Dietary ecology of the extinct cave bear: Evidence of omnivory as inferred from dental microwear textures

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The diet of the extinct European cave bear, *Ursus spelaeus*, has widely been debated. Diverging from the extant brown bear (*Ursus arctos*) approximately 1.2 million years ago, the cave bear is one of the most ubiquitous fossil bears occurring in Europe during the Middle and Late Pleistocene. Early morphological studies suggested that the cave bear was likely specialized on processing tough and/or abrasive foods, while later two-dimensional low-magnification microwear studies suggested that they were omnivorous and may have consumed more bone than *U. arctos*. Here, we used dental microwear texture analysis (DMTA) to further interpret the diet of the cave bear. Microscopic wear features were assessed and compared to modern ursids, including the cave bears' closest living relative, *U. arctos*. Results suggest that *U. spelaeus* consumed a diet with a diversity of textural properties, similar to most other bears and only distinguishable from the hyper-carnivorous polar bear (*Ursus maritimus*). Further, only *U. maritimus* can be distinguished from all bear species here examined (i.e., the giant panda bear, *Ailuropoda melanoleuca*; sun-bear, *Ursus malayanus*; spectacled bear, *Tremarctos ornatus*; American black bear, *Ursus americanus*; and *U. arctos*), with significantly greater area-scale fractal complexity (Asfc) of microwear surfaces. The DMTA of *A. melanoleuca* also has significantly lower Asfc than *T. ornatus* and *U. americanus*, consistent with observed dietary behavior. As modern bears vary their diets seasonally and across their range, it may be difficult to characterize the dietary ecology of extinct bears using dental microwear alone. Nevertheless, DMTA here demonstrates that *U. spelaeus* had a diet distinct from the hyper-carnivorous *U. maritimus* and instead likely consumed food with textural properties most similar to other herbivorous/omnivorous bears. Lastly, the European cave bear and North American giant short-faced bear (*Arctodus simus*) may have had similar diets as evident from DMTA, with *U. spelaeus* potentially eating tougher food items.

Key words: Mammalia, *Ursus spelaeus*, carnivore, dental microwear, Pleistocene, Europe.

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Introduction

Modern bears have been known to occupy a diversity of dietary niches, from primarily herbivorous (the giant panda bear, *Ailuropoda melanoleuca*) to hyper-carnivorous (the polar bear, *Ursus maritimus*; Dierenfeld et al. 1982; Stirling and McEwan 1975). Understanding the dietary ecology of extinct bears may aid in our understandings of bear evolution. One of the most ubiquitous extinct bears is the European cave bear, *Ursus spelaeus*, which is known to have occurred throughout Europe during the Middle and Late Pleistocene (Kurtén 1976). Genetic evidence suggests that *Ursus spelaeus* and its closest living relative the brown bear, *Ursus arctos*, diverged around 1.2 million years ago—potentially just prior to the major warm climatic period (Loreille et al. 2001; Mazza and Rustioni 1993). This diversion date is earlier than the ~850 000 years ago estimate suggested by Hanni et al. (1994). Despite having a broad geographic range that spanned from southern Europe to Northern Asia and from Eastern Europe to Altali, Russia, populations declined over 25 000 years before their extinction (Knapp et al. 2009; Stiller et al. 2010). Although the precise date of their extinction is still debated, Pacher and Stuart (2009) suggest their last known appearance was in the Alps ~24 000 years ago. The extinction of *U. spelaeus* is thought to be a result of climatic cooling which subsequently decreased vegetation productivity, intensifying competition with humans (Stiller et al. 2010).

The diet of *U. spelaeus* has been widely debated. Cranial dental morphology suggests that *U. spelaeus* most likely ate tough plants (e.g., Koby 1940; Kurtén 1976; Stiner et al. 1998). This interpretation is further supported by isotopic studies that suggest that *U. spelaeus* was primarily herbiv-

orous based on comparable or often lower $\delta^{15}N$ values than co-occuring herbivores (Bocherens et al. 1993, 1997, 2006). However, Richards et al. (2008) suggest that *U. spelaeus* may have consumed more meat, at least at some sites, as evidenced by higher and more variable $\delta^{15}N$ values than herbivores at Pestera cu Oase, Romania, in contrast to a diversity of European sites previously studied. Early dental microwear evidence is inconclusive, with two-dimensional (2D) low-magnification dental microwear analyses suggesting that *U. spelaeus* was processing bone to a greater degree than extant brown bears, while other low-magnification dental microwear studies indicate that they had a mixed omnivorous diet (Pinto-Llona 2006, 2013; Peigné et al. 2009).

