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Cougars' key to survival through the Late Pleistocene extinction: insights from dental microwear texture analysis

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Cougars (*Puma concolor*) are one of only two large cats in North America to have survived the Late Pleistocene extinction (LPE), yet the specific key(s) to their relative success remains unknown. Here, we compare the dental microwear textures of Pleistocene cougars with sympatric felids from the La Brea Tar Pits in southern California that went extinct at the LPE (*Panthera atrox* and *Smilodon fatalis*), to clarify potential dietary factors that led to the cougar's persistence through the LPE. We further assess whether the physical properties of food consumed have changed over time when compared with modern cougars in southern California. Using dental microwear texture analysis (DMTA), which quantifies surface features in three dimensions, we find that modern and Pleistocene cougars are not significantly different from modern African lions in any DMTA attributes, suggesting moderate durophagy (i.e. bone processing). Pleistocene cougars from La Brea have significantly greater complexity and textural fill volume than *Panthera atrox* (inferred to have primarily consumed flesh from fresh kills) and significantly greater variance in complexity values than *S. fatalis*. Ultimately, these results suggest that cougars already used or adopted a more generalized dietary strategy during the Pleistocene that may have been key to their subsequent success.

1. Introduction

Currently, cougars maintain the largest latitudinal range of any extant terrestrial mammal (aside from humans) in the Western Hemisphere [1]. Their broad geographical distributions are accompanied by highly generalized diets, dominated by the consumption of ungulates in temperate regions [2,3] to small- and medium-sized prey in the tropics [2,4]. Additionally, cougars are known to vary prey sources in response to the presence of sympatric competitively sized carnivores, including wolves [5,6] and jaguars [7]. While much is known about modern cougar diets, often in an effort to ensure their survival in the face of anthropogenic influences, little is known about cougar palaeoecology during the Pleistocene. As cougars are one of only two large cats, along with jaguars, to remain in North America after the Late Pleistocene extinction (LPE) [8], further study of their palaeoecology is necessary to clarifying how they survived.

The La Brea Tar Pits in southern California (USA) contains a high abundance of fossil carnivores during the Pleistocene, largely because it was a tar seep that attracted numerous carnivores once herbivorous prey became immobilized (much like flies on fly paper) [9]. Despite this rich fossil record, cougars are much less abundant than other sympatric carnivores at La Brea, especially carnivores inferred to have been social hunters (i.e. the sabre-toothed cat, *Smilodon fatalis* [9,10], and the dire wolf, *Canis dirus* [9]). While less information is available on the dietary ecology of Pleistocene cougars, dental microwear texture analysis (DMTA) can elucidate the textural properties of consumed food, including durophagy in extinct and extant carnivores [11,12].

Table 1. Descriptive statistics for each DMTA variable by species and/or subspecies. *n*, number of individuals sampled; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume.

taxon	statistics	<i>n</i>	<i>Asfc</i>	<i>epLsar</i>	<i>Tfv</i>
<i>Puma concolor</i> (fossil, La Brea Tar Pits)	mean	12	4.592	0.0035	12 860
	median		3.222	0.0027	14 008
	standard deviation		4.530	0.0021	3609
	skewness (Fisher)		1.814	0.870	−1.989
	<i>p</i> for normality (Shapiro–Wilk)		0.009	0.028	0.007
<i>Puma concolor cougar</i> (modern, California)	mean	17	4.113	0.0045	9554
	median		4.485	0.0051	10 454
	standard deviation		2.233	0.0016	4727
	skewness (Fisher)		0.638	−0.206	−0.459
	<i>p</i> for normality (Shapiro–Wilk)		0.299	0.229	0.684
<i>Puma concolor coryi</i> (modern, Florida)	mean	21	4.063	0.0027	8614
	median		3.871	0.0027	9409
	standard deviation		1.702	0.0015	4561
	skewness (Fisher)		0.715	0.339	0.047
	<i>p</i> for normality (Shapiro–Wilk)		0.305	0.400	0.530
<i>Puma concolor</i> (modern, combined CA and FL)	mean	38	4.086	0.0035	9035
	median		4.039	0.0034	9849
	standard deviation		1.929	0.0017	4597
	skewness (Fisher)		0.663	0.150	−0.168
	<i>p</i> for normality (Shapiro–Wilk)		0.273	0.248	0.278

Here, we compare dental microwear attributes of Pleistocene cougar specimens from the La Brea Tar Pits to sympatric felids that went extinct at the LPE, including *S. fatalis* and the American lion *Panthera atrox*. Additionally, we test the hypothesis that the diets of modern cougars are distinct from Pleistocene cougars—potentially in response to competitive release after the LPE.

