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Coupled social and ecological change drove the historical extinction of the California grizzly bear (*Ursus arctos californicus*)

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Large carnivores (order Carnivora) are among the world's most threatened mammals due to a confluence of ecological and social forces that have unfolded over centuries. Combining specimens from natural history collections with documents from archival records, we reconstructed the factors surrounding the extinction of the California grizzly bear (*Ursus arctos californicus*), a once-abundant brown bear subspecies last seen in 1924. Historical documents portrayed California grizzlies as massive hypercarnivores that endangered public safety. Yet, morphological measurements on skulls and teeth generate smaller body size estimates in alignment with extant North American grizzly populations (approx. 200 kg). Stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of pelts and bones ($n = 57$) revealed that grizzlies derived less than 10% of their nutrition from terrestrial animal sources and were therefore largely herbivorous for millennia prior to the first European arrival in this region in 1542. Later colonial land uses, beginning in 1769 with the Mission era, led grizzlies to moderately increase animal protein consumption (up to 26% of diet), but grizzlies still consumed far less livestock than otherwise claimed by contemporary accounts. We show how human activities can provoke short-term behavioural shifts, such as heightened levels of carnivory, that in turn can lead to exaggerated predation narratives and incentivize persecution, triggering rapid loss of an otherwise widespread and ecologically flexible animal.

1. Introduction

Understanding the past ecological dynamics of extirpated and currently endangered species is essential for facilitating their recovery, and where possible, their reintroduction (e.g. IUCN Green List [1,2]). Large mammalian carnivores (order Carnivora) are now at the centre of numerous global conservation initiatives—ranging from intentional re-introductions to natural re-expansions across their former distributions—and historical data are increasingly sought for guidance [3–5]. Primary historical sources, such as diaries, gazetteers and newspapers, can offer crucial conservation-relevant insights into an organism's ecology and interactions with humans [6,7]. But such sources rarely provide straightforward biological data because they were produced by authors writing with varying viewpoints during particular historical moments; they should be regarded with caution, placed in their social context, and cross-checked with other evidence to determine their veracity and interpret their meaning prior to their implementation in conservation decision-making [8,9]. This is especially true for historical observations of mammalian carnivores,