Although 2D low-magnification microwear has been able to clarify the diets of extinct and extant organisms, recent research has questioned the efficacy of 2D microwear for inferring diets in carnivorans (DeSantis et al. 2013). Three-dimension dental microwear texture analysis (DMTA) has been able to distinguish between more nuanced dietary niches in both herbivores and carnivores due to the inclusion of depth data and the analysis of surfaces using scale-sensitive fractal analysis (DeSantis et al. 2013; DeSantis 2016). Prior work on the 3D DMTA of bears concluded that the second lower molar grinding facet (on the hypoconulid), not the sheering facet (on the protoconid) of the lower carnassial tooth (m1), was able to distinguish between modern species with known dietary differences (Donohue et al. 2013). As the carnassial facet of modern bears does not record disparate DMTA features in bears with disparate diets, the results of Pinto-Llona (2006, 2013), Peigné et al. (2009), and Goillot et al. (2009) are called into question, as their investigations of ursid diets not only focused on the carnassial facet, but also employed 2D microwear methods.

To assess the dietary ecology of *U. spelaeus*, we compare the textural properties of its food to that of modern bears using DMTA. Specifically, we test the hypothesis proposed by Pinto-Llona (2006, 2013) that *U. spelaeus* consumed harder objects and potentially more bone and/or underground storage organs than *U. arctos*. Our study compares antemortem microwear of *U. spelaeus* from the Late Pleistocene to the modern baseline of bears examined by Donohue et al. (2013). As Donohue et al. (2013) did not examine *U. arctos*, we also examined extant specimens of *U. arctos* and additional specimens of *U. americanus*.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; FLMNH, Florida Museum of Natural History, Gainesville, USA; FMNH, Field Museum of Natural History, Chicago, USA; LACM, Los Angeles County Museum of Natural History, Los Angeles, USA; LACMHC, Los Angeles County Museum of Natural History Hancock Collection, Page Museum, Los Angeles, USA; NMNH, National Museum of Natural History (Smithsonian Institution), Washington, DC, USA; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, USA.

Other abbreviations.—Asfc, area-scale fractal complexity; DMTA, dental microwear texture analysis; epLsar, exact-proportion length-scale anisotropy of relief; SSFA, scale sensitive fractal-analysis; $HAsfc_{3\times3}$, $HAsfc_{9\times9}$, heterogeneity of area-scale fractal complexity as inferred by comparing 9 (3 × 3) and 81 (9 × 9) subsampled surfaces; Tfv, textural fill volume.

Material and methods

Antemortem microwear was examined on fossil specimens of the cave bear *Ursus spelaeus* from the FMNH (n = 7) and the AMNH (n = 5). These specimens were compared to published DMTA data of extant bears from Donohue et al. (2013) and additional extant bear specimens, including *Ursus americanus* (an additional 12 individuals were here analyzed and added to the 15 specimens previously examined) and *Ursus arctos* (n = 18, 8 specimens at the LACM and 10 from the NMNH; see SOM: table 1, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Jones_DeSantis_SOM.pdf). Extant ursids here examined, include: the giant panda bear, *Ailuropoda melanoleuca*; the spectacled bear, *Tremarctos ornatus*; the American black bear, *U. americanus*; the brown bear, *U. arctos*; the sun bear, *Ursus malayanus*; and the polar bear, *Ursus maritimus*.

Prior to molding, all wear facets were cleaned with cotton swabs soaked in acetone. Molds were created using a polyvinylsiloxane dental impression material (President's Jet, Coltène/Whaledent Corp., Altstätten, Switzerland). A polyvinylsiloxane dental putty was added to the mold to prevent any leaking when creating the replicas (President, Coltène). Replicas were subsequently cast using high-resolution epoxy well suited for imagining, including confocal microscopy (Epotek 301, Epoxy Technologies Corp., Billerica, MA, USA).

Replica casts were scanned using white light confocal profilometry with a Sensofar PLu NEOX (Solarius Development, Inc., Sunnyvale, CA, USA) under a 100× objective lens. Consistent with prior analyses (Donohue et al. 2013), the mesial facet of the lower second molar (m2) hypoconulid was analyzed on all extant and extinct bears. The replicas were scanned in four adjacent areas (2 × 2) for a total area of 204 × 276 μm^2. Resulting surface files were processed through ToothFrax and SFrax (Surfract Corporation) to assess textural properties via SSFA.

Dental wear surfaces were analyzed for complexity (Asfc), anisotropy (epLsar), heterogeneity (HAsfc), and textural fill volume (Tfv). Complexity is a measure of surface roughness and used to distinguish between taxa that consume softer versus harder food items (Scott et al. 2006; Schubert et al. 2010; DeSantis et al. 2012, 2015; Donohue et al. 2013; Haupt et al. 2013; DeSantis and Haupt 2014; DeSantis 2016). The consumption of either or both hard seeds or bone result in higher complexity values. Anisotropy quantifies the orientation of wear features with higher values occurring when

