

Invited Research Article

Dietary stability inferred from dental mesowear analysis in large ungulates from Rancho La Brea and opportunistic feeding during the late Pleistocene

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ABSTRACT

The Rancho La Brea locality is world famous for asphaltic deposits that trapped and preserved late Pleistocene megafauna over the last 50,000 years. This wealth of paleontological data allows for detailed investigation into paleoecological changes through the last glacial maximum into the Holocene. Here, we used dental mesowear analyses to infer dietary behavior in *Bison antiquus*, *Equus occidentalis*, and *Camelops hesternus* from five deposits ("pits") spanning the latest Pleistocene: pits 77, 91, 13, 3, and 61/67. Mesowear was compared among pits for each taxon and discriminant function and posterior probability analyses were conducted using a modern dataset to predict dietary categories at Rancho La Brea. Published mesowear scores from late Pleistocene *Bison*, *Equus* and *Camelops* from other localities were included in the discriminant function and posterior probability analyses to assess dietary variability among regions. Mesowear for each taxon did not differ among pits. Posterior probabilities and discriminant function analyses recovered *E. occidentalis* as a strict grazer with *B. antiquus* and *C. hesternus* recovered as mixed feeders. The stability of mesowear scores through the latest Pleistocene suggests average diets of these herbivores did not significantly change at Rancho La Brea. This is in contrast to documented changes in climate and flora proxies of southern California. However, it is unclear whether these proxies are representative of climate and floral changes at Rancho La Brea. Mesowear scores from late Pleistocene populations of *Equus*, *Bison*, and *Camelops* indicate little variability in diet in *Equus*, modest variability in *Bison*, and high variability in *Camelops*. These analyses suggest large ungulates may have been more opportunistic in their feeding strategies and highlights the need for using multiple proxies to clarify dietary behavior of herbivores

1. Introduction

The Rancho La Brea Tar Pits in Los Angeles, California are world famous asphaltic deposits preserving millions of latest Quaternary fossils that span a time period encompassing the Last Glacial Maximum (LGM) and the interglacial transition from the Pleistocene into the Holocene (Stock and Harris, 2001; Clark et al., 2009). Rancho La Brea (RLB) is

considered a carnivore trap with a high abundance of carnivores recovered, including: *Smilodon fatalis*, *Canis dirus*, *Canis latrans* and *Panthera atrox* (Stock and Harris, 2001). The overrepresentation of carnivores has led to the majority of paleoecological studies at RLB focusing on these taxa (e.g. Van Valkenburgh and Hertel, 1993; Binder et al., 2002; Meachen et al., 2014a; DeSantis et al., 2019), with only a few studies investigating the paleoecology of herbivores (Akersten et al.,

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1988; Coltrain et al., 2004; Feranec et al., 2009; Jones and DeSantis, 2017). Carnivore studies have found body size changes in *Smilodon fatalis* that are correlated with climate change, body size changes in *Canis latrans* correlated with the megafauna extinction event, and evidence that *Canis dirus* and *Smilodon fatalis* may have undergone nutrient stress, indicated by tooth breakage, tooth wear, and cortical bone thickness (Binder et al., 2002; Binder and Van Valkenburgh, 2010; Goswami et al., 2015; Meachen and Samuels, 2012; Meachen et al., 2014a, 2014b; O'Keefe et al., 2014; Binder et al., 2016; Van Valkenburgh and Hertel, 1993; Van Valkenburgh, 2009, but see Duckler and Van Valkenburgh, 1998; DeSantis et al., 2012, 2015 for an alternative hypothesis). While the causality of these changes in the carnivore guild at RLB has been debated, they can be informed by studies of paleoecological changes in their presumed prey. Elucidating temporal changes in the diet and paleoecology of large herbivores is important for understanding potential climatic effects on large mammals during the latest Pleistocene, and can help clarify paleoecological changes in carnivores at RLB and beyond (Ripple and Van Valkenburgh, 2010).

The majority of previous paleoecological studies of large herbivores at RLB have focused on interpreting their diets (Akersten et al., 1988; Coltrain et al., 2004; Feranec et al., 2009), with only one study investigating dietary changes through time in herbivores (Jones and DeSantis, 2017). These studies have used a variety of dietary proxies including dental boluses, stable isotopes, dental microwear, and dental mesowear (Akersten et al., 1988; Coltrain et al., 2004; Feranec et al., 2009; Jones and DeSantis, 2017; DeSantis et al., 2019; Fuller et al., 2019). Dental boluses provide direct evidence of plants eaten during the lifetime of an individual, but are rarely preserved. Many of the dental boluses found at RLB (up to 80%) are unidentifiable plant material, with the remaining plants being identifiable only to either monocotyledon or dicotyledon tissue (Akersten et al., 1988). Stable carbon isotopes help to inform the relative importance of the C₃ and C₄ photosynthetic pathways in plants that make up an organism's diet (Cerling et al., 1997; Clementz, 2012). Typically, $\delta^{13}\text{C}$ values less than -8‰ or -9‰ indicate the consumption of C₃ plants while values greater than -8‰ indicate some consumption of C₄ vegetation, signifying browsing and grazing behavior at latitudes $<37^\circ\text{N}$, respectively (Cerling et al., 1997; MacFadden, 1998; Kohn, 2010). However, stable carbon isotopes are less informative for taxa in Mediterranean climates from coastal California due to the presence of C₃ grasses and C₄ shrubs such as *Atriplex* (Sage and Monson, 1999; Feranec et al., 2009; Still et al., 2019). At RLB and other California localities, additional dietary proxies are required to differentiate between browsing and grazing, such as microwear and mesowear (Traylor, 2012; Jones and DeSantis, 2017). Microwear analysis examines the microscopic texture (the pits and scratches) on enamel that result from abrasion of ingested food, which typically form within the last few days to a week of life. This allows for a snapshot of the last meal of an organism (Grine, 1986; Teaford and Oyen, 1989; Hoffman et al., 2015; Ackermans et al., 2020). Mesowear is macroscopic wear that results from both attrition and abrasion, and can give insight into the average diet of an organism, making this proxy useful for investigating dietary change at the population level through time (Fortelius and Solounias, 2000; Ackermans et al., 2018). Combining all of these methods allows for a greater understanding of the average diet of an organism throughout its life, to shortly before death. Combining microwear and mesowear proxies can also indicate seasonal shifts in diet, with higher incongruence between the two proxies indicating higher seasonality in diets, either through migration or shifting plant communities (Sánchez-Hernández et al., 2016; Muhlbachler et al., 2018; Strani et al., 2018, 2019).

