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Article

# FEEDING HABITS OF A WHITE-TAILED DEER *Odocoileus virginianus cariacou* POPULATION AS INFERRED BY DENTAL WEAR AT A PROTECTED AREA OF THE COLOMBIAN ORINOQUIA

M. Fernanda Martínez-Polanco[1,2,3], Olga L. Montenegro[3], & Florent Rivals[1,2,4]

[1]Universitat Rovira i Virgili (URV), Departament d'Història i Història de l'Art, Tarragona, Spain. [Correspondence: M. F. Martínez-Polanco<mfmartinezp@gmail.com>].
[2]Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain.
[3]Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales, Grupo en Conservación y Manejo de Vida Silvestre, Bogotá D.C., Colombia.
[4]ICREA, Barcelona, Spain.

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**ABSTRACT.** In paleontology and also in archaeology, a direct comparison between the dentition of extant mammal species with known diets is currently used to infer the feeding habits of their ancient relatives. It is assumed, by analogy, that both species specialized in similar food, and determining the diet of a fossil mammal is helpful to identify the environmental context in which the animal inhabited. This type of approach allows us to know aspects of both the animals and the human groups that could benefit from hunting these animals, such as their behavior, environment, feeding preferences, and important events in their life history. At the same time, they provide a better knowledge of human palaeoecology, subsistence, and behavior. For these reasons, it is important to rely on modern data that allows this kind of approach. The aim of this paper is to establish baseline data to use in paleoecological studies from similar environments by studying the diet of an extant population of white-tailed deer (*Odocoileus virginianus cariacou*) from El Tuparro National Natural Park (PNN-El Tuparro) in Colombia. For this purpose, we used tooth mesowear and microwear as dietary proxies, which indicate the average annual diet and the diet at the time of death, respectively. The diet analysis of a deer extant population at the PNN-El Tuparro evidence that they consumed shrubs and herbs from both forests and savannas, but their diet changed seasonally. Tooth mesowear evidence of a grass-dominated diet in the last years of life and microwear browser diet at the moment of the death of the examined individuals.

**RESUMEN. INFERENCIAS SOBRE LOS HÁBITOS ALIMENTICIOS DE UNA POBLACIÓN DE VENADO DE COLA BLANCA *Odocoileus virginianus cariacou* A PARTIR DEL DESGASTE DENTAL EN UN ÁREA PROTEGIDA DE LA ORINOQUIA COLOMBIANA**. En paleontología y también en arqueología se realiza una comparación directa entre la dentición de especies actuales con dietas conocidas para inferir los hábitos alimenticios de especies de mamíferos en el pasado. Por analogía se asume que ambas especies se especializaron en alimentos parecidos. Al determinar la dieta de un animal fósil se está conociendo el medioambiente y el tipo de ecosistema donde vivió. Este tipo de aproximación permite conocer aspectos tanto de los animales como de los grupos humanos que pudieron beneficiarse de su caza. Aspectos de los animales, como su comportamiento, entorno, preferencias alimentarias y eventos importantes de la vida pueden ser estudiados. También proporcionan un mejor conocimiento de la paleoecología, la subsistencia y el comportamiento humanos. Por estas razones, es importante contar con datos actuales que permitan esta clase de inferencias. El objetivo de este trabajo es establecer una línea base para usar en estudios paleoecológicos en ambientes similares a partir del estudio la dieta de una población actual de venado cola blanca (*Odocoileus*

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*virginianus cariacou*) del Parque Nacional Natural El Tuparro (PNN-El Tuparro) en Colombia. Para tal fin utilizamos el mesodesgaste y el microdesgaste dental como técnicas. El análisis de la dieta evidencia que estos venados consumían arbustos y hierbas del bosque y también de las sabanas, y que su consumo estaba relacionado con la temporada. El mesodesgaste muestra un tipo de dieta dominada por el pastoreo en los últimos años de la vida de los individuos, mientras que el microdesgaste evidencia una tendencia al ramoneo en el momento de la muerte de los animales.

**Key words:** El Tuparro National Natural Park, dietary ecology, mesowear, microwear, paleoecology.

**Palabras clave:** Parque Nacional Natural El Tuparro, ecología nutricional, mesodesgaste, microdesgaste, paleoecología.

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## INTRODUCTION

Food habits of extant species are usually studied by several methods, such as direct observation and feces or stomach content examination, among others (Brokx & Andressen 1970; Sánchez-Rojas et al. 1997; Arceo et al. 2005). However, other methods are required for fossils or non-living animals (Rivals et al. 2016). A direct comparison between the dentition of extant mammals with known diets and their ancient relatives is used to infer past feeding habits. Such a tool is often used in paleontology and also in archaeology, under the assumption that extant and ancient animals specialized in similar foods (Faith & Lyman 2016). This, in turn, is useful to infer the environmental context where the ancient animals inhabited, their relationships with human groups that hunted them, as well as many other aspects of their behavior, feeding selection, and important events in their life history (Evans & Pineda Muñoz 2018). One of the methods for inferring diet is tooth wear. This method has allowed us to classify herbivorous ungulates as grazers, browsers, or intermediate feeders (Solounias & Semprebon 2002). This technique could be a useful alternative for inferring the feeding habits of an ungulate, white-tailed deer, living in a savanna environment in eastern Colombia.

### Tooth wear

Teeth are hard structures consisting of dentine and enamel (Hillson 1996). The shape and structure of teeth, as well as the precision of occlusion, allow herbivores to break plant cell walls to release their content for digestion (Evans & Pineda Muñoz 2018). The function of the molars directly relates to food processing, offering tooth wear as a strong dietary signal (Evans & Pineda Muñoz 2018). In recent years, animal tooth studies have been approached through different techniques related to ecological-biological, taphonomical, and archaeological areas (Rivals et al. 2016). Physical characteristics make teeth survive for a long time in the paleontological and archaeological records. Likewise, tooth structure allows the conservation of different information that contributes to a better understanding of human behavior through the study of animal remains (Reitz & Wing 2008). The diet of an animal is a subset of the environment in which the animal lives. For this reason, determining the diet of a fossilized mammal is helpful to identify the type of habitat and environment that the animal inhabited (Evans & Pineda Muñoz 2018). Teeth also offer information about animals, such as their behavior, environment, feeding preferences, and important life events (Evans & Pineda Muñoz 2018). From a broader perspective, as these animals were an important part of the human diet, they provide better knowledge of human paleoecology, subsistence, and behavior (Rivals et al. 2016).