features are oriented in a similar direction, such as many parallel scratches when consuming tougher food items like grass, leaves, or flesh. Heterogeneity describes the variation in complexity on a given surface. Specifically, heterogeneity quantifies the complexity of sub-sections of a given surface as compared to complexity of the entire surface; 9 and 81 sub-sections, when referring to $HAsfc_{3\times3}$ and $HAsfc_{9\times9}$, respectively. Higher heterogeneity values suggest variability in textural food properties (Scott et al. 2006); however, heterogeneity has not been useful in differentiating diet in extant bears, to date (Donohue et al. 2013). As we added to the extant baseline we have performed analyses of $HAsfc_{3x3}$ and $HAsfc_{9\times9}$ (and report all data in SOM: table 1). Textural fill volume quantifies the size of the features on the surface. It is calculated by quantifying the difference in volume filled by 10 μm^2 and 2 μm^2 diameter square cuboids (Scott et al. 2006). The higher the Tfv value the deeper the features on the tooth. This has been shown to be correlated with a smaller number of deep pits (DeSantis et al. 2013).

DMTA values are not normally distributed (Shapiro-Wilk tests). Therefore, non-parametric statistical tests (Kruskal-Wallis) were used to compare differences among taxa. We used Dunn's procedure to compare between multiple taxa, withholding the Bonferroni correction (to minimize Type II errors, see DeSantis et al. 2012 for a detailed discussion). Lower second molars of only two species were compared using Mann-Whitney tests.

Results

Dental microwear results of modern and extinct ursids are presented in Tables 1 and 2 and illustrated in Figs. 1 and 2. Of the extant ursids analyzed, *U. maritimus* has the greatest mean complexity value (8.847), followed by *U. americanus* (5.394) and *U. arctos* (4.405). *U. maritimus* has significantly higher complexity than all extant ursids here examined. *Ailuropoda melanoleuca* has significantly lower complexity than *T. ornatus*, *U. americanus*, and *U. maritimus*, but is indistinguishable from *U. arctos* and *U. malayanus*. *Ailuropoda melanoleuca* has significantly higher anisotropy values than *U. americanus*, *U. arctos*, and *U. maritimus* and significantly lower textural fill volume values than *T. ornatus*, *U. americanus*, and *U. maritimus*. All other extant ursids are indistinguishable from one another (Table 2). $HAsfc_{3\times3}$ and $HAsfc_{9\times9}$ are not significantly different between any extant ursids (all p-values are > 0.15, in agreement with Donohue et al. 2013) and thus not discussed further or compared to extinct ursids.

Ursus spelaeus has a mean complexity value of 2.951, significantly lower than *U. maritimus* ($p = 0.0003$) but indistinguishable from all other extant ursids (Kruskal-Wallis). Anisotropy values of *U. spelaeus* are significantly greater than *U. maritimus* ($p = 0.017$), but are indistinguishable from all other extant ursids. Mean textural fill volume values are similar to and statistically indistinguishable from all extant ursids.

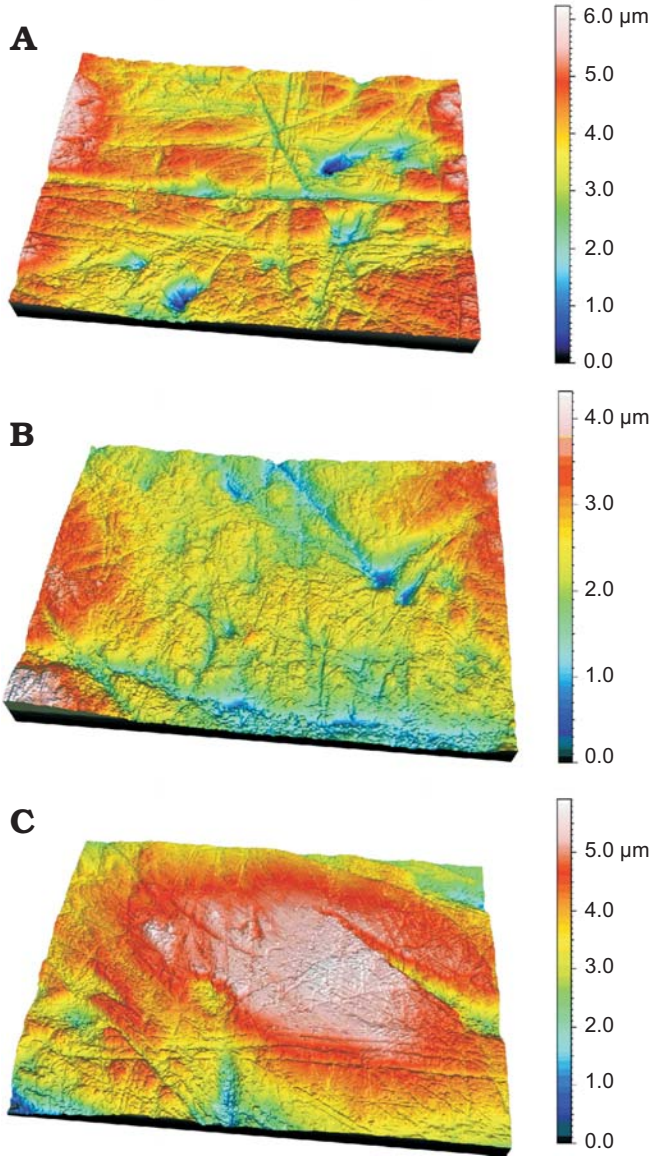

Fig. 1. Meshed axonometrics of digital elevation models showing microwear features. Examples include *Ursus americanus* (**A**), black bear (SBMNH 1381, modern specimen from California); *Ursus arctos* (**B**), brown bear (LACM 31256, modern specimen from Alaska), and *Ursus spelaeus* (**C**), cave bear (AMNH 11100, Pleistocene fossil specimen from Germany).