To date, one study (Jones and DeSantis, 2017) has investigated dietary change through time in *Bison antiquus*, *Equus occidentalis*, and *Camelops hesternus* at RLB using stable isotopes, microwear, and mesowear dietary proxies. This study included two time bins at RLB (Pit 77 and Pit 61/67), roughly equivalent to the pre-LGM glacial interval and the post-LGM interglacial interval, respectively (O'Keefe et al., 2009;

Fuller et al., 2014). Dietary differences in large herbivores were inferred from microwear and stable isotope proxies. *Bison antiquus* and *E. occidentalis* consumed more woody material during the pre-LGM glacial interval, while *C. hesternus* consumed browse from denser vegetation cover during the interglacial interval. However, no temporal changes in diet were detected via mesowear, although this may have been due to small sample size (sample sizes were below 10 for most comparisons). Here, we expand the mesowear analysis of RLB herbivores through time by adding additional time bins (additional pits), utilizing large sample sizes when possible for each pit, and by comparing these data against a broader, more robust dataset of modern taxa (see supplemental data). Understanding average dietary changes through time in herbivores can help clarify potential faunal responses to climate change or other environmental stressors during the latest Pleistocene, such as the transition from the LGM to the Holocene and changing plant communities (Templeton, 1964; Clark et al., 2009).

2. Materials and methods

2.1. Mesowear data collection

The mesowear dietary proxy was used to investigate dietary change through time in ungulates at RLB. Mesowear is a macroscopic method utilizing qualitative measures of cusp sharpness and relief (Fig. 1; Fortelius and Solounias, 2000). Mesowear relies on the difference in attritional wear versus abrasive wear to determine where ungulates fall along the browsing–grazing dietary spectrum. Attritional wear actively sharpens cusps via tooth-tooth contact, resulting in sharper cusps with high relief (indicative of browsing), while abrasive wear actively flattens cusps via tooth-food contact, resulting in blunter cusps with low relief (indicative of grazing; Fortelius and Solounias, 2000). At its core, the mesowear method is a relative measure of abrasives in an ungulate's diet. However, abrasives come from two sources: internal to the food source (i.e. phytoliths in plants) or external to the food source (i.e. dirt and grit on the surface). Mesowear may therefore be related to a number of variables beyond the browsing–grazing spectrum, such as feeding proximity to the ground, soil type, plant water content, and climatic variables such as annual temperature, rainfall, and aridity (Kaiser and Schulz-Kornas, 2006; Winkler et al., 2019). Studies investigating the effect of abiotic climate variables on mesowear, however, have found little correlation between drier, warmer climates (where exogenous grit is expected to be prevalent) and higher mesowear scores (Kubo and Yamada, 2014; DeSantis et al., 2018). Controlled feeding experiments on goats have also yielded little change in mesowear scores after the addition of higher percentages of exogenous grit and different sizes of grit (Ackermans et al., 2018). While Kaiser and Schulz-Kornas (2006)

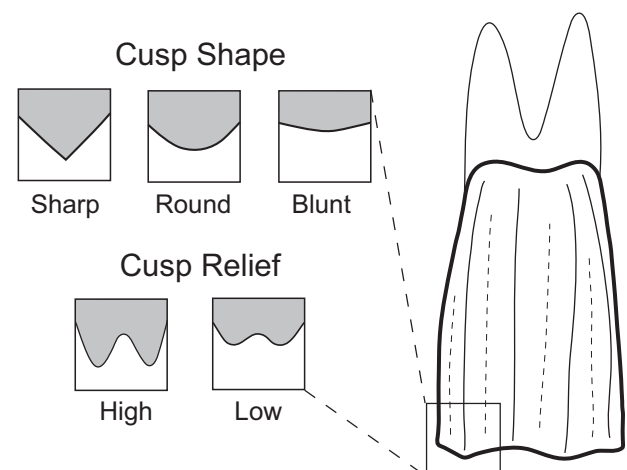


Fig. 1. Mesowear variables following Fortelius and Solounias (2000).

found that mesowear might be a good indicator of relative humidity (e.g. lower humidity can cause higher abrasives), this correlation may stem from differences in plant communities and not the relative amount of exogenous grit.

Mesowear shape and relief variables were scored following Fortelius and Solounias (2000). Since shape and relief variables are not independent, the variable scores were converted to a 0–3 mesowear numerical score (MNS) for each tooth. A sharp cusp and high relief corresponds with a score of 0, a round cusp and high relief corresponds with a score of 1, a sharp cusp and low relief corresponds with a score of 2, a round cusp and low relief corresponds with a score of 2.5, and a blunt cusp and low or high relief corresponds with a score of 3 (Croft and Weinstein, 2008; Rivals et al., 2007a, 2009; Louys et al., 2011; Kubo and Yamada, 2014). Sharp cusps and low relief is a rare combination with two different scoring mechanisms used in the literature: a 0–3 scale identified by 2.5 (Croft and Weinstein, 2008; Rivals et al., 2009; Louys et al., 2011; Kubo and Yamada, 2014) and a 0–4 scale identified by 3 (Tütken et al., 2013; Marín-Leyva et al., 2016; Dumouchel and Bobe, 2019). While both methods are valid and do not alter the results, we choose to use the 0–3 scale because it is more biologically meaningful. Strict grazers have high incidence of low relief while all other dietary categories have high relief, so a score over 2 for either the 0–3 or 0–4 scale typically corresponds with strict grazers (Fortelius and Solounias, 2000). However, previously used 0–3 scales scored round cusps and low relief as a 2 while sharp cusps and low relief was scored as a 2.5. This order of categories does not correspond with the attrition-abrasion spectrum that mesowear represents, so these categories were switched to accurately reflect the attrition-abrasion continuum (Fortelius and Solounias, 2000). Data collection followed Loffredo and DeSantis (2014), where five observers scored each specimen and the median value was taken in order to reduce interobserver error.