In paleontology and archaeology, a direct comparison of dentition between extant species with a known diet and tooth remains are used to infer the feeding habits of ancient mammals (Faith & Lyman 2016). For this reason, it is important to establish a robust reference dataset on modern animals to allow a reliable application of this method.

A good example of this kind of approach is the study of fallow deer (*Dama dama*) and red deer (*Cervus elaphus hispanicus*) at Sierra de Andujar Natural Park in Southern Spain, where a large sample (*C. elaphus*: n = 102, and *D. dama*: n = 174) was collected throughout all seasons in 2008 and 2009. The rumen content and the mandibles of all individuals were collected and preserved. This type of sample allows dietary studies on different levels, including stomach contents (Azorit et al. 2012), dental microwear texture analysis (Berlioz et al. 2017), and cementum analysis (Azorit et al. 2022). However, replicating this complete approach in neotropical deer populations is not possible considering the low population numbers in comparison with the populations from the Iberian Peninsula.

Fortelius & Solounias (2000) proposed a method known as mesowear to characterize the diet of a particular species from a particular location in space and time. They used the three main dietary categories of herbivores, such as browser, grazer, and mixed feeder, as defined by Hofmann & Stewart (1972). Mesowear is the result of attrition and abrasion over a long period, and it reflects the average annual diet of an animal (Fortelius & Solounias 2000; Ackermans et al. 2020). The relative contribution of attrition and abrasion to the total wear should be considered to understand this method, in which sharp cusps mean that attrition (tooth on tooth) predominates strongly, and blunt cusps are the product of abrasion (food on tooth). Leaf-browsing herbivores have an attritional wear pattern (producing sharp molar cusps), and grazing animals, with high abrasive diets, have blunt molar cusps (Fortelius & Solounias 2000).

Abrasion of food particles over the tooth enamel produces microscopic scars on the surface of the enamel, called the microwear pattern. This pattern is quickly produced and continuously overwritten as the teeth wear down, thus indicating the diet of the last days or weeks before death (Grine 1986). Taking into account that there is high variability in the hardness and abrasiveness of plants, as well as in the parts and age of the plant, all of these characteristics produce different patterns on the enamel of the tooth (Solounias & Semprebon 2002). These patterns respond to animal food preferences and their dietary ecology and bring insights about the paleoenvironmental conditions weeks or even days before the death of the animal (Solounias & Semprebon 2002; Davis & Pineda Muñoz 2016; Desantis 2016; Xafis et al. 2017). The microwear has been used to differentiate among browsers, grazers, and mixed feeders in extant ungulates and the fossil record by studying the microscopic features visible on the enamel of the tooth (Solounias & Semprebon 2002). Based on the quantification of microscopic pits and scratches, Solounias & Semprebon (2002) established a classification of the diets of extant ungulates. The microwear texture analysis, resource distribution, and seasonal variations in the diet of extant deer species are used to study differential feeding behavior between species and sexes under restricted conditions (Berlioz et al. 2017).

The microwear pattern is sensitive to seasonal, local, and individual variations in diet (Rivals et al. 2015; Semprebon et al. 2016). The variability of the microwear pattern in paleontological or archaeological contexts is correlated with the duration of the accumulation of the fossil assemblage (Rivals et al. 2009, 2015), allowing an estimation of human occupation duration in a specific location and during a precise period (Sánchez-Hernández et al. 2014; Rivals et al. 2011, 2015). Also, it allows us to identify if the archaeological assemblages are the result of single or multiple death events. Considering that the scratches are sensitive to seasonal variations and that each season could be associated with a specific food, it is expected that each season produces a specific microwear signal. If the mortality events took place across seasons, the range of food and the microwear signal will be more diverse (Rivals et al. 2009, 2011; Rodríguez-Hidalgo et al. 2016).

Rivals et al. (2015) proposed a methodology to study the variations in scratches using the standard deviation and the coefficient of variation, according to their position in the heat map coefficient of variation and the standard variation of the number of scratches. This allows us to distinguish three types of human occupations: 1) seasonal or shorter events; 2) events longer than a season; and 3) separate events.

## White-tailed deer

The white-tailed deer (*Odocoileus virginianus* Zimmermann 1780) is an important species across America both in Pre-Columbian [e.g., Canada (Berg & Bursey 2000), the United States of America (Byrd 2011), Mexico (Blasco Martín et al. 2019), Guatemala (Emery 2008), Belize (Boileau & Stanchly 2020), the West Indies (Giovas 2018), Panama (Cooke 2004), Colombia (Correal 1990), and Ecuador (Stahl & Athens 2002)] and in modern times [e.g., the United States of America (Campbell et al. 2005), Mexico (Barrera-Bassols & Toledo 2005; Weber 2014), and Colombia (Martínez Salas et al. 2016)].

This species is distributed from southern Canada to Brazil (Eisenberg 1989; Smith 1991). It is a polytypic species that has become well-adapted to a wide range of habitats, from temperate to subtropical and semi-arid environments to rainforests and savannas (Eisenberg 1989; Emmons 1999). Although, indeed, the white-tailed deer is perhaps the most studied species of mammal in America, there are still gaps in its taxonomic identification in South America. For instance, in Venezuela, Molina et al. (1999), based on a morphological and morphometrical study, stated that white-tailed deer from South America are not conspecific with those from North America, and they proposed to raise to a species level several subspecies designed for that country. Following such argument, authors such as Solari et al. (2013) and Ramírez-Chaves et al. (2016) used three subspecies names as full species (*O. goudoutti, O. ustus*, and *O. cariacou*) for white-tailed deer populations in Colombia. However, this taxonomy needs molecular analysis on Colombian specimens to be well-supported (López Arévalo et al. 2020). Due to this taxonomic uncertainty and until more work on the subject is available, we used the name *O. virginianus* for these deer in Colombia in this paper. For the populations of white-tailed deer in the Colombian Orinoquia region, we use the name *O. virginianus cariacou*, partially following Molina et al. (1999) but without rising jet this subspecies to a full species.