Complexity values of *Arctodus simus* are indistinguishable from *U. spelaeus*. Anisotropy and textural fill volume, however, are significantly different in *A. simus* as compared to *U. spelaeus* ($p = 0.022$ and $p = 0.008$, respectively).

Discussion and conclusions

Our analyses of dental microwear textures of lower second molars was able to distinguish several extant bear species from one another. Most notably, textural attributes correlated with hard object feeding (i.e., complexity) are the

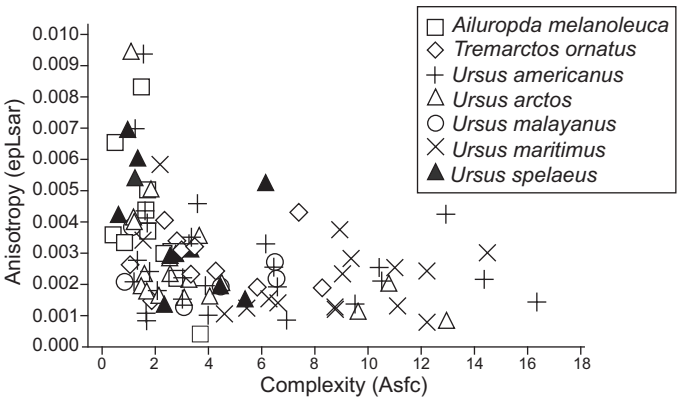

Fig. 2. Bivariate plot of complexity (Asfc) and anisotropy (epLsar) of extant ursids and *Ursus spelaeus*.

most revealing. As previous work by Donohue et al. (2013) showed that complexity is the most useful for inferring diets in extant wild bears and as this is in agreement with our additional analyses with an improved baseline, we focus our discussion primarily on complexity. While Donohue et al. (2013) discussed relationships between DMTA and diet in extant bears, our results are slightly different due to the inclusion of brown bears (*U. arctos*) and additional specimens of *U. americanus* in this analysis.

Ailuropoda melanoleuca has the lowest complexity and Tfv values (Table 1 and 2; significantly lower than *T. ornatus*, *U. americanus*, and *U. maritimus*) and greatest anisotropy (significantly greater than *U. arctos*, *U. americanus*, and *U. maritimus*; Table 2), consistent with the consumption of predominantly tough bamboo leaves (Hansen et al. 2010). This result is consistent with Donohue et al. (2013) who originally noted this pattern. Also consistent with Donohue et al. (2013), *U. maritimus* has significantly higher complexity than all other extant species (Table 2), indicative of the consumption of brittle object consumption, like bone. The hyper-carnivorous polar bear, *U. maritimus* predominantly feeds on the ringed seal, *Phoca hispida* in Arctic waters (Stirling and McEwan 1975; Thiemann et al. 2008). Although they often prefer the blubber, in times of desperation, or when feeding their own small polar bear cubs, polar bears will scavenge the entire carcass (Stirling and McEwan 1975). Despite occasional consumption of terrestrial plants and berries during the summer months (as noted to occur inland from northwest Hudson Bay; Derocher et al. 1993), polar bears are most commonly observed eating marine mammals (also including harbor seals: *Phoca vitalina*, bearded seals: *Erignathus barbatus*, walruses: *Odobenus rosmarus*, and narwhals: *Monodon monoceras*) and sometimes Arctic char, *Salvelinus alpinus* (Stirling and McEwan 1975; Derocher et al. 1993; Thiemann et al. 2008; Dyck and Kebreab 2009)—food items capable of leaving microwear textures of high complexity.

In contrast to Donohue et al. (2013), *U. maritimus* here has significantly greater complexity than *U. americanus*. This is likely due to the inclusion of *U. americanus* specimens from California, as they show lower complexity values than the

Table 1. Descriptive statistics for each ursid examined, including data previously reported in Donohue et al. (2013). Asfc, area-scale fractal complexity; epLsar, exact-proportion length-scale anisotropy of relief; n, sample size; Tfv, textural fill volume.