2.2. Fossil specimens and time bins

In order to track dietary changes through time at RLB, time bins were chosen to represent glacial, LGM, and the interglacial transition into the Holocene, roughly corresponding with pits at RLB (O'Keefe et al., 2009; Fuller et al., 2014). Five pits at RLB were used as time bins, including pits 77 (~28–37 radiocarbon kyr B.P.), 91 (~23–45 radiocarbon kyr B.P.), 13 (~16 radiocarbon kyr B.P.), 3 (~12–15 radiocarbon kyr B.P.), and 61/67 (~12 radiocarbon kyr B.P.; Friscia et al., 2008; O'Keefe et al., 2009; Fuller et al., 2014). These pits were chosen for three reasons: 1) the pits represent separate time intervals, 2) the time intervals potentially represent different climatic regimes, and 3) these pits have relatively large sample sizes available (Andersen et al., 2004; Clark et al., 2009; O'Keefe et al., 2009). The three most common ungulates, *Bison antiquus*, *Equus occidentalis*, and *Camelops hesternus*, were scored for mesowear in each time bin (Stock and Harris, 2001). Upper cheek teeth (P4M3) were scored to increase sample size in each time bin, following Kaiser and Solounias (2003). Not all time bins or taxa yielded large sample sizes, however, with the most notable being *E. occidentalis* in pits 91 and 13, and *C. hesternus* in all pits (low sample size is defined as $n <$

10, following Fortelius and Solounias, 2000; Table 1). Recent mesowear studies have attempted to resolve issues of low sample sizes by including adult lower cheek teeth, with mixed success (Franz-Odenaal and Kaiser, 2003; Rivals et al., 2009; Fraser et al., 2014; Dumouchel and Bobe, 2019). Adult lower cheek teeth tend to have blunter cusps than adult upper cheek teeth in the same specimens, leading to an interpretation of increased grazing from lower cheek teeth compared to upper cheek teeth (Franz-Odenaal and Kaiser, 2003). However, mesowear for adult upper and adult lower cheek teeth may give slightly different signals for the same individual (Franz-Odenaal and Kaiser, 2003; Kaiser and Fortelius, 2003). At RLB, low sample sizes were in large part due to a high percentage of juvenile specimens lacking worn adult teeth (Friscia et al., 2008; Jefferson and Goldin, 1989). In order to boost sample sizes in these depauperate time bins, deciduous upper fourth premolar (DP4) mesowear scores were compared with adult cheek teeth mesowear scores in an attempt to increase sample size. Incorporating deciduous premolars with adult cheek teeth may help solve low sample size issues in this study and future mesowear studies.

2.3. Deciduous premolars

Mesowear studies typically use moderately worn adult teeth, avoiding young and old individuals with little worn or extremely worn teeth (Fortelius and Solounias, 2000). However, mesowear scores from moderately worn deciduous premolars may give similar signals to the adult mesowear scores, if adult and juvenile ungulates have broadly similar diets (as is the case for *Bison bison*; Rosas et al., 2005). While ontogenetic differences in diet inferred from mesowear have been observed in moose, this analysis was based on the adult dentition and did not consider deciduous teeth (Rivals et al., 2007b; Winkler and Kaiser, 2011). Mesowear depends on the physical attributes of food on tooth wear, so all that is required to develop a mesowear signal is sufficient time to wear down the teeth. Since ungulate DP4s are morphologically similar to M1s and M2s and share a similar function during the first few years of life, mesowear signals among these teeth should be similar. As with adult teeth, minimally worn teeth or extremely worn teeth should be avoided (Fortelius and Solounias, 2000). Mesowear captures the last few months to years of an animal's diet, which is consistent with the onset of fully worn DP4s in modern ungulates (Ackermans et al., 2018; Fortelius and Solounias, 2000; Grant, 1982; Jefferson and Goldin, 1989; Joubert, 1972; Payne, 1973; Penzhorn, 1982; Sánchez-Hernández et al., 2016; Wheeler, 1982).

Ungulates at RLB are overrepresented by juveniles and provide a large dataset to employ for testing mesowear scores between adult and juvenile dentitions (Jefferson and Goldin, 1989). Progression of wear on the DP4 has been correlated with known ages of closely related modern taxa, including *Equus zebra*, *Equus quagga*, *Lama* spp., *Vicugna* spp., and *B. bison* (Jefferson and Goldin, 1989; Joubert, 1972; Smuts, 1974; Reher and Frison, 1980; Penzhorn, 1982; Wheeler, 1982). DP4s of modern bison, horses, and camelids erupt at birth and begin to wear shortly afterwards (Frison and Reher, 1970; Smuts, 1974; Reher and Frison, 1980; Wheeler, 1982). Wear facets on the DP4 paracone are formed by three months in *Lama* spp. and *Vicugna* spp., and by two months in *B. bison* (Wheeler, 1982; Jefferson and Goldin, 1989). Both the metacone and the paracone of the DP4 is fully in wear by six months of age in *Lama* spp. and *Vicugna* spp., and by five months of age in *Bison bison*, representing a minimum of three months of wear on the paracone of the DP4 in these taxa (Wheeler, 1982; Jefferson and Goldin, 1989). The DP4 of *E. quagga* appears to wear at a faster rate, beginning to wear shortly after birth with fully developed wear facets by three months of age (Smuts, 1974). DP4s are replaced around 3.5 years of age in *Lama* spp. and *Vicugna* spp., and 3 years of age in *E. quagga*, *E. zebra*, and *B. bison*. Based on these replacement times, DP4s are present in the jaw a minimum of 2.5 years, a period of time long enough for a reliable mesowear score to develop (Jefferson and Goldin, 1989; Joubert, 1972; Penzhorn, 1982; Reher and Frison, 1980; Smuts, 1974; Wheeler, 1982). In order to

Table 1
Dental mesowear sample sizes for each taxon, ontogenetic stage, and pit.

Taxon	Ontogenetic stage	Pit 77	Pit 91	Pit 13	Pit 3	Pit 61/67
<i>Bison antiquus</i>	Adult	16	11	10	19	36
	Juvenile	6	13	14	18	18
	Total	22	24	24	37	54
<i>Camelops hesternus</i>	Adult	2	0	3	5	4
	Juvenile	2	0	1	8	18
	Total	4	0	4	13	22
<i>Equus occidentalis</i>	Adult	14	7	4	30	14
	Juvenile	4	2	10	18	18
	Total	18	9	14	48	32

decrease any ontogenetic effects, only DP4s with fully formed wear facets on both the paracone and the metacone were used, with mesowear scored from the paracone (consistent with a minimum of 3–6 months of wear, depending on the taxon). No study has yet compared mesowear scores between the deciduous dentition and the adult dentition, and if mesowear scores are consistent between ontogenetic groups, the inclusion of DP4s should allow for higher sample sizes in future mesowear studies.