An archaeological record of white-tailed deer in Colombia was found in Sabana de Bogotá, where this species has been a very important prey since 12.000 years ago; their bones are found in all pre-ceramic sites in the area (Peña & Pinto 1996; Peña & Rincón-Rodríguez 2020). Ancient people used deer as a food source, and the bones were used to manufacture tools, while furs were made into clothing for protection from cold weather (Peña & Pinto 1996; Peña & Rincón-Rodríguez 2020). White-tailed deer are also present in archaeological assemblages from different parts of the country [e.g., Atlántico (Angulo Valdés 1988) and Tolima (Peña et al. 2007; Peña 2013)].

White-tailed deer abundance varies along its range, but in South America, they are less abundant compared with North America and with other deer species in the world. In Colombia, Gómez et al. (2016) estimated deer abundance at El Tuparro National Natural Park (PNN-El Tuparro) using an occupancy model and found that Ψ = 0.43. This means that deer are not very abundant in this area (Gómez et al. 2016). In a classic study (1973-1977) of the mammals of the Guatopo National Park (State of Guarico, Venezuela), the density of the population of white-tailed deer was estimated by direct observation –frequency of sightings– to be 3-4 deer/km$^2$ (Eisenberg et al. 1979).

Habitat use by white-tailed deer is predicated by the quality, quantity, and heterogeneity of available forage (Sánchez-Rojas et al. 1997; Gallina et al. 2010; Ramírez Lozano 2012). Diet varies among seasons due to discontinuities in food availability, cover, and water (Sánchez-Rojas et al. 1997). During high rainfall periods, a large quantity of food resources becomes available to deer, although, paradoxically, dietary diversity may be diminished at the beginning of the rains when the animals become more selective, choosing young leaves of trees, shrubs, and vines (Sánchez-Rojas et al. 1997; Bello et al. 2001, 2004; Arceo et al. 2005). Dry seasons are critical periods during which the deer orientate their foraging towards the most nutritious fruits and leaves of trees, shrubs, and herbs that are available at the time (Sánchez-Rojas et al. 1997; Bello et al. 2001, 2004; Arceo et al. 2005). In some populations of white-tailed deer in North America, females differ from males in their diet quality (McCullough 1985; Beier 1987). However, it is poorly known if such variation occurs in the neotropical populations.

Nevertheless, there is still a gap in the knowledge of the dietary ecology of living deer populations that may bias comparisons with archaeological assemblages. For this reason, this paper aims to study the feeding habits of an extant population of white-tailed deer (*Odocoileus virginianus cariacou* from El Tuparro National Natural Park (PNN-El Tuparro) in Colombia using mesowear and microwear as proxies. We tested dietary variations depending on sex, considering their different physiological requirements. This work is expected to be a reference for interpreting data from paleontological or archaeological contexts in similar areas.

## MATERIALS AND METHODS

### Study area

The area where the white-tailed deer examined in this paper were collected is located in the northeastern Colombian Orinoquia region. In the 1970s, this area was known as the Tuparro faunal territory, but in 1980, part of this area was designed as a national park (El Tuparro National Natural Park [PNN-El Tuparro]). In 1982, El Tuparro was declared the Biosphere Reserve by the United Nations Educational, Scientific and Cultural Organization (UNESCO). The core area of the reserve corresponds to PNN-El Tuparro, which, with an area of 5,480 km$^2$, covers close to 60% of the area of the reserve (Patiño et al. 2007). El Tuparro is located in the Colombian Orinoquia in the extreme east of the high plains in the Department of Vichada (**Fig.** 1). It is limited by the Orinoco River to the east, the Tomo River to the north, and the Tuparrito, Tuparro, and El Caño Cunavero Rivers to the south (Patiño et al. 2007; Villarreal & Maldonado 2007). To the west, the limits correspond to the Hormiga and Janipa creeks in the town known as El Tapón, between the Tomo and Tuparrito Rivers (Patiño et al. 2007; Villarreal & Maldonado 2007). The park is immersed in a large water network, as can be seen by the limits of this area (Gómez et al. 2009).

The climate in Tuparro is classified as tropical rainy savanna that is slightly humid with less than 60 mm of precipitation in the driest month and an annual maximum of 2,500 mm (Gómez et al. 2009), which is characterized by the monomodal annual distribution of precipitation with