Taxon	n	Statistic	Asfc	epLsar	Tfv
Ailuropoda melanoleuca (extant)	11	mean	1.996	0.0039	8229.699
		median	1.915	0.0038	11433.068
		standard deviation	1.010	0.0021	5506.812
		minimum	0.618	0.0004	210.985
		maximum	3.895	0.0083	14591.464
		total range	3.277	0.0079	14380.479
		skewness (Fisher's)	0.338	0.6317	-0.303
Arctodus simus (extinct)	16	mean	4.586	0.0022	15027.685
		median	4.115	0.0020	15394.578
		standard deviation	2.295	0.0010	1753.254
		minimum	1.160	0.0009	11985.388
		maximum	8.292	0.0041	17652.226
		total range	7.133	0.0032	5666.838
		skewness (Fisher's)	0.185	0.6148	-0.412
Tremarctos ornatus (extant)	11	mean	4.172	0.0028	12986.927
		median	3.538	0.0026	13012.031
		standard deviation	2.288	0.0009	4409.971
		minimum	1.256	0.0014	4029.080
		maximum	8.478	0.0043	19630.217
		total range	7.223	0.0028	15601.137
		skewness (Fisher's)	0.871	0.3170	-0.534
Ursus americanus (extant)	27	mean	5.394	0.0028	12205.405
		median	3.560	0.0022	12894.469
		standard deviation	4.401	0.0019	3829.890
		minimum	1.401	0.0008	3140.259
		maximum	16.550	0.0093	16981.355
		total range	15.148	0.0085	13841.096
		skewness (Fisher's)	1.214	1.9660	-0.886
Ursus arctos (extant)	16	mean	4.405	0.0028	12022.700
		median	2.749	0.0021	12284.561
		standard deviation	3.542	0.0020	2919.079
		minimum	1.288	0.0008	5372.738
		maximum	13.152	0.0094	17014.341
		total range	11.864	0.0086	11641.604
		skewness (Fisher's)	1.745	2.4046	-0.407
Ursus malayanus (extant)	6	mean	3.964	0.0023	10638.874
		median	3.972	0.0021	11727.468
		standard deviation	2.519	0.0009	3714.545
		minimum	1.052	0.0012	4242.606
		maximum	6.672	0.0038	13791.051
		total range	5.710	0.0026	9548.445
		skewness (Fisher's)	-0.012	0.9714	-1.146
Ursus maritimus (extant)	16	mean	8.847	0.0022	13036.051
		median	9.055	0.0019	13358.147
		standard deviation	3.640	0.0013	2135.500
		minimum	1.740	0.0007	10574.162
		maximum	14.690	0.0058	18800.075
		total range	12.950	0.0050	8225.913
		skewness (Fisher's)	-0.340	1.3911	1.185
Ursus spelaeus (extinct)	12	mean	2.951	0.0037	11176.850
		median	2.651	0.0030	12376.704
		standard deviation	1.776	0.0018	4647.631
		minimum	0.815	0.0013	1450.149
		maximum	6.352	0.0069	16379.763
		total range	5.537	0.0056	14929.614
		skewness (Fisher's)	0.780	0.4273	-1.350

Table 2. Pairwise comparisons between modern ursids, including previously published data by Donahue et al. (2013) and new *Ursus americanus* and *Ursus arctos* data here analyzed. * denotes significant p-values ($p < 0.05$). Asfc, area-scale fractal complexity; epLsar, exact-proportion length-scale anisotropy of relief; Tfv, textural fill volume.

	Taxon	*Tremarctos ornatus*	*Ursus americanus*	*Ursus arctos*	*Ursus malayanus*	*Ursus maritimus*
Asfc	*Ailuropoda melanoleuca*	0.034*	0.007*	0.095	0.162	< 0.001*
	Tremarctos ornatus		0.846	0.492	0.704	0.028*
	Ursus americanus			0.275	0.561	0.012*
	Ursus arctos				0.882	0.001*
	Ursus malayanus					0.028*
epLsar	*Ailuropoda melanoleuca*	0.222	0.035*	0.040*	0.069	0.006*
	Tremarctos ornatus		0.517	0.487	0.427	0.150
	Ursus americanus			0.909	0.704	0.293
	Ursus arctos				0.772	0.387
	Ursus malayanus					0.737
Tfv	*Ailuropoda melanoleuca*	0.047*	0.039*	0.144	0.604	0.032*
	Tremarctos ornatus		0.763	0.452	0.250	0.990
	Ursus americanus			0.554	0.292	0.744
	Ursus arctos				0.530	0.410
	Ursus malayanus					0.227

black bears analyzed by Donahue et al. (2013). California black bears may have consumed fewer hard objects, such as saw palmetto hearts (*Serenoa repens*), than black bears in Florida consumed. It is possible that California black bears also consumed fewer carcasses than black bears in Alaska, all while consuming more vegetation and fruit, as observed in Yosemite National Park (Graber and White 1983). All of these scenarios can explain the lower complexity values seen in the California black bears. The widely varied diet of *U. americanus* (Graber and White 1983; Hatler 1967; Raine and Kansas 1990; Roof 1997; Stratman and Pelton 1999) is here captured in their dental microwear. Future work focused on assessing *U. americanus* diets throughout their range and across various seasons is needed to better understand the nature of their highly variable DMTA values (e.g., total range in complexity of 15.148, with a standard deviation of 4.401; Table 1).