2.4. Statistical analysis

A three-way ANOVA and Tukey's post hoc test comparing MNS among pits, taxa, and ontogenetic stage (juvenile and adult) was conducted using R v3.3.3. A discriminant function analysis was also employed to classify RLB ungulates in each pit into four dietary groups: browsers, mixed feeders, non-strict grazers, and strict grazers following Díaz-Sibaja et al. (2018). The four groups were based on published mesowear scores for modern ungulates from 48 taxa where sample sizes for each taxa was $n > 10$ (Fortelius and Solounias, 2000; Rivals et al., 2007a; Schulz and Kaiser, 2013; Jones and DeSantis, 2017). Dietary classifications in the discriminant function analysis were based on four variables: % Sharp, % Round, % Blunt, and % High (Fig. 1). Published mesowear scores for Pleistocene *Equus* spp., *B. antiquus*, and *Camelops* spp. from localities throughout North America, ranging from the Yukon to south-central Mexico, were added into the discriminant function analysis to explore diet variability in these taxa, using the raw cusp shape and relief scores (Rivals et al., 2007a; Semprebon and Rivals, 2010; Bravo-Cuevas et al., 2011; Barrón-Ortiz et al., 2014; Barrón-Ortiz, 2016; Marín-Leyva et al., 2016; Díaz-Sibaja et al., 2018; Jiménez-Hidalgo et al., 2019). Pleistocene taxa diet groups were characterized as unknowns in the dataset and classified into the four dietary groups using posterior probabilities. The discriminant function analysis and posterior probabilities were conducted using the MASS package in R v3.3.3.

3. Results

3.1. Deciduous premolars vs. adult cheek teeth

No differences in MNS between deciduous and adult dentitions were found among all pits and taxa ($p > 0.05$). These results allow for the combination of deciduous and adult teeth, so all further analyses were conducted using the combined deciduous premolars and adult cheek teeth dataset. This allowed for an additional 150 specimens to be included in the analysis, with 69 additional *B. antiquus*, 52 additional *E. occidentalis*, and 29 additional *C. hesternus* specimens (Table 1).

3.2. Mesowear through time and Pleistocene dietary classifications

While *B. antiquus* and *E. occidentalis* were divided into five time bins, no specimens for *C. hesternus* were available for Pit 91, limiting *C. hesternus* to only four time bins (Fig. 2; Table 1). No significant differences were found among pits for all three taxa, so mesowear scores for each taxon were pooled together for subsequent analyses. *E. occidentalis* differed significantly from both *B. antiquus* and *C. hesternus* in all pits ($p < 0.0001$). Mesowear percentages used in the discriminant function analysis were combined into average RLB values for *B. antiquus*, *C. hesternus*, and *E. occidentalis* (Table 2). Following jackknife resampling procedures, mesowear percentages for modern ungulates were accurately classified into their given groups 100% of the time in the discriminant function analysis. The four dietary groups were well defined in ecospace, with the first function explaining 75.9% and the second function explaining 23.8% of the variance (Fig. 3A). Biplots indicating major differences between browsers, mixed feeders, and non-strict grazers were derived from cusp sharpness and roundness, while major differences between strict grazers and all other dietary categories were derived from cusp relief and cusp bluntness. Browsers have a higher percentage of sharp cusps and non-strict grazers have a higher percentage of round cusps, with mixed feeders situated between these two groups. Strict grazers were separated from all other groups with

Table 2

Summary of mesowear percentages per pit and combined Rancho La Brea.

Taxon	Pit	n	% Sharp	% Round	% Blunt	% High	% Low
<i>Bison antiquus</i>	61/67	36	30.6	63.9	5.5	80.6	19.4
	3	19	31.6	63.1	5.3	84.2	15.8
	13	24	45.8	41.7	12.5	79.2	20.8
	91	24	41.7	58.3	0	83.3	16.7
	77	22	27.3	54.5	18.2	72.7	27.3
	RLB	125	35.2	56.8	8	80	20
<i>Camelops hesternus</i>	61/67	22	50	45.5	4.5	77.3	22.7
	3	13	53.8	38.5	7.7	92.3	7.7
	13	4	50	50	0	50	50
	77	4	50	25	25	75	25
	RLB	43	51.2	41.9	6.9	79.1	20.9
	RLB	103	30.1	47.6	22.3	8.7	91.3
<i>Equus occidentalis</i>	61/67	32	46.9	37.5	15.6	6.3	93.7
	3	30	30	60	10	16.7	83.3
	13	14	14.3	57.1	28.6	0	100
	91	9	33.3	33.3	33.3	22.2	77.8
	77	18	11.1	44.4	44.4	0	100
	RLB	103	30.1	47.6	22.3	8.7	91.3

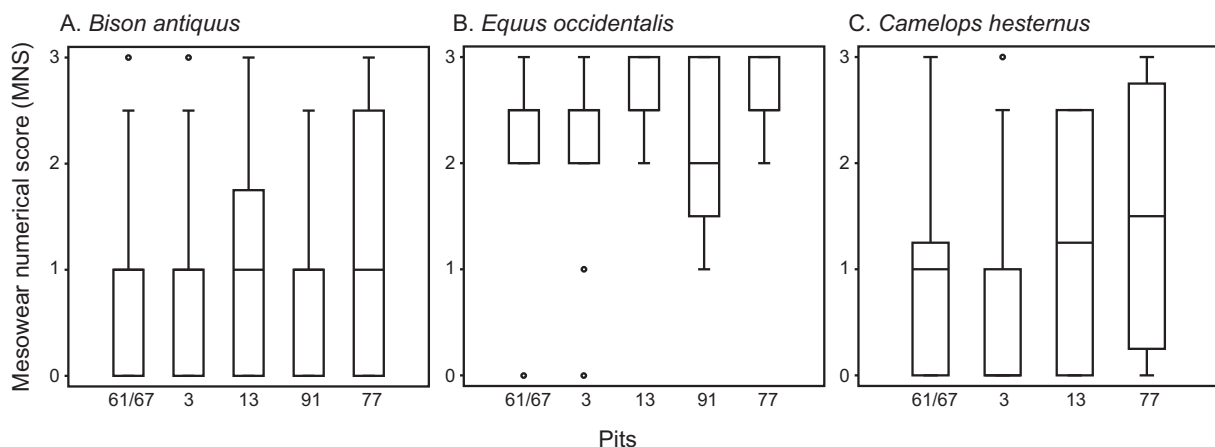


Fig. 2. Boxplots of MNS (mesowear numerical score) for Rancho La Brea taxa in each time bin (pit). A. *Bison antiquus*. B. *Equus occidentalis*. C. *Camelops hesternus*.