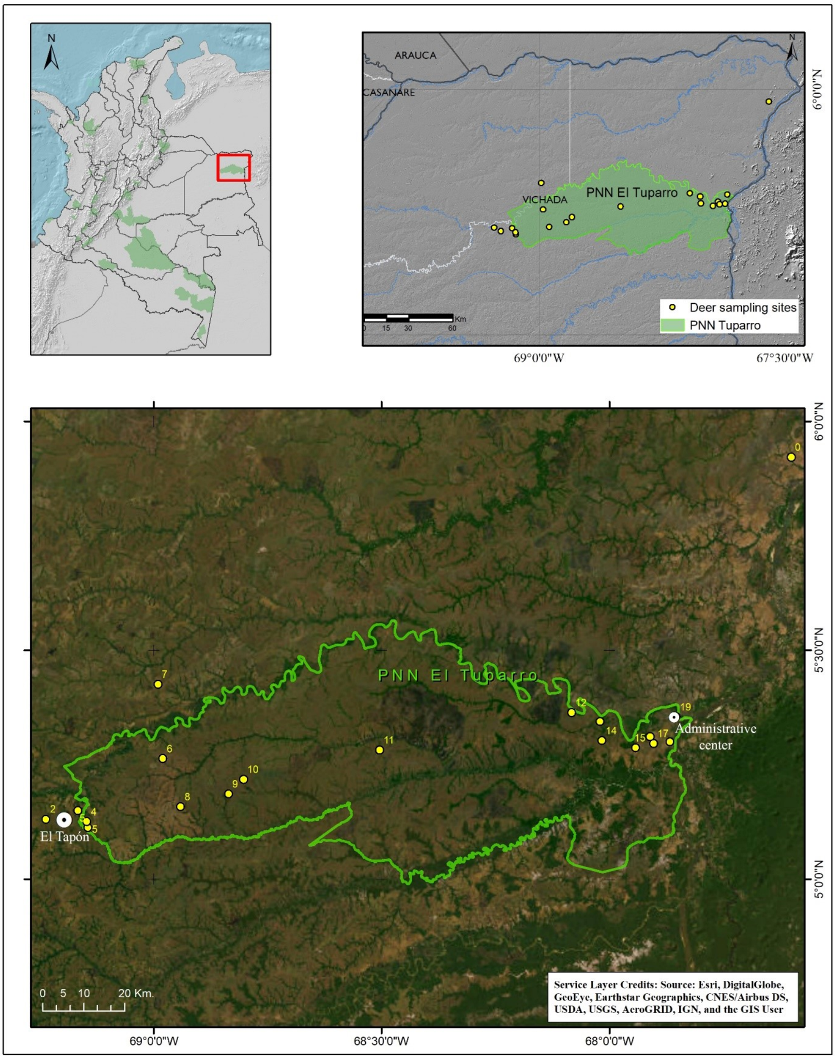


**Fig. 1.** Geographical location of PNN-El Tuparro, Colombia.

a very marked dry period between November and March (Villarreal & Maldonado 2007). These climatic conditions generate a severe water deficit that begins in November and lasts until mid-March-April. The rainy season occurs from April to October. During this period, an excess of humidity that can last up to seven months is observed, since about 50% of the rains correspond to over raining in these months. Precipitation in the park ranges from 1,559 mm/year to the east (Bocas del Tomo Station) and 3,000 mm/year towards the west (El Tapón Station) (Patiño et al. 2007; Villarreal & Maldonado 2007). The average annual temperature is 27.2 °C (Patiño et al. 2007; Villarreal & Maldonado 2007).

El Tuparro is considered a transition zone between the highlands, the jungle, and the savannas of the Guiana Shield (Molano 1998). Its landscape is characterized by a matrix of high, flooded natural savannas where they are found immersed in patches of flooded forest, terra firme, and rocky outcrops (Molano 1998; Patiño et al. 2007; Villarreal & Maldonado 2007).

The vegetation of El Tuparro corresponds to a mosaic of savannas and forests with variants that are regulated by the microrelief, type of soil, and degree of flooding, which is associated with the rise and descent of main river channels in the area. Savannas are characterized by the absence of continuous tree cover and the presence of a continuous herbaceous stratum (Molano 1998). Vincelli (1981) describes seven types of savannas in the El Tuparro National Natural Park, depending on whether they are in non-flooded areas (highland savannas) or flooded areas. The same author found five types of wooded vegetation. He observed forests associated with rivers, creeks, or other water bodies. These kinds of forests suffer periodic flooding, in some cases higher than 5 m. Other types of forests are those immersed in a matrix of savanna or rocky outcrops (Vincelli 1981).

## Materials

We selected all available white-tailed deer dental material from the mammal collection of the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH-M) in Villa de Leiva (Colombia). The second lower molars (m2) in intermediate dental wear, which were not fragmented and/or damaged, were selected. In total, 26 individuals were studied, 11 females and 15 males. Most of them were collected during the rainy season (n = 22). These individuals were collected between 1970 and 1975 (**Table** 1). Considering current abundance estimates for PNN-El Tuparro (Gómez et al. 2016) and the historical data from Venezuela (Eisenberg et al. 1979), the sample size of white-tailed deer that is kept at IAvH-M is impressive. The Mammal Collection of the Humboldt Institute is the third-largest collection in the country (Lozano-Flórez et al. 2020). It is important to mention that this collection is unique to Colombia, and in no other collection are there so many specimens from the same geographical area together. We estimated the geographical coordinates of each deer specimen examined, based on the localities named on the tags and the collection database. All collection sites are located in savanna vegetation type, and most of the deer were sampled during the rainy season (**Table** 1).

## Methods

Tooth mesowear: Mesowear analysis involves the observation of cusp morphology and proceeds by describing the sharpness and relief of molar tooth cusps (Fortelius & Solounias 2000). These attributes are scaled from 0 (sharp cusps and high relief) to 6 (blunt surfaces); mesowear is scored on each specimen then averaged for each sample (MWS) (Mihlbachler et al. 2011; Rivals et al. 2013, 2017). We compare the mesowear scores between males and females using a *t*-test, if the assumptions are fulfilled, or an *F*-test, if not. For these analyses, we used PAST software (Hammer et al. 2001).

Tooth microwear: We followed the method proposed by Solounias & Semprebon (2002) and Semprebon et al. (2004). Microwear analysis was comprised of several steps: 1) selecting teeth; 2) making a mold of the occlusal surface using a material appropriate for high-resolution dental impressions, such as polyvinylsiloxane; and 3) making a cast using transparent epoxy. 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 the mesiobuccal cusp of the second molar within a standard (0.4 x 0.4 mm) area using an ocular reticle. The quantification of scratches allows us to distinguish three dietary categories: 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 & Semprebon 2002). In this article, the (RStudio 2022) code proposed by Rivals (2019) was used to create the bivariate plots. This code used the packages “readxl”, “ggrepel”, “plyr”, “lattice”, “Rmisc”, and “ggplot2” for drawing plots (RStudio 2022). To compare the variability of the scratches and the pits between males and females, we performed a *t*-test because the data met the assumptions to conduct this test. For this analysis, we used PAST software (Hammer et al. 2001).

Other features could be identified on the enamel bands, including 1) cross scratches, which are oriented in different directions than the majority of the scratches; 2) large pits (LP), which are double-sized pits; and 3) gouges, which are similar to large pits with irregular edges but are 2 or 3 times larger and deeper. The scratch textures are ranked using the scratch width score (SWS): 0 (fine scratches); 1 (mixture of fine and coarse scratches); and 2 (coarse scratches). The SWS is obtained by taking each individual value and averaging it (Solounias & Semprebon 2002; Semprebon et al. 2011).