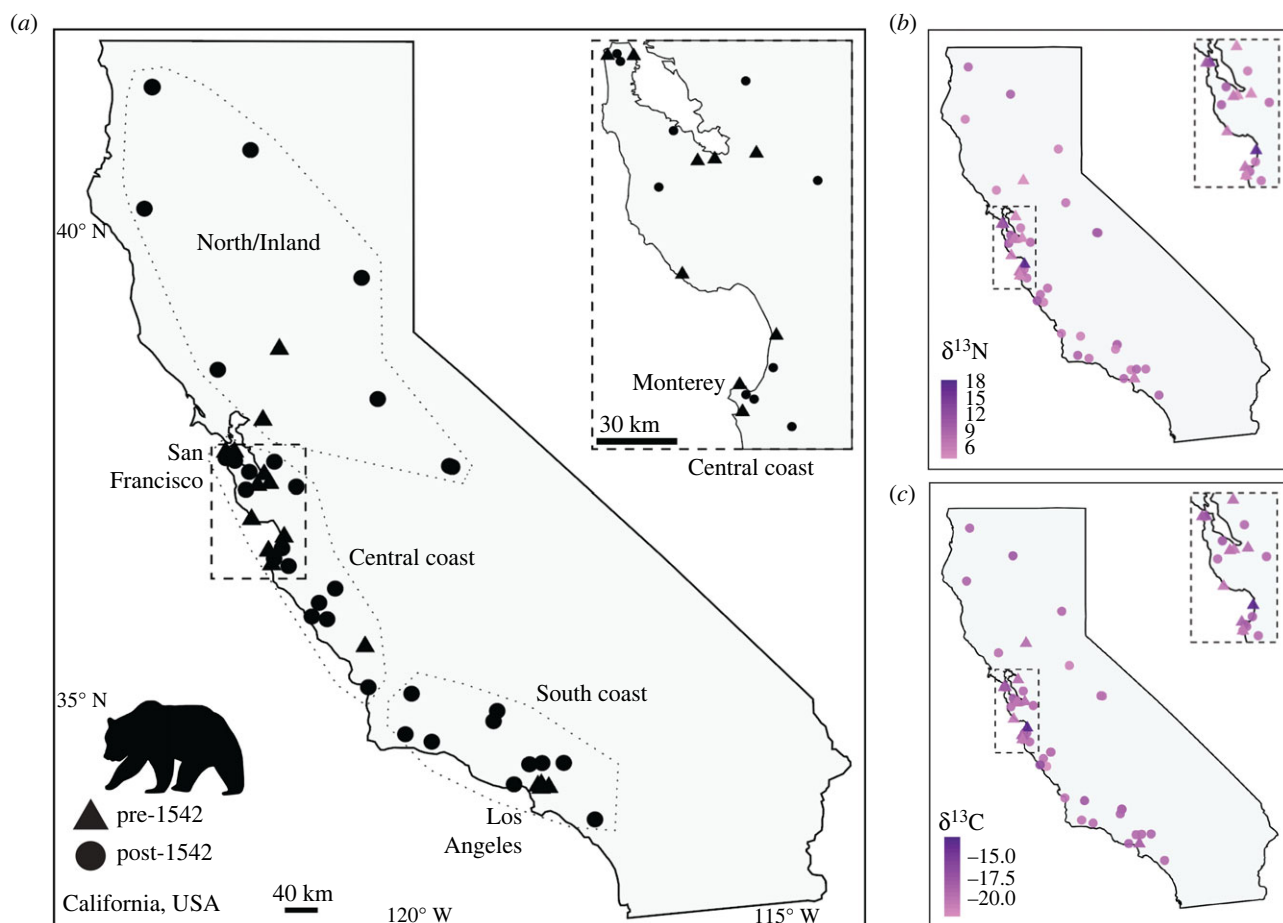


Figure 1. Geographical distribution of California grizzly bear (*Ursus arctos californicus*) specimens used in this study. (a) Specimens represent pre- ($n = 17$) and post- ($n = 40$) 1542 time bins (time of European colonization) and are grouped into North/Inland, Central Coast (including detailed inset maps) and South Coast regions. Spatial patterns in stable isotope values of (b) nitrogen ($\delta^{15}\text{N}$) and (c) carbon ($\delta^{13}\text{C}$), with inset map featuring a portion of the Central Coast in all panels. Symbols courtesy of Phylopic (<http://phylopic.org>).

many of which have complex social, political and economic associations that may influence their perceived niches and behaviours [10,11].

In this study, we used primary historical sources to form hypotheses about the ecology of the California grizzly bear (*Ursus arctos californicus*, Merriam 1896). We compared these expectations with data generated by palaeobiological research methods to yield the first new ecological information about the subspecies since eye-witness observations were made nearly a century ago. All brown bears once found in California were assigned to the subspecies *U. a. californicus* (see electronic supplementary material for a note on taxonomy), which was last credibly sighted in 1924 on the western slope of Sequoia National Park in the southern Sierra Nevada [12]. The disappearance of this subspecies resulted in the loss of *U. arctos* mitochondrial lineages from California [13], with possible attendant losses of unique ecological, physiological and/or behavioural attributes that could exert lingering influences on ecosystem processes today. Knowing what habitats and food resources California grizzlies used through time in response to changing socioecological landscapes is essential both for understanding their past decline and for assessing the prospects for reintroduction [14,15].

By the time the California grizzly went extinct, it had been featured in a vast archive of documents and images [12]. Written sources pertaining to grizzlies begin with the Vizcaíno expedition of 1602, two centuries before Lewis and Clark's infamous encounters with grizzlies along the

Missouri River [16], and consistently describe California's 'golden bears' as huge, aggressive and hypercarnivorous. Grizzlies were accused of attacking people and preying on the livestock that proliferated on the open range during California's Spanish Mission and Mexican Rancho eras (1769–1848) [12]. The Gold Rush of 1849, followed by California's admission as a US state in 1850, sparked a massive influx of settlers and wildlife persecution, resulting in the loss of not just grizzlies but other larger mammals, such as wolves [17,18].

To address the historical perception that California grizzlies were, for brown bears, unusually large, aggressive and carnivorous, we examined all that remains of the subspecies: skulls, teeth and pelts stored in natural history museums. We generated a 'menu' of potential food items derived from written documents in which authors had recorded first-hand observations of these animals foraging or eating (electronic supplementary material, table S1). We then evaluated how the frequency of these observations compared with values yielded by stable isotope analyses (nitrogen, $\delta^{15}\text{N}$, and carbon, $\delta^{13}\text{C}$) of historical, zooarchaeological and palaeontological bear specimens across three regions (figure 1a) [19] and two time bins, as constrained by radiocarbon dating or archival documentation. Using these methods coupled with morphological measurements, we asked three questions in the service of aligning historical narratives with palaeobiological datasets: (1) whether grizzly diets changed following the initial European colonization of California (pre- versus

post-1542); (2) whether historical records from the post-1542 time bin accurately reflected isotopic evidence for grizzly resource use, especially livestock predation; and (3) morphologically, whether California grizzlies were abnormally large compared to brown bears in other geographical regions, as was reported in historical sources.