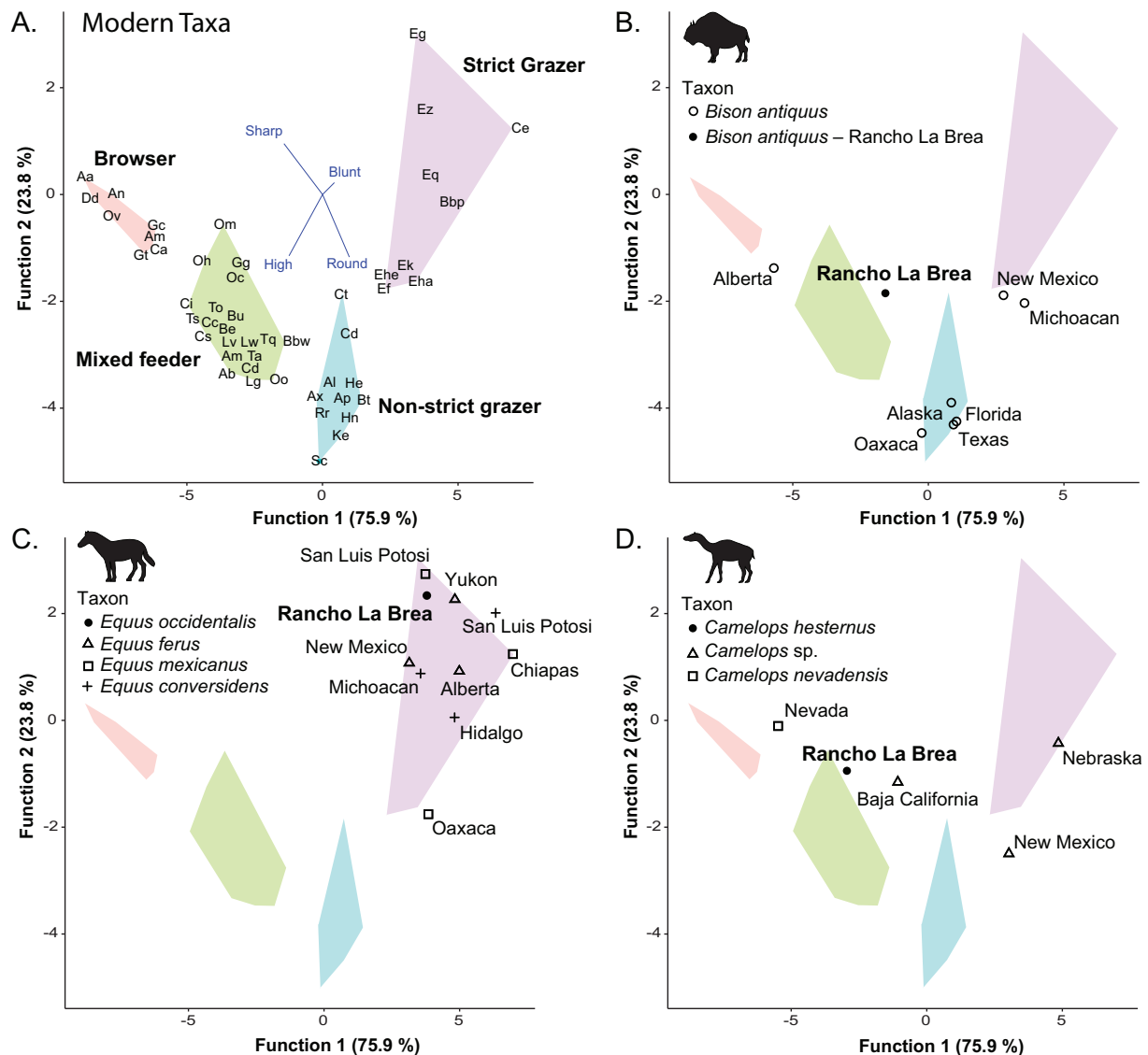


Fig. 3. Discriminant function plots of mesowear variables from modern and Pleistocene taxa. Convex hulls indicate dietary categories defined by modern taxa. A. Modern ungulate mesowear dietary categories with biplots. B. Pleistocene *Bison* mesowear scores. C. Pleistocene *Equus* mesowear scores. D. Pleistocene *Camelops* mesowear scores.

high percentages of low cusp relief and bluntness.

Posterior probability classifications of RLB recovered *E. occidentalis* in all pits as a strict grazer (100% strict grazer), *B. antiquus* as primarily a mixed feeder (95.0% mixed feeder, 5.0% non-strict grazer), and *C. hesternus* as a mixed feeder (100% mixed feeder; Fig. 3B–D). *Bison*, *Equus*, and *Camelops* specimens from late Pleistocene localities beyond RLB were also incorporated into the discriminant function analysis, with posterior probability classifications indicating additional variability in diets. The majority of *B. antiquus* were recovered as non-strict grazers with the exception of specimens from Alberta (74.1% browser, 25.9% mixed feeder), Michoacán (98.2% strict grazer, 1.8% non-strict grazer), and New Mexico (88.4% strict grazer, 11.6% non-strict grazer; Fig. 3B). All *Equus* were classified as strict grazers at 100% (Fig. 3C). *Camelops* diets were highly variable, with specimens from Nebraska recovered as strict grazers (100%), specimens from New Mexico recovered as primarily strict grazers (64.9% strict grazer, 35.1% non-strict grazer), specimens from Baja California recovered as mixed feeders (90.1% mixed feeder, 9.9% non-strict grazer), and specimens from Nevada recovered as browsers (93.3% browser, 6.7% mixed feeder; Fig. 3D).