2. Material and methods

Extant cougar (*Puma concolor*) specimens were examined from both southern California (*Puma concolor cougar*, *n* = 17; Santa Barbara Museum of Natural History) and from Florida (*Puma concolor coryi*, *n* = 21; Florida Museum of Natural History, some noted in reference [13]). These specimens were compared with the following extant species: *Acinonyx jubatus* (cheetah, *n* = 9), *Panthera leo* (African lion, *n* = 15) and *Crocuta crocuta* (spotted hyaena, *n* = 12) from reference [12]. Fossil cougar specimens (*Puma concolor*, *n* = 12) from the La Brea Tar Pits in southern California (Los Angeles Museum of Natural History, Page Museum, Hancock Collection) were examined and compared with published [12] DMTA data of extinct *S. fatalis* (*n* = 15, sabre-toothed cat) and *Panthera atrox* (*n* = 15, American lion).

The enamel region of the lower carnassial shearing facet of the m1 trigonid ([11,12]) was examined on all specimens. The entire shearing facet was cleaned with acetone, moulded with polyvinylsiloxane dental impression material, and tooth replicas were prepared using Epotek 301 epoxy resin and hardener. Dental microwear texture analysis was performed on all replicas that preserved antemortem microwear using white-light confocal profilometry and scale-sensitive fractal analysis (SSFA) [14,15]. All specimens were scanned in three dimensions in four adjacent fields of view, for a total sampled area of 204 × 276 µm². All scans were analysed using SSFA software (ToothFrax and

SFrax, Surfract Corp., www.surfract.com) to characterize tooth surfaces according to the following variables: (i) complexity (*Asfc*), which distinguishes taxa that consume brittle foods from taxa that consume softer and/or tougher ones, assesses the change in surface roughness across changing scales of observation; (ii) anisotropy (*epLsar*), the degree to which features share similar orientations, such as a dominance of parallel striations (as can be formed by carnassial action in meat slicing given constraints of tooth-on-tooth movement during occlusion) yielding more anisotropic surfaces and (iii) textural fill volume (*Tfv*), a measure of the difference in volume filled by large (10 µm) and small (2 µm) diameter square cuboids (high values indicate many deep features between these sizes) [14,15]. In the case of extant carnivorous taxa, increased complexity, decreased anisotropy and increased textural fill volume are associated with increased durophagy [11] (see the electronic supplementary material, Methods for a more detailed discussion of DMTA).

As the majority of DMTA variables are typically not normally distributed (Shapiro–Wilk tests, table 1 and [12]), we used non-parametric statistical tests (Kruskal–Wallis) to compare differences between cougars, both spatially and temporally. We used Dunn's procedure to conduct multiple comparisons (either between taxa or between like taxa across time) absent of the Bonferroni correction (see [12] for a discussion regarding the exclusion of the Bonferroni correction), and Mann–Whitney tests to compare between two taxa or the same species through time. Levene's test (medians), also known as the Brown–Forsythe test, was used to compare variance between extinct and extant taxa.

3. Results

Results are presented in table 1 and illustrated in figures 1 and 2 (all primary data are included in the electronic

Figure 1. Three-dimensional photosimulations of microwear surfaces of modern and fossil cougars analysed, demonstrating similar textural attributes. Examples include (a) *Puma concolor cougar* (SBMNH 886, modern specimen from southern California, USA), (b) *Puma concolor coryi* (FLMNH 27148, modern specimen from southern Florida, USA) and (c) *Puma concolor* (LACMHC x9466, fossil specimen from the La Brea tar pits).