2. Methods

(a) Primary historical sources

As our research centres on understanding how Euro-American practices led to the subspecies' historical extinction, we focus on written accounts centering those groups, while recognizing that a diverse range of Indigenous peoples also interacted with California's grizzlies and landscapes for millennia. The historical record of written documents pertinent to Europeans begins in 1542, with the arrival of Juan Rodriguez Cabrillo. We began our search process by using the classic text on this subject, *California Grizzly* [12], to identify and track down large numbers of cited primary sources. We then moved on to a host of other well-known primary sources, including published diaries, journals, and other records of explorers, settlers, naturalists and government surveyors. We then turned to more than 300 collections searchable through the Online Archive of California, which we queried using 13 key terms in both English and Spanish (bear, grizzly, grizly, grisly, silver tip, bruin, cinnamon bear, brown bear, ursus, ursine, sow, cubs/yearlings, oso/osa/osos/osas; see electronic supplementary material for further methodological details). Through this iterative process, we were able to build a robust database consisting of 330 California grizzly observations, 136 of which described grizzlies foraging or eating (electronic supplementary material, data file).

(b) California grizzly bear specimens

All *U. arctos* specimens found in California are designated as *U. arctos californicus* and/or its older synonymies by relevant taxonomic authorities and museum collections. California grizzly subspecies skeletons, skulls and hair were obtained from three main sources through accessing museum collections or were taken from the published literature: (1) natural history (mammalogy) collections, mostly comprised of skulls and pelts that were identified as *U. arctos* prior to death by the collector; (2) zooarchaeological collections, primarily bones from coastal archaeological middens; and (3) palaeontological collections, such as the asphaltic deposits of Rancho La Brea. Specimens were only included in analyses if they met morphological criteria separating *U. arctos* from *U. americanus* (electronic supplementary material, methods) and California provenance could be confirmed through catalogue, accession, archival and/or historical narrative information.

(c) Designating regional and temporal bins

The $\delta^{13}\text{C}$ value of atmospheric CO_2 was -6.4‰ in the Pleistocene epoch, -6.5‰ before 1880 and -7.7‰ by 1989 [20]. All samples were Suess-corrected to facilitate direct comparisons through time [19], though the need to do so was very minimal as all specimens used in this study were collected before atmospheric $\delta^{13}\text{C}$ signatures changed substantially (prior to 1930, resulting in a correction of less than 0.25‰). We divided all samples into pre- and post-1542 eras, delimiting European colonization; this cut-off is conservative as the livestock practices that could alter grizzly behaviour would not begin until the later Rancho period. Our pre-1542 population encompassed the Early-Late Holocene (approx. 7500 to 550 calibrated years before present) and our earliest post-1542 specimen was radiocarbon dated to approximately 1676 (1645–1800 95.4% calibrated range,

UCIAMS-201913) (electronic supplementary material, table S2). We recognize that the cultural practices of Indigenous peoples varied through the Early-Late Holocene period; however, our sampling resolution precluded us from interrogating this record as it related to grizzlies in more detail. Spatially, we defined three geographical sampling regions within California (South Coast, Central Coast and North/Inland including the Sierra Nevada) following current California Department of Fish and Wildlife designations and a previous historical carnivore study by [19] and references therein (figure 1a).

(d) Potential food sources (pre-1930)

All food stable isotope values used in this study either represent zooarchaeological/palaeontological specimens or specimens from natural history and herbarium collections for which we have generated new data or which previously existed in the literature. We used stable isotope values from the published literature for all pre-1542 food items and, where possible, for many post-1542 food items (e.g. [21]) (electronic supplementary material, data file). We generated new stable isotope values for historical foods (earlier than 1930) for six deer bone specimens (*Odocoileus hemionus*), 17 oak acorn and leaf specimens (*Quercus chrysolepis*, *Quercus lobata*), 10 livestock bone specimens (2 *Capra hircus*, 3 *Bos taurus*, 5 *Ovis aries*) and 13 salmonid fin clip and muscle specimens (6 *Onconrhnchus* spp. and 7 *Salmo* spp.). We categorized three of the fish samples as coming from anadromous adult or estuarine juvenile specimens (hereafter marine fish; mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values = 12‰ (s.d. = 1.9) and -20‰ (1.9)), and the others as small stream fish (mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values = 6.3‰ (1.6) and -23.9‰ (2.6)). Because stable isotope signatures for migrating salmon are more like marine mammal than terrestrial prey signatures [22,23], we cautiously interpreted the signatures for marine mammals as a general signature for marine predators (marine mammals, anadromous salmonids). We were unable to locate suitable Holocene plant material, so we used historic herbarium plant specimens as the Suess-corrected baseline signatures for plants (as in [24]). Although baseline shifts in the stable nitrogen signature of primary producers have been documented across the Late Pleistocene (e.g. [25]), our sampling does not span glacial transitions and specimens were collected prior to extensive Haber-Bosch synthetic fertilizer use. Thus, we relied on our pre- and post-1542 dataset for the primary consumer, *Odocoileus hemionus*, to assess whether shifting food resource baselines could account for any change in the trophic level of California grizzly bears. Our C3 plant endpoint is a proxy for plant foods including berries, pine nuts, acorns, roots, tubers, and native and non-native grasses and forbs. Our average *Quercus* stable isotope values aligned with those of vegetation categories used in previous grizzly bear diet studies (e.g. [26]).