4. Discussion

4.1. Combining deciduous fourth premolars with adult mesowear scores and modern mesowear dataset

Our results indicate that juvenile DP4s can be used in conjunction with adult cheek teeth in mesowear analyses. Future studies are necessary to confirm the use of both DP4s and adult cheek teeth in a broader range of taxa and/or localities. In *B. antiquus* and *C. hesternus* from RLB, we controlled our sample to only include specimens older than about six months of age. Wear studies suggest *Equus* fully develops wear facets by three months, far faster than either *Bison* or camelids, which is consistent with wear rates of grazers (Smuts, 1974; Wheeler, 1982; Jefferson and Goldin, 1989; Damuth and Janis, 2014). At this age, the paracone should be in wear for a minimum of three months in *Equus* and six months in *Bison* and *Camelops*, suggesting that a reliable mesowear signal could develop in that time. While studies looking at seasonal differences between mesowear and microwear scores and experimental feeding trials in goats suggest mesowear records an annual diet, both datasets were looking at dietary shifts in teeth that presumably were already in wear

for an extended period of time (Sánchez-Hernández et al., 2016; Ackermans et al., 2018). While no experimental studies have been conducted to investigate the time it takes for an initial mesowear signal to develop from an unworn tooth, the results from our analysis suggest that a minimum of 3–6 months (depending on the taxon) may be sufficient to develop an initial mesowear score. Experimental studies investigating the initial development of mesowear scores are required to test this hypothesis.

The modern taxa dataset incorporates data from a number of sources and focuses on incorporating datasets with $n > 10$ samples per taxa (Supplemental Data; Fortelius and Solounias, 2000; Rivals et al., 2007a; Schulz and Kaiser, 2013; Jones and DeSantis, 2017). In the DFA, the modern taxa were correctly classified into their given group 100% of the time, suggesting dietary differences are adequately demonstrated in the dataset (Fig. 3A). Browsers, mixed feeders, and non-strict grazers are all situated along a similar axis identified by cusp shape. Browsers tend to have sharp cusps while mixed feeders and non-strict grazers tend to have more rounded cusps. Strict grazers are largely separated from browsers, mixed feeders, and non-strict grazers by having high percentages of low cusp heights, with some influence of increased blunt cusps. Non-strict grazers also appear to be influenced by some degree of low cusp height, with browsers exhibiting the highest cusp height.

4.2. Dietary change and climate at RLB

No changes in mesowear scores were detected in *B. antiquus*, *E. occidentalis*, and *C. hesternus*, suggesting that average diets did not change between 45 ka and the end of the Pleistocene. While *C. hesternus* appears to have high MNS values in Pit 13 (Fig. 2C), this is likely due to low sample size and not due to increased grazing (Table 1). Climate and floral reconstructions of southern California indicate a number of changes during this time interval, including the Last Glacial Maximum (LGM), the Younger-Dryas, and the transition to the Holocene (Heusser, 1998; Andersen et al., 2004; Heusser et al., 2015; Kirby et al., 2018). The majority of Late Pleistocene climate reconstructions of southern California are based on palynological and stable isotope records from Lake Elsinore and the Santa Barbara Basin, indicating similar palynological patterns across southern California (Heusser, 1998; Hendy et al., 2002; Heusser et al., 2015; Kirby et al., 2018). Southern California pollen records indicate a floral transition after the LGM, from a more mesic closed-cone pine forests to more xeric oak woodlands and chaparral (Heusser et al., 2015; Kirby et al., 2018). While the southern California flora appears to transition to a more open landscape, no dietary shifts towards increased grazing are found in large ungulates at RLB. However, pollen proxies are unknown and stable oxygen isotope proxies are not well established from RLB, making direct comparisons difficult between dietary change in large herbivores at RLB to floral and climate changes in southern California. General trends in southern California pollen proxies may not be representative of RLB because of the geographically driven diversity of microclimates present in southern California (Heusser, 1998). Both the Santa Barbara Basin and Lake Elsinore records are highly influenced by runoff from the Santa Ynez and Santa Ana mountain ranges, respectively. Both of these mountain ranges exceed 1200 m in elevation and today, the local plant communities found in these ranges differ from those found in the low-lying plains of coastal southern California (where RLB is located). Even today, cypress-pine forests are common in southern California at higher altitudes, so the palynological changes observed in the pollen record may be a signal of expansion and contraction of elevation gradients of cypress-pine forests, rather than large-scale floral changes across southern California. Additionally, Lake Elsinore is located on the leeward side of the Santa Ana Mountains, so is generally warmer and drier than RLB in the Los Angeles basin.

Currently, the only study to investigate climate changes through time locally at RLB utilized ^{14}C dated insect communities (Holden and Southon, 2016; Holden et al., 2017a, 2017b). The local insect

community indicates a relatively stable Mediterranean climate at RLB, broadly similar to that of the modern Los Angeles basin, though somewhat cooler and wetter (Holden et al., 2017a, 2017b). The local insect proxy does not support the presence of a more mesic, closed-cone pine forest at RLB during the last 45 ka, as all of the Pleistocene insect taxa recovered are locally found today in Los Angeles, suggesting similar chaparral xeric conditions (Holden et al., 2017a, 2017b). However, with the insect record for both pre-LGM and post-LGM indicating similar climates and environments and no insects recovered during the LGM at RLB, inferences on climate and floral changes through time are difficult. It is possible that environmental and climatic changes may not have been drastic at RLB through the end of the Pleistocene, so a lack of dietary changes in large ungulates may be expected.

Fossil plants from RLB, however, indicate floral differences between the Pleistocene and the present, with the presence of taxa at RLB typically found within closed-cone pine plant communities reminiscent of the Monterey Bay peninsula and the mountains of southern California during the Pleistocene (Frost, 1927; Templeton, 1964; Warter, 1976). Unfortunately, plant remains were not systematically collected, with the exception of Pit 91 and Project 23, making floral changes through time difficult to ascertain (Shaw, 1982; Shaw and Quinn, 1986). Furthermore, aside from dates on unidentified wood, published radiocarbon dates on plant specimens from RLB are almost entirely from *Juniperus* specimens (Ward et al., 2005). These have yielded dates ranging from 60,000 to 8462 yr cal BP, suggesting this taxon was present throughout the latest Pleistocene and early Holocene, but any changes in the relative abundance through time is unknown (Ward et al., 2005; O'Keefe et al., 2009; Fuller et al., 2014). Plant fossils at RLB indicate some differences between the Pleistocene plant communities and modern plant communities found in the Los Angeles basin today, similar to palynological records from southern California and in contrast with the conclusions from the insect proxy record (Templeton, 1964; Heusser et al., 2015; Holden et al., 2017a, 2017b; Kirby et al., 2018). Overall floral records from southern California indicate that changes in plant communities occurred after the LGM, but the exact timing and the extent of which the floral community at RLB changed is unknown.