Much like *U. americanus*, *U. arctos* has one of the more varied diets amongst extant bears (Cicnjak et al. 1987; Mowat and Heard 2006; Persson et al. 2001; Welch et al. 1997). In Alaska, salmon can be a dominant component of their diet (as inferred from carbon and nitrogen isotopes; Mowat and Heard 2006). When salmon is not available, the brown bear often consumes larger ungulates, such as *Alces alces,* moose and *Rangifer tarandus*, reindeer (Persson et al. 2001). Seasonally, as *U. arctos* prepares to hibernate, berries become an importance resource (Persson et al. 2001). Although it is common for *U. arctos* to consume mostly salmon and berries, depending on the season, vegetation is often a component of their diet (Cicnjak et al. 1987; Mowat and Heard 2006; Munro et al. 2006; Persson et al. 2001). For example, *U. arctos* in Yugoslavia consume more vegetation than animal biomass (Cicnjak et al. 1987) while those in Alberta, Canada consume grasses from late April to late June, ungulates from May to early June, and berries from early August to early October (Munro et al. 2006). With this varied diet, we expect highly variable DMTA attributes including a large range in complexity values as seen here (e.g., total range of complexity values is 11.864, 1.288–13.152; Table 1).

U. spelaeus has significantly lower complexity and higher anisotropy than *U. maritimus*, suggesting that *U. spelaeus* was not a hyper-carnivore. Instead, DMTA values are indistinguishable from all other extant bears and are instead consistent with a dietary interpretation of omnivory. The lack of any significant differences between *U. spelaeus* and its closest living relative, *U. arctos,* suggests that dietary differences between these taxa were likely minor, at least in regards to the textural properties of food consumed. These data are consistent with prior isotopic work done by Bocherens et al. (1993, 1997, 2006), which suggested that *U. spelaeus* consumed primarily vegetation, due to low $\delta^{15}N$ values. These data are consistent with a largely omnivorous diet as inferred from prior 2D microwear studies (Pinto-Llona 2006, 2013; Peigné et al. 2009), but in contrast to Pinto-Llona (2006, 2013) do not present evidence for increased bone consumption (i.e., harder-object feeding) in *U. spelaeus* as compared to *U. arctos*. The data of prior authors (Pinto-Llona 2006, 2013; Peigné et al. 2009) relied on the counting of pits and scratches, which in carnivores may be problematic for the recognition of bone consumption. As shown by previous comparative work of 2D and 3D methods (DeSantis et al. 2013), pit frequencies can decrease with increased bone consumption (due to the increased size of pits, as seen in durophagous hyenas). Thus, divergent dietary interpretations between our study and that of authors using 2D methods, may stem from different methodologies.

We also compared the European cave bear to the North American giant short-faced bear in order to understand if they both filled similar ecological niches. *Arctodus simus*

was not distinguishable from *U. spelaeus* in complexity, but had significantly lower anisotropy, suggesting that *U. spelaeus* ate tougher food items (such as tough grass or leaf material) than *A. simus*. In combination with prior isotopic data (Bocherens et al. 1993, 1996, 2008; Matheus 1995), these dietary comparisons suggest potential dietary differences between these extinct cave bears, with *U. spelaeus* potentially consuming tougher vegetation than *A. simus*; although, both are interpreted as consuming significant amounts of plant matter (here and Donohue et al. 2013).

Similar to prior work (Donohue et al. 2013), DMTA is able to distinguish between an herbivorous diet, a hyper-carnivorous diet, and a mixed/omnivorous diet. It is difficult, however, to further distinguish between ursids with differential consumption of plant and animal matter—in large part due to the highly variable nature of extant ursid diets. Nuts, seeds, and bone, all hard food items, are indistinguishable from one another via textural attributes like complexity. Similarly, flesh and tough plant matter can be hard to distinguish as both can result in higher anisotropy (high anisotropy in felids is indicative of flesh consumption while high anisotropy in ursids is exhibited by herbivorous panda bears; see Schubert et al. 2010; DeSantis et al. 2012; DeSantis and Haupt 2014; DeSantis 2016; Donohue et al. 2013). However, the DMTA data discussed here clearly demonstrate that *U. spelaeus* was not a hyper-scavenger or hyper-carnivore and is in agreement with nitrogen isotope data (Bocherens et al. 1993, 1996, 2008). While hypotheses regarding hyper-carnivory can be assessed in extinct bears (much like was done by Donohue et al. 2013), inferring precise proportions of plant matter is unlikely to be resolved or captured using DMTA. While further work aimed at clarifying relationships between dietary variability and DMTA attributes in extant ursids may be revealing, the highly variable nature of bear diets complicates paleobiological interpretations of extinct ursids.