(e) Stable isotope processing

We used approximately 150 mg of nasal turbinate bones where available or gently removed fragments from damaged areas of the skull. Asphaltic material from Rancho La Brea required several additional pre-treatments and filtering steps to remove asphaltenes and other hydrocarbon contaminants [27]. Bone fragments were sonicated in 2:1 chloroform/methanol, then methanol, then MilliQ water to remove excess lipids. Bone then was decalcified overnight in 1 N HCl and gelatinized at 60°C in 0.01 N HCl. Gelatinized collagen was then ultra-filtered to obtain a high molecular weight fraction of greater than 30 kDa and lyophilized in a vacuum centrifuge. A small number of our post-1542 specimens consisted of pelts (electronic supplementary material, table S3). Only hairs > 9 cm in length were sampled to ensure they were fully grown [28]. Hairs were rinsed in a 2:1 chloroform:methanol solution, then sonicated

with methanol and de-ionized water and dried in a vacuum [29], then sectioned and combined.

Both hair and bone collagen were run as 0.7 mg samples in 8×5 mm tin capsules. Samples were run on a Delta-Plus CFIRMS (continuous flow isotope ratio mass spectrometer) interfaced with a Fisons NA-1500 for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope analyses. Values are presented as per mil (‰), expressed as delta (δ) values: $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ (‰) = $(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} \times 1000$, where R represents the ratio of the heavy to the light isotope ($\delta^{15}\text{N}/\delta^{14}\text{N}$, $\delta^{13}\text{C}/\delta^{12}\text{C}$), and standards were Pee Dee Belemnite and air, respectively. Analytical precision was $<0.1\%$ and less than 0.2% for C and N, respectively.

(f) Radiocarbon dating

Accelerator mass spectrometry was performed on graphite derived from CO_2 produced by combusting approximately 2 mg of purified bone collagen using a National Electrostatics Corporation 0.5 MV 1.5SDH-1 Pelletron with a 60-sample modified MC-SNICS ion source at the UC Irvine Keck-CCAMS facility. All radiocarbon dates were calibrated using OxCal v4.4.4 [30] and the IntCal20 curve [31], unless otherwise noted for marine contributions [32].

(g) Spatio-temporal and dietary analyses

We analysed the relationship between grizzly stable isotope signatures and sample age (years before present) using Spearman's rank correlation analysis for each period separately and both periods combined (electronic supplementary material, table S4). We assessed the spatial distribution of stable isotope signatures by using (1) Mantel tests, (2) the multiple response permutation procedure (MRPP) and (3) maps of stable isotope values (figure 1*b,c*). We examined the direct and interactive effects of regions and time bins using two-way ANOVAs (electronic supplementary material, table S5). We also compared stable isotope signatures between time bins for individual and collective regions, between regions within each time bin, and among food types and competitor taxa within each time bin using one-way ANOVAs and Tukey's HSD tests, as well as non-parametric analogues (Mann-Whitney U-test or Wilcoxon rank sum test, Steel-Dwass test) or permutation tests (MRPP) because parametric assumptions were not always met (see electronic supplementary material, tables S6 and S7).

We used the Bayesian stable isotope mixing model package MixSIAR [33,34] to reconstruct and compare the probable nutritional contributions of plants, ungulates and marine food sources to grizzly bear tissues. Concentration dependence was incorporated into the models using data from [35]. End member values were defined using mean time and tissue-corrected ^{13}C and ^{15}N isotope values and associated standard deviations for food groups from each region and time period. Mixing models were run with an uninformative prior, three Markov chain Monte Carlo (MCMC) chains of 300 000 draws, and a burn in of 200 000 draws. Satisfactory model convergence was evaluated using Gelman and Geweke diagnostics. Probable food source contributions to grizzly nutrition are presented as means (with standard deviations), medians, and 95% Bayesian credible intervals. To assess the effect of the introduction of livestock in the post-European period, and discern potential contributions associated with livestock and salmon, we built three contrasting models that included the following food sources: (a) C3 plants, deer, livestock and marine animals (pinnipeds); (b) C3 plants, deer, marine animals (pinnipeds); and (c) C3 plants, deer and salmon. We also used the R package 'trophicPosition', which incorporates a Bayesian model to calculate consumer trophic position at the population level [36]. We ran 200 000 iterations and two chains for each model and checked model convergence using MCMC trace files.