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. The CV and SD bivariate plots indicate the mortality period in ungulates. According to Rivals et al. (2015), the 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 animals were hunted. On the left side of the graph are short events; in the middle, there are long-continued events; and on the right side, there are two separate short events (Rivals et al. 2015).

# RESULTS

## Tooth mesowear

Mesowear analysis showed medium values (MWS = 2.38), indicating that the diet of the white-tailed deer at PNN-El Tuparro was not very high in abrasiveness. In comparison to other ungulate species (Fortelius & Solounias 2000), the mesowear scores for the white-tailed deer are located in a medium point, overlapping with grazers and grass-dominated mixed feeders. It indicates a mixed feeder diet tending to be grass-dominated in the last years of the life of the deer (**Table** 2; **Figs**. 2 and 3). The *F*-test shows no significant differences among the mesowear scores between males and females ($F = 1.03$; $p = 0.92$).

## Tooth microwear

The enamel surfaces are characterized by a microwear pattern with more scratches than pits (**Figs**. 3 and 4). The percentage of individuals with cross scratches (%XS = 7.69%) is low in the sample, and the scratch width (SWS) is 0.92 indicating a mixture of fine and coarse scratches (**Table** 2). The percentages of large pits in the complete sample are 76.92%, but if we only consider the individuals that are coming from the rainy season, the percentage is higher (86.36%). Gouges and puncture pits were not found in the sample. The number of scratches and

**Table 1**

Geolocation information of the white-tailed deer (*Odocoileus virginianus*) from PNN-El Tuparro, based on the catalogues of the IAvH-M. Abbreviations: M: male; F: female; R: Rainny; D: Dry.

| Map ID | Cat. Number | Deer sampling sites | Latitude | Longitude | Sex | Season | Year |
|---|---|---|---|---|---|---|---|
| 1 | IAvH-M-00491 | PNN El Tuparro, Territorio Faunístico, Bajo La Pica 8 Km al NW, del Tapón | 5.15336800000 | -69.27840500000 | M | R | 1971 |
| 2 | IAvH-M-00476 | PNN El Tuparro, Territorio Faunístico, 5 Km al W, de El Tapón | 5.13197397788 | -69.23621968180 | F | D | 1971 |
| 3 | IAvH-M-00489 | PNN El Tuparro, Territorio Faunístico, El Tapón, 1 Km al SE, del puente sobre El caño La Hormiga | 5.15000000000 | -69.16666700000 | F | R | 1971 |
| 4 | IAvH-M-00472 | PNN El Tuparro, Territorio Faunístico, 5 Km al E, del Tapón, 85 Km | 5.12597337752 | -69.14647444360 | M | D | 1971 |
| 5 | IAvH-M-00525 | PNN El Tuparro, Territorio Faunístico, El Tapón | 5.11227000000 | -69.14441500000 | F | R | 1971 |
| 5 | IAvH-M-00526 | PNN El Tuparro, Territorio Faunístico, El Tapón | 5.11227000000 | -69.14441500000 | F | R | 1971 |
| 6 | IAvH-M-05996 | PNN El Tuparro, A 28 Km al NE del Tapon | 5.26382329492 | -68.97993880860 | M | R | 1972 |
| 7 | IAvH-M-01517 | PNN El Tuparro, Territorio Faunístico, a 40 Km del Tapón | 5.42614076721 | -68.99067907470 | M | R | 1973 |
| 8 | IAvH-M-05995 | PNN El Tuparro, A 28 Km al NE del Tapon | 5.15835636631 | -68.94116979500 | M | R | 1974 |
| 9 | IAvH-M-01292 | PNN El Tuparro, Territorio Faunístico, 40 Km al este del Tapón | 5.18618771249 | -68.83590830150 | M | R | 1975 |
| 10 | IAvH-M-00484 | PNN El Tuparro, Territorio Faunístico, Bajo Los Topios, 45-50 Km, al W, del Tapón | 5.21828272816 | -68.80297742680 | F | R | 1971 |
| 11 | IAvH-M-00490 | PNN El Tuparro, Territorio Faunístico, Bajo Las Tapias, 45-50 Km al W, del Tapón | 5.28242800000 | -68.50433200000 | F | R | 1971 |
| 12 | IAvH-M-01295 | PNN El Tuparro, Territorio Faunístico, 25 Km al oeste del Centro Administrativo | 5.36407854472 | -68.08232938950 | F | R | 1975 |
| 13 | IAvH-M-01356 | PNN El Tuparro, Territorio Faunístico, a 11 Km del Centro Administrativo | 5.34436880000 | -68.01998070000 | M | R | 1973 |
| 14 | IAvH-M-01001 | PNN El Tuparro, Territorio Faunístico, 10 Km suroeste del Centro Administrativo | 5.30277200000 | -68.01640200000 | M | R | 1974 |
| 15 | IAvH-M-00552 | 15 Km al W del río Orinoco y 2 Km al S, del río Tomo | 5.28723461865 | -67.94195006490 | F | R | 1972 |
| 16 | IAvH-M-00562 | PNN El Tuparro, Territorio Faunístico, 5 Km al S, del Centro Administrativo | 5.31141400000 | -67.91110800000 | F | R | 1972 |
| 17 | IAvH-M-01000 | PNN El Tuparro, Territorio Faunístico, 8 Km suroeste del Centro Administrativo | 5.29669962599 | -67.90239219220 | M | R | 1974 |
| 18 | IAvH-M-01024 | PNN El Tuparro, Territorio Faunístico | 5.30000000000 | -67.86666670000 | F | R | 1975 |
| 18 | IAvH-M-01447 | PNN El Tuparro, Territorio Faunístico | 5.30000000000 | -67.86666670000 | M | R | 1973 |
| 19 | IAvH-M-00496 | PNN El Tuparro, Territorio Faunístico, Puerto Nuevo, río Tomo, 14 Km, al N del Tapón | 5.35509710000 | -67.85310540000 | M | R | 1971 |
| 19 | IAvH-M-05999 | PNN El Tuparro, Rio Tomo | 5.35509710000 | -67.85310540000 | M | R | 1970 |
| 0 | IAvH-M-00461 | Fundo Canaima, caño Las Sardinas | 4.89801000000 | -71.03407500000 | M | R | 1970 |
| 0 | IAvH-M-00471 | PNN El Tuparro, El tapón, 85 Km, al E, del fundo Canaima, Territorio Faunístico El Tuparro | 4.89367742942 | -70.24735940310 | M | D | 1971 |
| 0 | IAvH-M-00481 | PNN El Tuparro, Territorio Faunístico, El Tapón, 5 Km al E, del puente sobre El caño La Hormiga | 5.92228456666 | -67.60091619850 | F | R | 1971 |
| 0 | IAvH-M-00433 | 40-50 Km al E, del Fundo Canaima | 4.91472787806 | -70.59726790020 | M | D | 1970 |