The lack of average dietary change in *B. antiquus*, *E. occidentalis*, and *C. hesternus* is surprising when considering the documented changes in climate and floral proxies. There are several potential explanations for why no dietary change via mesowear is observed: 1) time-averaging in pits may be overriding any dietary change, 2) floral and climate changes were not large enough to lead to measurable average dietary change, or 3) local diets at RLB did change through time, but the overall average diet of each taxon did not. The only pits at RLB that have been systematically radiocarbon dated are Pit 91 and Project 23 Deposit 1 (Friscia et al., 2008; Fuller et al., 2019). Time averaging differs between these two deposits, with dates from Pit 91 possibly encompassing two deposition events ranging from 45,000–35,000 radiocarbon years B.P. and 28,000–23,000 radiocarbon years B.P., and Project 23 Deposit 1 representing a single main deposit ranging from 36,000–35,000 radiocarbon years B.P. (Friscia et al., 2008; Fuller et al., 2019). None of the other pits in this study have undergone systematic radiocarbon dating, so the temporal ranges of these pits are not well constrained and may potentially represent as much as 4000 years of time averaging (O'Keefe et al., 2009; Fuller et al., 2014). Extensive radiocarbon dating within each pit is required to solidify our understanding of time averaging at RLB. Conflicting climate and floral proxies makes it difficult to know the extent of floral change before, during, and after the LGM at RLB (Templeton, 1964; Warter, 1976; Heusser, 1998; Heusser et al., 2015; Holden et al., 2017a, 2017b; Kirby et al., 2018). Since the insect proxy record does not include the LGM, inferences about any change during this time interval is impossible (Holden et al., 2017a, 2017b). Palynological studies from RLB are needed to better understand floral and climatic changes locally. As mesowear represents an average annual diet of an individual, it is possible that while floral and climatic changes were occurring in southern California, the overall plant community within the

home ranges of these taxa did not significantly differ. Alternatively, it is also possible that the home ranges of these taxa may have changed according to shifts in floral microhabitats. In order to tease apart local dietary changes from annual diets, studies incorporating well-constrained radiocarbon dates and microwear changes through time are required, and are ongoing.

4.3. *Bison* paleoecological reconstructions

Mesowear scores for *B. antiquus* were primarily consistent with modern mixed feeders, similar to previous studies for *B. antiquus* at RLB (Akersten et al., 1988; Feranec et al., 2009). Analysis of dental boluses of *B. antiquus* at RLB indicate a browse-dominant mixed feeder, with 86.7% of identifiable plant material recovered from gymnosperms and dicotyledons, and the remaining 13.4% from monocotyledons (Akersten et al., 1988). No analysis looking at dental bolus change through time has been conducted at RLB. Stable carbon isotope analyses have found *B. antiquus* subsisted on C₃ plants with up to 10% of their diet incorporating C₄ plants, potentially during cooler months (Feranec et al., 2009; Jones and DeSantis, 2017; DeSantis et al., 2020). Similar to mesowear, stable carbon isotopes do not change significantly over time in *B. antiquus* (Jones and DeSantis, 2017). Microwear indicates a browsing or mixed feeding diet at RLB, with a significant decline in the consumption of woody browse between Pit 77 and Pit 61/67 (Jones and DeSantis, 2017). All dietary proxies largely agree that *B. antiquus* was a mixed feeder to browser at RLB.

Our mesowear analysis indicates a mixed feeding diet for *B. antiquus* from RLB, differing from the majority of *B. antiquus* populations from the late Pleistocene of North America (Fig. 3B). Most *B. antiquus* populations are recovered as non-strict grazers, with exceptions from Alberta (recovered as browsers), Michoacán (recovered as strict grazers), and New Mexico (recovered as strict grazers), indicating dietary variability existed within *B. antiquus* during the Pleistocene. Our analyses further confirm and agree with previous studies suggesting dietary variability in Pleistocene and Holocene bison populations from both North America and Europe (Widga, 2006; Rivals et al., 2007a; Jones and DeSantis, 2017; Díaz-Sibaja et al., 2018; Hofman-Kamińska et al., 2018, 2019). Pleistocene dietary variability is most likely a function of differences in plant communities, similar to modern *B. bison* today, but requires further testing by directly comparing ancient plant communities and *B. antiquus* mesowear scores from the same localities (Larter and Gates, 1991).

4.4. *Equus* paleoecological reconstructions

E. occidentalis mesowear scores are consistent with modern strict grazers. These results agree with prior mesowear analyses, but are inconsistent with other proxy data (e.g., microwear and dental bolus studies) from *Equus* at RLB (Akersten et al., 1988; Jones and DeSantis, 2017). While only preliminary results from dental boluses have been conducted (a single specimen), *E. occidentalis* at RLB appeared to incorporate a significant amount of browse, with 55.6% of plant materials originating from gymnosperms and dicotyledons and 44.4% from monocotyledons, however without additional specimens sampled, this data should be used with caution (Akersten et al., 1988). Stable isotope analyses of collagen and enamel indicate both C₃ and C₄ plants were consumed, although this result does not eliminate grazing diets (Coltrain et al., 2004; Feranec et al., 2009; Jones and DeSantis, 2017; Fuller et al., 2019; DeSantis et al., 2019, 2020). Jones and DeSantis (2017) documented a significant dietary shift from mixed feeding in Pit 77 to grazing in Pit 61/67 inferred from microwear analyses. However, mesowear results (both here and Jones and DeSantis, 2017) do not indicate any major dietary shifts over time, suggesting local diets of *E. occidentalis* at RLB may have changed seasonally, but average diets did not. Current evidence suggests *E. occidentalis* did not migrate out of southern California, so microwear-mesowear incongruences may be due to these

seasonal differences (Feranec et al., 2009; Sánchez-Hernández et al., 2016; Mhihlbachler et al., 2018). Since microwear and mesowear incongruences are present at Pit 77 but not at Pit 61/67, this suggests two possible explanations: 1) seasonal changes in the plant community was more extreme during Pit 77 deposition than Pit 61/67 deposition, or 2) entrapment occurred during different seasons between Pit 77 and Pit 61/67. Pit 77 and Pit 61/67 were deposited during different climatic regimes (O'Keefe et al., 2009). While differences in plant communities should be expected, the degree that seasonal plant communities differed between the two pits is unknown (Heusser, 1998; Hendy et al., 2002; Heusser et al., 2015). Entrapment episodes should also be more common during warmer climate regimes when the asphalt is at its stickiest, so microwear-mesowear congruence in Pit 61/67 (warmer) may be indicative of entrapment through multiple seasons (and therefore more indicative of an average diet), while microwear-mesowear incongruence in Pit 77 (cooler) may indicate seasonal entrapment only. Entrapment over multiple seasons during a warmer regime would result in microwear capturing a more average diet, rather than a seasonal diet, due to increased time (seasonal) averaging.