(h) Body size estimates

We used digital calipers (Mitutoyo) to measure relevant dental, cranial and postcranial elements for use in equations developed to calculate Ursidae and Caniformia mass: humeral and femoral length [37], total length of skull [38] and lower first molar area (length \times width of molar [39]). We compared body mass estimates for a subset of bears that had both skull and molar measurements ($n = 9$) (electronic supplementary material, data file). Because skulls provided the largest number of body mass estimates, we compared the distribution of body masses generated from our adult skull measurements with the distribution of historical body mass reports collated [12] from newspapers and other contemporary sources.

3. Results

(a) Historical documents reference frequent consumption of livestock

Of the 136 documented observations of California grizzlies foraging or eating (out of 330 total historical records), livestock was most commonly reported as a food item (59 quoted entries, approximately 43%), followed by wild plants (approx. 27%), native terrestrial mammals (approx. 5%), marine mammals (approx. 4%) and fish (approx. 1%), with remaining observations pertaining to honey, crops and other unspecified foods (electronic supplementary material, table S1). These primary sources lead to the hypothesis that the California grizzly was a highly carnivorous animal that regularly consumed newly abundant European livestock [18].

(b) The California grizzly's isotopic menu

We generated 48 new stable isotope values for historical (before 1930) oak leaves and acorns (*Quercus* spp.), deer (*Odocoileus hemionus*) and livestock (goat, sheep, cow) bones, and fish muscle and fin clips (figure 2). We augmented this dataset with greater than 60 published stable isotope values for food sources from both the pre- and post-1542 time bins [21,24,40–43] (electronic supplementary material, data file). Bivariate stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic space) were significantly different among food categories in both eras (MRPP; pairwise comparisons followed by Benjamini-Hochberg (B-H) corrections: pre-1542 foods, all $p < 0.0005$; post-1542 foods, all $p < 0.00002$; electronic supplementary material, table S2) [44]. Bivariate stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) differed among livestock in the post-1542 time bin and deer in the pre- and post-1542 time bins (MRPP with B-H corrections, all $p < 0.02$) with $\delta^{15}\text{N}$ values showing the pattern post-1542 livestock $>$ pre-1542 deer $>$ post-1542 deer (all $p < 0.006$; Steel-Dwass test). Pre-1542 deer and post-1542 livestock had similar $\delta^{13}\text{C}$ values, and both were greater than those for post-1542 deer (Steel-Dwass test, both $p < 0.002$, electronic supplementary material, table S8). Although some stable isotope values differed regionally within food categories (MRPP uncorrected $p < 0.06$, for regional deer differences within time bins; livestock and marine mammals in the post-1542 time bin), subsequent analyses were unaffected because we matched stable isotope data for periods and regions for animal foods and grizzly bears (electronic supplementary material, figure S1).