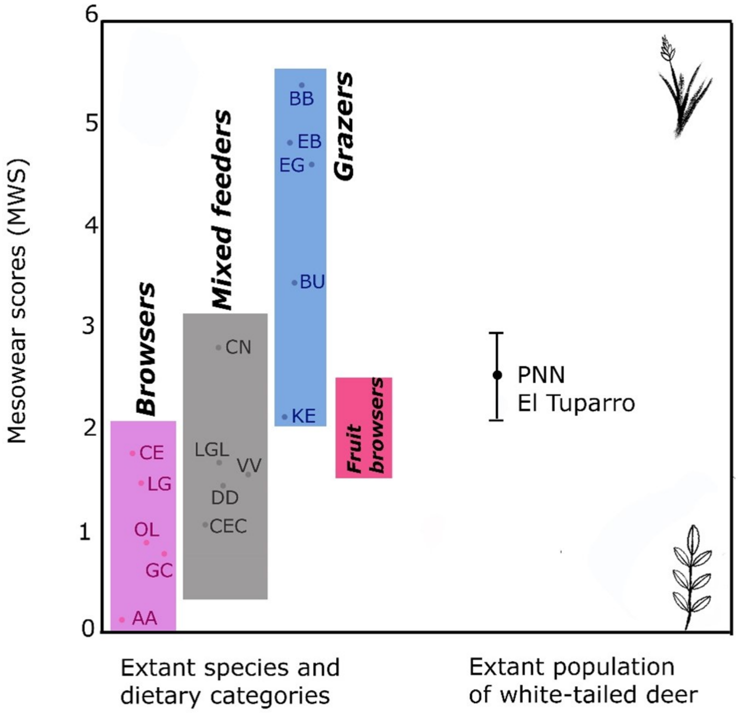


**Fig. 2.** Mesowear results for the white-tailed deer (*Odocoileus virginianus*) from PNN-El Tuparro in comparison with data on ungulates with known diet: Grazers: BB *Bison bison bison*, BU *Bubalus mindorensis*, EB *Equus quagga*, EG *Equus grevyi*, KE *Kobus ellipsiprymnus*; Leaf browsers: AA *Alces alces*, CE *Cervus elaphus*, GC *Giraffa camelopardalis*, LG *Lama guanicoe*, OL *Capreolus capreolus*; Mixed feeders: CEC *Cervus elaphus canadensis*, CN *Cervus nippon*, DD *Dama dama*, LGL *Lama glama* VV *Vicugna vicugna*. Data from Fortelius & Solounias (2000); Rivals et al. (2010, 2013, 2014, 2017). Error bar correspond to standard error of the mean (±1 SEM).

the medium number of pits (**Table** 2), locating their values in the medium part of the 95% confidence ellipse in comparison to the reference browsers (**Fig**. 4). Microwear analysis indicates that the deer were typical browsers at the time of death. The *t*-test shows no significant differences between males and females, both in the number of scratches ($t$ = 0.19; $p$ = 0.85) and pits ($t$ = 1.01; $p$ = 0.32). In **Figure** 3, the microwear pattern is observed in two individuals, a. collected in the rainy season and b. in the dry season.

### Scratch variability

Scratch variation, quantified by the SD and CV, presents intermediate values. The sample from PNN-El Tuparro falls in area b of the heat map, thus indicating several events distributed over one or several years (**Fig**. 5).

## DISCUSSION

The mesowear analysis performed in this paper evidenced that the diet of deer in their last years of life was that of a mixing feeder tending to be grass-dominated. Our results fit with Mateus-Gutiérrez & López-Arévalo (2020) general observation about the herbaceous diet of white-tailed deer. Mateus-Gutiérrez & López-Arévalo (2020) reviewed the available scientific literature regarding the diet of the white-tailed deer in Colombia. They recorded a total of 112 plant species, most of them belonging to the families Cyperaceae and Poaceae. The authors pointed out that the diverse diet of deer in Colombia corresponds with its wide geographic and altitudinal distribution. This research also showed that the most frequent type of vegetation in the diet of the white-tailed deer in Colombia was herbaceous. These results are also observed in Costa Rica, Mexico, and