supplementary material, table S1). Detailed descriptive statistics and comparisons between *A. jubatus*, *Panthera leo* and *C. crocuta* are noted in reference [12] and not included here. All modern feliforms examined, as well as fossil *Puma concolor* specimens, have median complexities significantly greater than that of *A. jubatus* (1.767; table 1), indicating the consumption of more brittle food items in all taxa except *A. jubatus*. Modern and fossil *Puma concolor* complexity values are most similar to *Panthera leo* (4.690), which is known to engage in more generalized dietary behaviour including moderate durophagy [11], and have significantly lower complexity than the predominant scavenger *C. crocuta* (7.070; figure 2a and the electronic supplementary material, table S2). Anisotropy of fossil and modern *Puma concolor* specimens is significantly lower than the primarily flesh consuming *A. jubatus* (0.0027, 0.0034 and 0.0047, respectively; figure 2a and the electronic supplementary material, table S2) and indistinguishable from *Panthera leo* and *C. crocuta* (with median values of 0.0033 and 0.0034, respectively). Median textural fill volume is lowest in *A. jubatus* (2581), followed by modern *Puma concolor* (9849), *Panthera leo* (11 358), fossil *Puma concolor* specimens (14 008) and *C. crocuta* (14 142).

Fossil specimens of *Puma concolor* from the La Brea tar pits are not significantly different from modern southern California *Puma concolor cougar* specimens in complexity or anisotropy (including both median values and variance). However, fossil specimens from the La Brea Tar Pits have significantly greater textural fill volume ($p = 0.034$) than modern specimens from similar geographical areas, potentially suggesting that fossil

Figure 2. (a) Bivariate plot of anisotropy ($epLsar$) and complexity ($Asfc$) of extant cougars and African carnivores [12] and (b) fossil specimens from the La Brea Tar Pits, with daggers indicating extinct taxa.

populations processed coarser food items. Fossil specimens of *Puma concolor* from the La Brea Tar Pits have significantly greater complexity and variance ($p = 0.009$) than *Panthera atrox* (figure 2b and the electronic supplementary material, table S3). *Puma concolor* is indistinguishable from *S. fatalis* in complexity values; however, it has significantly greater variance ($p = 0.016$; figure 2b). *Puma concolor* has significantly greater textural fill volume than *Panthera atrox* (electronic supplementary material, table S3), but is indistinguishable from *S. fatalis*. Anisotropy is not significantly different between the three cats examined at La Brea (figure 2b and the electronic supplementary material, table S3).

4. Discussion

Collectively, DMTA data (i.e. intermediate complexity and low anisotropy) suggest that Pleistocene and modern cougars engaged in moderate durophagy, similar to extant African lions. Pleistocene cougars from La Brea have more variable complexity than sympatric extinct felids, further suggesting that cougars had more generalized dietary behaviour; specifically, some individuals may have consumed primarily tougher flesh, whereas others engaged in a greater degree of brittle food item processing, including bone. This highly generalized dietary behaviour is consistent with observed dietary behaviour in modern cougars [2]. Specifically, cougars today are both opportunistic predators [2] and scavengers of their own kills from cache sites or abandoned carrion [2,16], more fully consuming carcasses of smaller- to medium-sized prey and/or juveniles [2,17]. Similar dental microwear attributes in

modern and Pleistocene cougars suggest that dietary behaviour was likely consistent through time, at least, in southern California. However, as textural fill volume is greater in Pleistocene cougars, it is possible that Pleistocene individuals, on average, consumed food items that left coarser features, suggestive of more durophagous behaviour during the Pleistocene.

None of the extinct carnivorans at La Brea (including the felids, the canid *Canis dirus* and the short-faced bear *Arctodus simus*) provide evidence that carnivorans more fully consumed carcasses owing to 'tough times' prior to the LPE [12,18], as was suggested by Van Valkenburgh & Hertel [19]. Interestingly, cougars from La Brea demonstrate the highest degree of carcass utilization, which may have provided this surviving

large cat with greater resilience to LPE events, in contrast to more specialized felids [12]. While cougars may not have sailed through the LPE without consequences (e.g. severe genetic bottlenecks in North America and/or localized extinctions [20]), these findings suggest that more variable dietary behaviour may have actually been a key to their survival.

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