Mesowear scores for horses from southern Mexico to northern Canada and Alaska were all consistently recovered as strict grazers (Fig. 3C). Our results suggest latest Pleistocene horses from North America were primarily strict grazers, however, mixed feeding *Equus* species from the Pleistocene is not unheard of, so dietary guild hypotheses should continue to be tested within *Equus* (Kaiser and Franz-Odenaal, 2004).

4.5. *Camelops* paleoecological reconstructions

C. hesternus mesowear scores at RLB were consistent with modern mixed feeders. Previous studies at RLB have suggested a browsing to mixed feeding diet for *C. hesternus* based on dental boluses, microwear, mesowear, and stable carbon isotopes (Akersten et al., 1988; Coltrain et al., 2004; Jones and DeSantis, 2017). Dental boluses of *C. hesternus* yielded 89.5% of recovered material from dicotyledons and gymnosperms, and 10.5% of recovered material from monocotyledons, suggesting a mixed feeding to browsing diet (Akersten et al., 1988). Stable carbon isotope analyses indicate mostly C₃ vegetation was consumed through time at RLB, with a significant decline in $\delta^{13}\text{C}$ values from Pit 77 to Pit 61/67 (Coltrain et al., 2004; Jones and DeSantis, 2017). The decline in $\delta^{13}\text{C}$ values likely indicates either a decrease in consumption of C₄ vegetation or the consumption of vegetation from within a denser canopy (i.e. a decline in mean $\delta^{13}\text{C}$ values from $-8\text{‰} \pm 0.6\text{‰}$ to $-10.2\text{‰} \pm 0.5\text{‰}$; Jones and DeSantis, 2017). Microwear results did not differ between Pit 77 and Pit 61/67 and are consistent with a browsing diet (Jones and DeSantis, 2017). While all previous dietary proxies are consistent in recovering *C. hesternus* at RLB as primarily browsing, mesowear points towards a mixed feeding diet. However, *C. hesternus* has on average a higher percent of sharp cusps than most modern mixed feeders, indicating that browse is an important component of their diet. Alternatively, the slight incongruence between mesowear and microwear may be due to differences in the seasonal plant communities, seasonal entrapment, or migration, but no studies have investigated whether *C. hesternus* migrated into RLB.

Camelops has been the subject of multiple studies to determine diet, incorporating a number of different proxies, including premaxillary shape, stable isotopes, hypsodonty index, mesowear, and microwear (Dompierre and Churcher, 1996; Semperebon and Rivals, 2010; Yann et al., 2016; Jones and DeSantis, 2017). Studies have variably classified *Camelops* as anything from an obligate browser to a mixed feeder (Dompierre and Churcher, 1996; Yann et al., 2016; Jones and DeSantis, 2017); however, our analysis of published mesowear data indicates *Camelops* was also capable of grazing, with populations from Nebraska and New Mexico recovered as strict grazers and non-strict grazers, respectively (Semperebon and Rivals, 2010). From the analysis of mesowear data, *Camelops* appears to be an opportunistic feeder ranging from high amounts of browse to high amounts of grass into its diet. This

diversity in diet may be explained one of two ways: 1) *Camelops* was highly opportunistic and fed from a variety of different plant communities, or 2) there are too few localities where mesowear scores have been reported in order to predict general dietary patterns for Pleistocene *Camelops*. Mesowear scores from additional localities that yield Pleistocene *Camelops* specimens are required to test this hypothesis. Enamel carbon isotope analysis of serially sampled teeth from the McKittrick asphalt seeps in California have also shown dietary variability for *Camelops*, but it is unclear whether this variation originates from changes in the plant community or changes in browsing behavior (Trayler et al., 2015). Modern New World camelids show a high diversity in diet related to habitat use and seasonal differences in use of food plants, suggesting modern camelids may also be opportunistic feeders (Puig et al., 2001; Soler et al., 2013). However, modern wild Old World camelids are primarily browsers, but this may be due to low plant and habitat variability in their home range (Mengli et al., 2006; Sugimoto et al., 2018). Only four localities outside of RLB have published mesowear scores from *Camelops*, so additional mesowear samples throughout North America are required to test for high dietary variability in Pleistocene *Camelops*.

5. Conclusions

Average herbivore diets inferred from mesowear did not change through time for *B. antiquus*, *E. occidentalis*, and *C. hesternus* at RLB. *Bison antiquus* and *C. hesternus* were both recovered as mixed feeders, and *E. occidentalis* was recovered as a strict grazer. A mesowear analysis of late Pleistocene populations for *Bison*, *Equus*, and *Camelops* indicates dietary variability in each taxon across populations, highlighting the importance of utilizing dietary proxies rather than relying on taxonomic assignment for dietary categorization. *Equus* appears to be the least variable in diet with the all populations recovered as strict grazers. *B. antiquus* had a more variable diet, ranging from browser-mixed feeding to strict grazing, with the majority of *B. antiquus* populations sampled recovered as non-strict grazers (66.6%), suggesting a strong propensity for grazing. *Camelops* also appears to be variable in diet, ranging from browsing to non-strict grazing. However, *Camelops* was the least sampled taxon, which may be contributing to the variable dietary nature recovered from our analyses, indicating more research needs to focus on understanding the paleoecology and diet of *C. hesternus* in order to assess potential competition with *B. antiquus* and *E. occidentalis* at RLB. Collectively, an extensive dental mesowear study at RLB provides additional dietary proxy data of ancient herbivores during the Late Pleistocene, shedding light on ancient mammalian ecology and bringing attention to areas of dietary disagreement that require further investigation.

Declaration of Competing Interest

Conflict of Interest Statement for “Dietary stability inferred from dental mesowear analysis in large ungulates from Rancho La Brea and opportunistic feeding during the Late Pleistocene”.

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

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