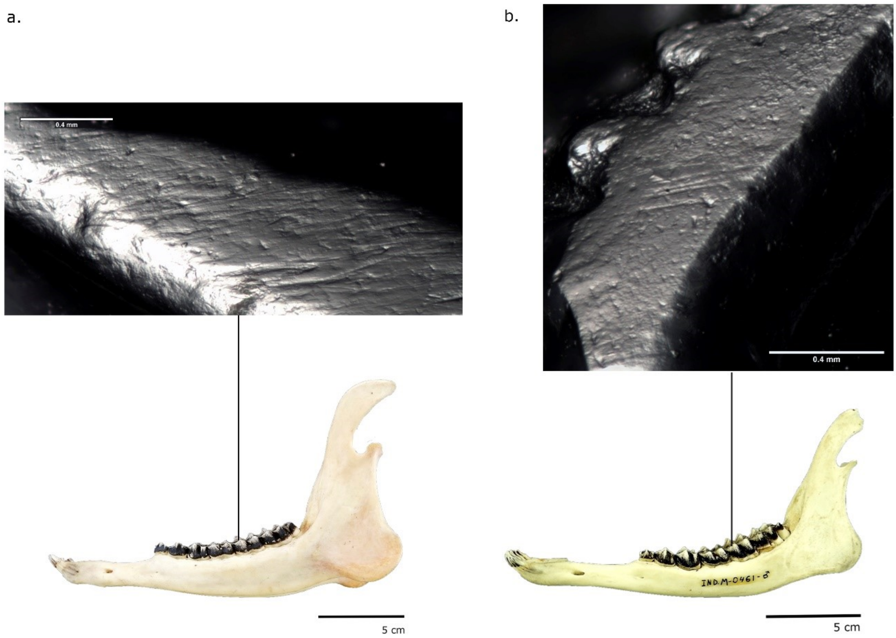


**Fig. 3.** Examples of microwear features on the enamel bands of the occlusal surface of white-tailed deer (*Odocoileus virginianus*) m2 from PNN-El Tuparro. a. Small and large pits and fine and coarse scratches (specimen IAvH-M; 526) collected during the rainy season; b. Coarse scratches and mixed pits (specimen IAvH-M; 471) collected during the dry season.

Venezuela. Another point in common is the consumption of crops such as pumpkin, chili, broad bean, beans, corn, and sorghum, among others (Mateus-Gutiérrez & López-Arévalo 2020).

In a recent study of the vegetal cover of the PNN-El Tuparro, it was found that the savanna vegetation is highly diverse since about 190 species of vascular plants are associated with this ecosystem (Mendoza-Cifuentes & Córdoba-Sánchez 2018). Consequently, the white-tailed deer have access to a high diversity of herbaceous plants for their diet, in particular during the dry seasons. The white-tailed deer is a species that prefers open areas and avoids mature forests, which it uses as a refuge, which is reflected in the occupation of 43% of the sites with forest in the PNN-El Tuparro (Gómez et al. 2016). Deer are forest-edge animals, having more than one type of habitat for food and shelter (Brokx & Andressen 1970).

The white-tailed deer studied in this paper were found to be browsing during the last days or weeks before their death. From the records of the collection, we knew that most of them were collected during the rainy season. In this season, food resources increase, and deer select the young leaves of trees (Sánchez-Rojas et al. 1997; Bello et al. 2001, 2004; Arceo et al. 2005). Young leaves represent a higher nutritional quality and fewer secondary compounds than mature leaves that grow up later in the dry season, losing their quality (Arceo et al. 2005). Therefore, it makes sense that deer were typically browsers at the time of their death at PNN-El Tuparro. These results also coincide with those of Rotti et al. (2018) who studied microwear on extant deer from Peru and Venezuela from the collection of the Museo de La Plata (Argentina), which evidenced that deer were browsers at the moment of their death.

Near the study area, there is only one study of the stomach contents of white-tailed deer (*O. virginianus gymnotis*). This was performed between 1967 and 1968 on the Altos and Bajos Llanos of Western Guarico, Cojedes, and Apure in Venezuela. The authors collected deer during the wet and dry seasons. They found that the leaves and terminal branches of various *Mimosa* sp. were the most important single item, followed by grasses and flowers. This study evidenced that deer used the same plants in different degrees in both seasons (Brokx & Andressen 1970).

The absence of gouges and puncture pits in the microwear traits of PNN-El Tuparro deer implies that they did not include fruits and seeds in their

**Table 2**

Summary of mesowear and microwear data for the white-tailed deer (*Odocoileus virginianus*) from PNN-El Tuparro. Abbreviations: n: sample size; MWS: mesowear score; NS: number of scratches; NP: number of pits; %LP: percentage of specimens with large pits; % XS: percentage of specimens with cross scratches; SWS: scratches width score (from 0, fine scratches only, to 2, coarse scratches only).

| | | **Mesowear** | | | | **Microwear** | | |
|---|---|---|---|---|---|---|---|---|
| | **n** | **MWS** | **n** | **NP** | **NS** | **%LP** | **%XS** | **SWS** |
| M | | 2.38 | | 8.34 | 12.4 | | | |
| SD | 26 | 2.06 | 26 | 3.45 | 2.41 | 76.92 | 7.69 | 0.92 |
| CV | | 0.86 | | 0.41 | 0.19 | | | |

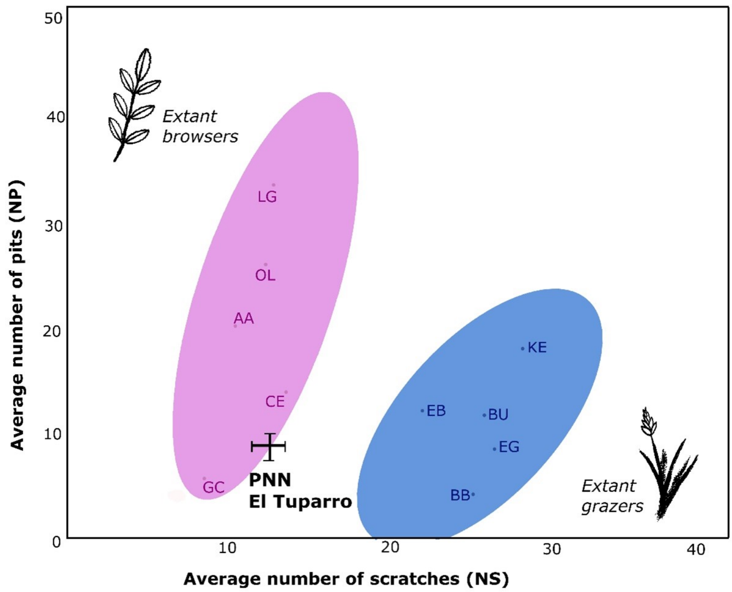


**Fig. 4.** Bivariate plot of the average numbers of pits and scratches of the white-tailed deer (*Odocoileus virginianus*) from PNN-El Tuparro. Error bars correspond to the standard error of the mean (±1 SEM). Ellipses correspond to the Gaussian confidence ellipses (p = 0.95) on the centroid for the extant leaf browsers and grazers from Solounias & Semprebon (2002). Grazers: BB *Bison bison bison*, BU *Bubalus mindorensis*, EB *Equus quagga*, EG *Equus grevyi*, KE *Kobus ellipsiprymnus*; Leaf browsers: AA *Alces alces*, CE *Cervus elaphus*, GC *Giraffa camelopardalis*, LG *Lama guanicoe*, OL *Capreolus capreolus*; Data Solounias & Semprebon (2002).