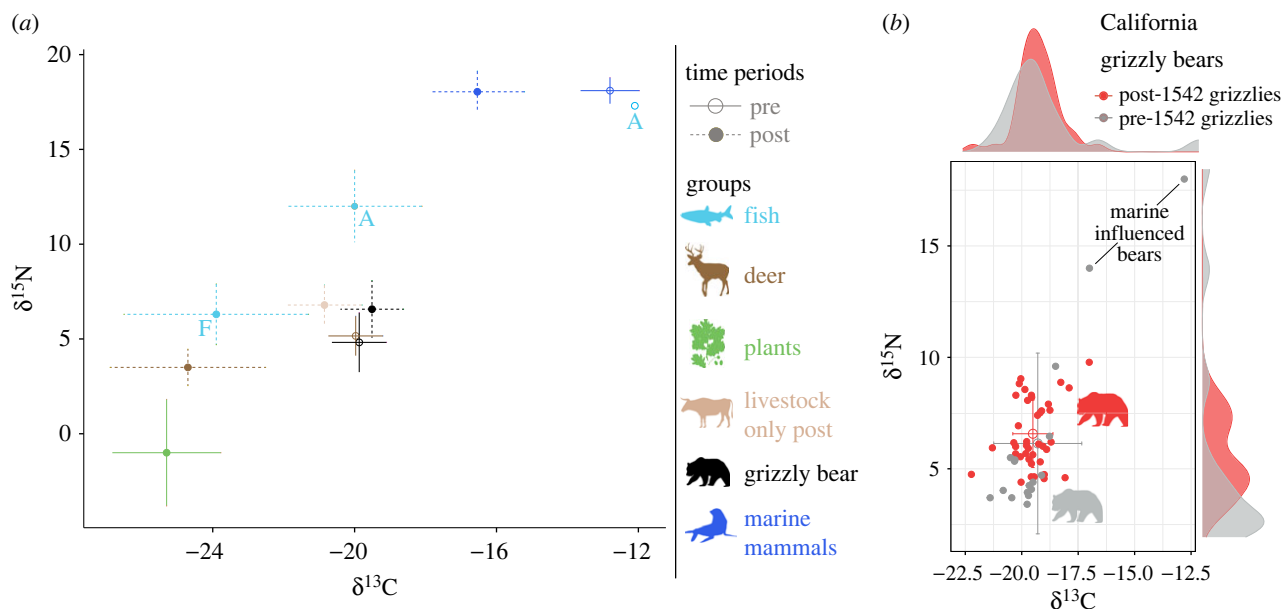


Figure 2. (a) Biplot showing stable isotope values ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) for California grizzlies and their potential food items (mean \pm s.d.) statewide across the pre and post periods, not including trophic discrimination factor but with all relevant tissue and Suess corrections. Note that the same plant value was used across periods (see also electronic supplementary material, figure S7). A = anadromous fish, F = freshwater fish. (b) Biplot showing the individual grizzlies in the pre (grey) and post (red) 1542 periods, as well as their means ± 1 s.d. (produced using the R package tRophicPosition [36]). Also shown in the margins are the distributions of $\delta^{15}\text{N}$ (right) and $\delta^{13}\text{C}$ (top) values for these two groups. Symbols courtesy of Phylopic (<http://phylopic.org>).

(c) California grizzly resource use through time

Combined analyses of stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) values for 40 post-European and 17 pre-1542 California grizzlies indicate that grizzlies were primarily herbivorous across regions and periods (electronic supplementary material, table S9). We combined all adult specimens as only a small subset of individuals were reliably sexed at the time of death (electronic supplementary material, table S10). We did not identify any pre-Holocene individuals—the oldest confirmed specimen is 7528 ± 29 calibrated years before present (cal ybp) from Rancho La Brea, Los Angeles (electronic supplementary material, table S2). Grizzly stable isotope values did not differ across regions when periods were considered separately (MRPP p 's > 0.10), with spatial distance (figure 1*b,c*; Mantel tests, $p > 0.05$; see also electronic supplementary material, table S6), nor with specific year of collection within each time period (Spearman's rank correlation (r 's = -0.11 to $+0.20$, p 's = 0.22 to 0.91), allowing us to geographically group all grizzlies into a single state-wide population for comparisons between pre- and post-1542 time bins (figure 2).

Two specimens from the pre-1542 time bin, both from the Central Coast region, had values consistent with marine resource use ($\delta^{15}\text{N} = 14$ and 18‰ , $\delta^{13}\text{C} = -17$ and -12.8‰ ; hereafter called 'marine bears'), but marine resource use was not apparent in any of the grizzlies collected during the post-1542 time bin, despite a larger sample size with strong coastal representation (see also electronic supplementary material, figure S2). Grizzly bivariate stable isotope signatures differed between the time bins (MRPP, p ca 0.003 and $p < 0.0001$ for analyses including or excluding the two marine bears), owing to an increase in grizzly $\delta^{15}\text{N}$ values (Mann–Whitney U -tests with and without marine bears: $\delta^{15}\text{N}$ $p < 0.005$ and < 0.0001 , respectively; $\delta^{13}\text{C}$ $p > 0.30$ and > 0.07), suggesting an increase in carnivory through time and a consistent reliance on terrestrial food. Similarly,

Table 1. The mean (± 1 s.d.), median and 95% Bayesian credible interval for the percentage contributions of different food types (plants, ungulates, marine animals) to grizzly diets across all regions in the pre-1542 (pre) and post-1542 (post) time bins.

source	time bin	mean \pm s.d.	median	95% CI*
plant	pre	88.6 ± 4.4	89.1	79.2–95.4
	post	70.8 ± 6.0	70.7	59.3–83.1
ungulate	pre	9.2 ± 5.0	8.8	1.5–19.6
	post	26.3 ± 7.0	26.4	11.8–39.3
marine	pre	2.2 ± 1.6	1.9	0.1–5.8
	post	2.9 ± 1.4	2.8	0.4–5.9

we found that $\delta^{15}\text{N}$ values increased through time whether marine bears were included or not ($\delta^{15}\text{N}$ values versus years before present (ybp), Spearman's ρ 's = $+0.41$ and $+0.50$, p ca 0.002 and 0.0002, respectively) and that $\delta^{13}\text{C}$ values (Suess corrected) and years before present were related when marine bears were excluded ($\rho = +0.34$, $p = 0.012$), but not when marine bears were included ($\rho = +0.26$, $p = 0.06$).