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References

Bocherens, H., Billiou, D., Patou-Mathis, M., Bonjean, D., Otte, M., and Mariotti, A. 1997. Paleobiological implications of the isotopic signature (^{13}C, ^{15}N) of fossil mammal collagen in Scladina Cave (Sclayn, Belgium). *Quaternary Research* 48: 370–380.

Bocherens, H., Drucker, D., Billiou, D., Geneste, J., and van der Plicht, J. 2006. Bears and humans in Chauvet Cave (Vallon-Pont-d'Arc, Ardèche, France): insights from stable isotopes and radiocarbon dating of bone collagen. *Journal of Human Evolution* 50: 370–376.

Bocherens, H., Fizet, M., and Mariotti, A. 1993. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. *Paleogeography, Paleoclimatology, Paleoecology* 107: 213–225.

Cicnjak, L., Huber, D., Roth, H.U., Ruff, R., and Vinovrski, Z. 1987. Food habits of brown bears in Plitvice Lakes National Park, Yugoslavia. *Bears: Their Biology and Movement* 7: 221–226.

Derocher, A., Andriashek, D., and Stirling, I. 1993. Terrestrial foraging by polar bears during the ice-free period in Western Hudson Bay. *Arctic* 46: 251–254.

DeSantis, L.R.G. 2016. Dental microwear, textures: reconstructing diets of fossil mammals. *Surface Topography: Metrology and Properties* 4: 023002.

DeSantis, L.R.G. and Haupt, R. 2014. Cougars' key to survival through the Late Pleistocene extinction: insights from dental microwear texture analysis. *Biology Letters* 10: e20140203.

DeSantis, L.R.G., Schubert, B.W., Schmitt-Linville, E., Ungar, P., Donohue, S., and Haupt, R.J. 2015. Dental microwear textures of carnivorans from the La Brea Tar Pits, California and potential extinction implications. *Science Series of the Natural History Museum of Los Angeles County* 42: 37–52.

DeSantis, L.R.G., Schubert, B., Scott, J., and Ungar, P. 2012. Implications of diet for the extinction of saber-toothed cats and American lions. *PLoS One* 7: e52453.

DeSantis, L.R.G, Scott, J., Schubert, B., Donohue, S., McCray, B., Van Stolk, C., Winburn, A., Greshko, M., and O'Hara, M. 2013. Direct comparisons of 2D and 3D dental microwear proxies in extant herbivorous and carnivouros mammals. *PLoS One* 8: e71428.

Dierenfeld, E., Hintz, H., Robertson, J., Soest, P., and Oftedal, O. 1982. Utilization of bamboo by the Giant Panda. *The Journal of Nutrition* 112: 636–641.

Donohue, S., DeSantis, L.R.G., Schubert, B., and Ungar, P. 2013. Was the giant short-faced bear a hyper-scavenger? A new approach to dietary study of ursids using dental microwear textures. *PLoS One* 8: e77531.

Dyck, M. and Kebreab, E. 2009. Estimating the energetic contribution of polar bear (*Ursus maritimus*) summer diets to the total energy budget. *Journal of Mammalogy* 90: 585–593.

Goillot, C., Blondel, C., and Peigné, S. 2009. Relationship between dental microwear and diet in Carnivora (Mammalia)—Implications for the reconstruction of the diet of extinct taxa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 271: 13–23.

Graber, D. and White, M. 1983. Black bear food habits in Yosemite National Park. *Bears: Their Biology and Management* 5: 1–10.

Hanni, C., Laudet, V., Stehelin, D., and Taberlet, P. 1994. Tracking the origins of the cave bear (*Ursus spelaeus*) by mitochondrial DNA sequencing. *Proceedings of National Academy of Sciences in the United States of America* 91: 12336–12340.

Hansen, R., Carr, M., Apanavicius, C., Jiang, P., Bissell, H., Gocinski, B., Maury, F., Himmelreich, S., Ouellette, J., and Kouba, A. 2010. Seasonal shifts in giant panda feeding behavior: relationships to bamboo plant part consumption. *Zoo Biology* 28: 1–14.

Hatler, D. 1967. *Some Aspects in the Ecology of the Black Bear (*Ursus americanus*) in Interior Alaska.* 121 pp. Unpublished M.Sc. Thesis, University of Alaska, Fairbanks.

Haupt, R., DeSantis, L.R.G., Green, J., and Ungar, P. 2013. Dental microwear texture as a proxy for diet in xenarthrans. *Journal of Mammalogy* 94: 856–866.

Knapp, M., Rohland, N., Weinstock, J., Baryshnikov, G., Sher, A., Nagel, D., Rabeder, G., Pinhasi, R., Schmidt, and H., Hofreiter, M. 2009. First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. *Molecular Ecology* 18: 1225–1238.