diet at the moment of their death. However, this result should be taken with caution, taking into account that the study of the stomach contents of white-tailed deer in Venezuela evidenced that fruit intake was very important in the diet of the deer during the dry season on the Bajo Llano and during the wet season on the Alto Llano. The fruits of palm (*Copernicia tectorum*), genipa (*Genipa caruto*), and certain Leguminosae trees were particularly consumed. Although, in Apure, no fruits were found, perhaps because these fruit trees either do not occur or are rare in the areas where deer were collected (Brokx & Andressen 1970). This must be taken into account because the consumption of fruits may not leave marks on the teeth. It will be necessary to study this aspect deeper in the next studies.

The scratch texture (SWS) evidenced a mixture of fine and coarse scratch patterns related to the mixed feeders tending to be grazers. However, the %XS is low, indicating an unspecialized grazer diet, and the

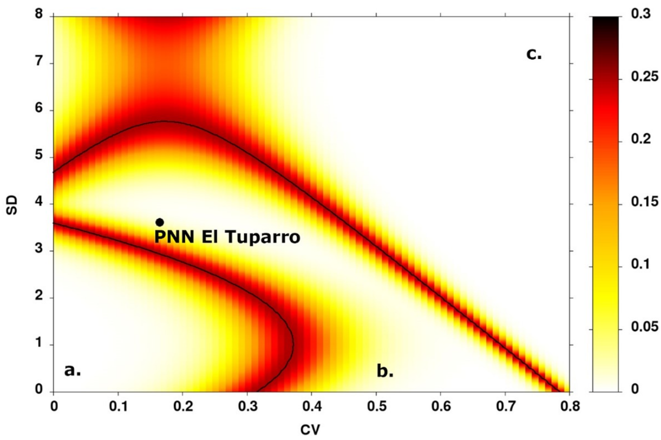


**Fig. 5.** Heat map (boundary lines of the three regions with the error probability) and the sample from PNN-El Tuparro. a. Seasonal or shorter events; b. Longer than a season events; c. Separate events (data from Rivals et al. 2015).

%LP is high, in particular during the rainy season. This trend could indicate the dietary preferences of the browsers in particular in this season, taking into account that the food resources increase and deer select young tree twigs and leaves as food (Sánchez-Rojas et al. 1997; Bello et al. 2001, 2004; Arceo et al. 2005).

Ecological studies of white-tailed deer in the Orinoco basin in Colombia reported that the most used habitats correspond to forest edges and shrubs that border savannas (González-Hernández 2001 cited by Pérez-Moreno et al. 2020). Rojas (2010) pointed out that deer prefer savannas over forests. Pérez-Moreno et al. (2020), talking about deer habit use, observed that a complementary use exists between the habitats because each one offers different resources to the deer populations. Through the study of diets, it can be observed that deer consume shrubs and herbs from forests and savannas, but their consumption changes depending on the season.

A classical study (1967-1974) of white-tailed deer diet based on the botanical composition at E.S. George Reserve Michigan evidenced no significant differences in food habits between sex and age classes (McCullough 1985). In this study, we also demonstrated that there are no significant differences in the mesowear scores and microwear patterns (pits and scratches) between females and males. In the case of the tropics, Buenrostro-Silva (2005) studied sexual segregation and its relationship with the quality of the diet in a tropical dry forest in the Sierra de Huautla, Morelos, Mexico. Females consumed a higher-quality diet (with high fecal nitrogen values) compared to males (cited by: Gallina et al. 2010; Mandujano et al. 2014; Weber 2014). More studies on dietary differences between sexes in live deer populations are needed to clarify this point.

Through the study of diets, it can be observed that deer consume shrubs and herbs from forests and savannas, but their consumption changes depending on the season. The study of the diet of archaeological deer from Panama at Cerro Mangote (7,800-4,600 cal BP) and Cerro Juan Díaz (300 BCE-1,600 CE) evidenced that deer were typically browsers. Both methods, mesowear, and microwear, showed 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 (2,200-500 cal BP), another archaeological site, the microwear signal evidences the opposite trend, which implies that deer were hunted in the dry season since scratches and pit variation has a higher value in these samples than in those from Cerro Mangote and Cerro Juan Diaz (Martínez-Polanco et al. 2020).

In the case of the tropics, the scratch variation could indicate the periodicity of the hunting events more than the duration of occupation of the site. If we consider, for example, that Cerro Juan Díaz was a village (Martínez-Polanco et al. 2020), the periodicity of hunting was short events at different times of the year. Contrarily, at Sitio Sierra, another village, hunting was practiced repeatedly during the same period each year. If we take into account that this site has been interpreted as the result of a communal feasting event at which deer meat was consumed in large quantity, holding communal feasts of this nature would have been more practical and appealing between late December and late April than during the rainy and stormy months (Martínez-Polanco & Cooke 2019). The periodicity of hunting is also supported by the present study because we knew the exact date of capture of the individuals and determined that there were different events during the same season (wet season) over several years (1970-1975).

## CONCLUSIONS

The analysis of the diet of an extant population of white-tailed deer that inhabited PNN-El Tuparro between 1970-1975 through mesowear and microwear evidenced that deer consumed shrubs and herbs from forests and savannas. Moreover, we established that their consumption was related to the season. Mesowear evidenced a grass-dominated diet in the last years of the life of the individuals, and microwear evidenced that deer were browsers at the moment of their death. This study showed that deer had a browsing diet during the rainy season. There was no evidence of differences in the diet of females and males in both microwear and mesowear. The results we obtained on modern white-tailed deer are strongly relevant for the study of fossil deer from archaeological sites. It allowed us to establish a reference to characterize seasonality in human hunting activities in the past. This work provided the first database to analyze seasonality in the diet of fossil deer from the Neotropics.

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