Although plants provided the dominant nutritional support for grizzly populations in both the pre-1542 (mean $88.6 \pm 4.4\%$ (s.d.) and post-1542 time bins ($70.8 \pm 6.0\%$), terrestrial animal contributions to grizzly diets more than doubled from $9.2 \pm 5.0\%$ in the pre-1542 time bin to $26.3 \pm 7.0\%$ in the post-1542 time bin, as indicated by mixing model analyses (Bayesian MixSIAR, [33,34]) (table 1). Using a four end-member model (i.e. four sources of nutrition, such as plant, ungulate, livestock, marine mammal), we calculated that the dietary contributions of livestock and wild ungulates were $7.9 \pm 5.1\%$ and

14.9 ± 6.8%, respectively, during the post-1542 time bin. Marine mammal or anadromous salmon contributions to grizzly nutritional support were minor (less than 2%) in both time bins (see electronic supplementary material, table S11 for additional post-1542 model results).

We examined isotopic niche width for grizzlies across space and time by calculating standard ellipse areas (SEA_c, small sample size corrections) [45] (electronic supplementary material, table S9). When including the two 'marine' bears, the isotopic niche of the pre-1542 population was larger than that for the post-1542 population (10.54 versus 4.16 ‰²) (electronic supplementary material, figure S3); however, when the two marine outliers were removed, the isotopic niche width estimates suggest a slight expansion from the pre- to post-1542 periods (see electronic supplementary material, figure S4 for post-1542 regional niche comparisons). Concordantly, grizzly trophic position increased through time, both statewide and regionally, regardless of whether plant (trophic position shift from 3.55 ± 0.41 to 4.30 ± 0.38) or deer baselines were used (trophic position shift from 2.08 ± 0.07 to 2.73 ± 0.09), whereas the trophic position of deer decreased over time (electronic supplementary material, figure S5).

(d) The biggest bears in North America?

We assessed historical claims that the California grizzly was among the largest brown bear subspecies—sometimes reaching 2000 lbs (approx. 900 kg) [12]—by comparing morphological measurements of adult California grizzly specimens with those of other brown bears. Our California grizzly body mass estimates varied depending on the skeletal features used in body mass-skeletal measurement regressions, ranging from an average of 104 kg (± 27 kg s.d.) based on lower first molar measurements ($n = 16$, [39]) to 145 kg (± 56 kg s.d.) based on humeral and femoral lengths ($n = 3$, [37]) to 252 kg (± 54 kg s.d.) based on skull lengths ($n = 21$) [38]) (electronic supplementary material, figure S6). Both morphological measurements and body mass estimates align with the known sizes of male and female grizzlies in Yellowstone (Wyoming) and Alaska [28,46,47]. Grizzly body mass distributions and means differed between skull-based mass estimates ($n = 21$) and historical newspaper reports ($n = 37$) ($p < 0.001$, Kolmogorov–Smirnov and Wilcoxon rank sum tests) (figure 4c). Although it is possible that body size scaling equations generate underestimates of size, our raw morphological measurements of teeth and skulls are also in alignment with those of other living brown bears (electronic supplementary material, data file).

4. Discussion

(a) Addressing historical perceptions

Primary historical sources for grizzlies in the state, spanning from 1602 to 1924, contain 136 mentions of grizzlies feeding, 43% of which involve livestock and 5% of which refer to other terrestrial mammals. Nineteenth century American culture did not generally value large carnivores, and most farmers, ranchers, hunters and settlers sought to either control or eradicate them. Within this cultural context, documents and images portraying grizzlies as threats to public safety and private property provided a specific rationale for shooting, trapping and poisoning. Our isotopic data, however, show that even after decades of access to free-ranging European

livestock (barbed wire used to contain and protect cattle was not widely adopted until 1880), California grizzlies remained largely herbivorous, with increasing, though still modest, nutritional contributions from livestock and other terrestrial animals.