Koby, F.E. 1940. Les usures séniles des canines d'*Ursus spelaeus* et la préhistoire. *Verhandlungen der naturforschenden Gesellschaft* 51: 76–95.

Kurtén, B. 1955. Sex dimorphism and size trends in the cave bear, *Ursus spelaeus* Rosenmüller and Heinroth. *Acta Zoologica Fennica* 90: 1–48.

Kurtén, B. 1976. *The Cave Bear Story*. 163 pp. Columbia University Press, New York.

Loreille, O., Orlando, L., Patou-Mathis, M., Phillippe, M., Taberlet, P., and Hanni, C. 2001. Ancient DNA analysis reveals divergence of the cave bear, *Ursus spelaeus*, and brown bear, *Ursus arctos*, lineages. *Current Biology* 11: 200–203.

Matheus, P.E. 1995. Diet and co-ecology of Pleistocene short-faced bears and brown bears in eastern Beringia. *Quarternary Research* 44: 447–453.

Mazza, N. and Rustioni, M. 1993. On the phylogeny of Eurasian bears. *Palaeontographica Abstracts A*: 230: 1–38.

Mowat, G. and Heard, D.C. 2006. Major components of the grizzly bear diet across North America. *Journal of Zoology* 84: 473–489.

Munro, R., Nielsen, S., Price, M., Stenhouse, G., and Boyce, M. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy* 87: 1112–1121.

Pacher, M. and Stuart, A.J. 2009. Extinction chronology and palaeobiology of the cave bear. *Boreas* 38: 189–206.

Peigné, S., Goillot, C., Germonpre, M., Blondel, C., Bignon, O., and Merceron, G. 2009. Predormancy omnivory in European cave bears evidenced by a dental microwear analysis of *Ursus spelaeus* from Goyet, Belgium. *Proceedings of National Academy of Sciences in the United States of American* 106: 15390–15393.

Persson, I., Wilkan, S., Swenson, J.E., and Mysterud, I. 2001. The diet of the brown bear *Ursus arctos* in the Pasvik Valley, northeastern Norway. *Wildlife Biology* 7: 27–37.

Pinto-Llona, A. 2006. Comparitive dental microwear analysis of cave bears *Ursus spelaeus* Rosenmuller, 1794 and brown bears *Ursus arctos* Linnaeus, 1758. *Scientific Annals, School of Geology Aristotle University of Thessalonki* 98: 225–230.

Pinto-Llona, A. 2013. Macrowear and occlusal microwear on teeth of cave bears *Ursus spelaeus* and brown bears *Ursus arctos*: Inferences concerning diet. *Palaeogeography, Palaeoclimatology, Palaeoecology* 370: 41–50.

Raine, R. and Kansas, J. 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. *Bears: Their Biology and Management* 8: 297–304.

Richards, M., Pacher, M., Stiller, M., Quilès, J., Hofreiter, M., Constantin, S., Zilhão, J., and Trinkaus, E. 2008. Isotopic evidence for omnivory among European cave bears: Late Pleistocene *Ursus spelaeus* from the Peştera cu Oase, Romania. *Proceedings of National Academy of Sciences in the United States of America* 105: 600–604.

Roof, J. 1997. Black bear food habits in the lower Wekiva river basin of Central Florida. *Florida Field Naturalist* 25: 92–97.

Schubert, B., Ungar, P., and DeSantis, L. 2010. Carnassial microwear and dietary behavior in large carnivorans. *Journal of Zoology* 280: 257–263.

Scott, R., Teaford, M., and Ungar, S. 2006. Dental microwear texture and anthropoid diets. *American Journal of Physical Anthropology* 147: 551–579.

Stiller, M., Baryshnikov, G., Bocherens, H., Grandal d'Anglade, A., Hilpert, B., Susanne, M. C., Pinhasi, R., Rabeder, G., Rosendahl, W., Trinkaus, E., Hofreiter, M., and Knapp, M. 2010. Withering away—25,000 years of genetic decline preceded cave bear extinction. *Molecular Biology and Evolution* 27: 975–978.

Stiner, M., Achyuthan, H., Arsebuk, G., Howell, F. Clark, Josephson, S., Juell, K., Pigati, J., and Quade, J. 1998. Reconstructing cave bear paleoecology from skeletons: a cross-disciplinary study of middle Pleistocene bears from Yarimburgaz Cave, Turkey. *Paleobiology* 24: 74–98.

Stirling, I. and McEwan, E. 1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behavior. *Canandian Journal of Zoology* 53: 1021–1027.

Stratman, M. and Pelton, M. 1999. Feeding ecology of black bears in northwest Florida. *Florida Field Naturalist* 27: 95–102.

Thiemann, G., Iverson, S., and Stirling, I. 2008. Polar bear diets and arctic marine food webs: insights from fatty acid analysis. *Ecological Monographs* 78: 591–613.

Welch, C., Keay, J., Kendall, K., and Robbins, C. 1997. Constraints on frugivory by bears. *Ecology* 78: 1105–1119.