Similarly, our body size estimates of bears from natural history collections were smaller than both newspaper records documenting individually killed bears as well as the oft-cited number of 2000lbs (e.g. 'the bear tipped the beam-forbid it that anyone should question the reading of the scales!-at two thousand, three hundred and fifty pounds' [12]). Hunted animals do not necessarily represent a random sample of the population due to the preferences of hunters [48]. The bears reported in newspaper clippings were often killed as trophies, as part of publicity stunts, or even sold for meat. Therefore, there were both monetary and reputational incentives to both capture the largest animals possible and to exaggerate the size and aggressiveness of captured animals [49]; indeed, the animals captured were often males [12]. It is also possible that trophy hunters selectively removed the largest individuals from the population before they could otherwise enter natural history collections, potentially acting as a selective force [50]. Many natural history specimens had visible bullet holes; some were noted as purchases while others were taken by scientific expeditions or simply 'picked up' from the ground, and thus our morphological sample may have been more representative of the entire population than the bears killed by hunters. Regardless of the cause of the discrepancy, the common perception of California grizzlies engendered by newspaper reports had negative consequences for coexistence with people.

(b) Contemporary comparisons

Brown bears are wide-ranging omnivores with diets that vary seasonally, interannually, and geographically [22,51]. A California grizzly diet dominated by plants is consistent with the diets of present-day brown bears in parts of the world with similar Mediterranean climates, such as southern Europe and the Middle East, as well as many other regions (e.g. interior North America, Europe, Asia) where herbaceous vegetation, fruits, berries and hard mast (nuts, acorns) are abundant [52,53]. Such a diet is consistent with the average skull lengths and body size estimates for California grizzlies, approximating the sizes of bears in Yellowstone National Park and interior Alaska. California grizzlies were thus smaller than bears living on Kodiak Island and along the Alaskan coast—populations that primarily consume marine or anadromous foods [22,28,47,54].

Brown bears living in some coastal areas use salmon runs as protein sources [55], and opportunistically consume marine mammal carcasses [56]. Yet, even where salmon runs are present, they do not always constitute a major component of brown bear diets [26]. Robust salmon runs once occurred in the streams of California's Central Valley, North and Central Coasts, and San Francisco Bay areas, but during the mid-nineteenth century, most were diminished by overfishing, dam construction, habitat degradation and pollution [56]. In Southern California, anadromous salmonid bones are rare in archaeological middens, presumably owing to inconsistent and variable river flow regimes, making these fish an inconsistently available resource [57,58]. Marine mammal carcasses were once common along California

beaches and were likely consumed by scavengers including California condors [21]. The number of beached carcasses likely waned, however, during the nineteenth century, owing to regional declines in several pinniped and whale species [42]. Our data suggest that such resources were only a very minor part of California grizzly diets, with only two bears from the pre-1542 period showing substantial marine resource use. However, it is possible that (1) our sample largely did not include individuals that used marine or anadromous protein sources, such as bears living along large rivers in northern coastal California that may have competed with humans for salmonids [16], and/or (2) our use of bone collagen provided a long-term, potentially lifetime, average of bear nutritional support [59], potentially missing use of pulsed marine resources or rare carcasses.

Brown bear consumption of terrestrial protein is also variable and tends to be more important for populations living at higher latitudes [60,61]. Although ungulates comprise only a small proportion of average brown bear diets across Europe (approx. 10.5%) and Asia (approx. 6.8%) [62], studies have reached differing conclusions about the importance and extent of brown bears' meat consumption in North America. Two studies conducted in the vicinity of Yellowstone National Park, for example, estimated that vertebrate protein provided either 51% [23] or 9% [63] of nutritional support, with the remainder consisting of other resources such as whitebark pine nuts (approx. 25%) and other plants (approx. 56%). Native ungulates are typically consumed through scavenging, but brown bears may also hunt calves [64]. Predation on domestic ungulates (i.e. livestock) is an opportunistic and individually variable behaviour and a key source of human conflict [65–67].

(c) Human-grizzly interactions over time in California

We compared bear resource use before and after the addition of livestock, representing a past experiment in human–wild-life conflict. The earliest verified presence of California grizzlies within our new radiocarbon chronology is approximately 7500 cal ybp—many millennia after humans arrived in the area now known as California. Grizzly bones and claws are occasionally found in Late Holocene middens, and Indigenous cultural traditions relating to grizzlies include shamans and stories preserved in dances, artworks, oral histories and enduring rituals [12]. Unfortunately, the spatio-temporal distribution of our samples precluded meaningful statistical analysis across cultures and lifeways within the pre-1542 period, but many Indigenous people harvested resources also favoured by grizzlies, including green vegetation, roots, bulbs and hard mast, especially acorns produced by California's 19 species of native oaks [68,69].

Following European contact in 1542, and especially after the onset of the Spanish Mission era in 1769, California grizzlies roughly doubled their consumption of terrestrial animal protein, including some livestock, but continued to derive most of their nutrition from plants. The earliest post-1542 grizzly in our dataset was dated to 1676 (1645–1800 95.4% calibrated range), falling into the initial period of European 'exploration' (1542–1769), and our dataset contains six grizzly individuals for which the median calibrated date falls within the Spanish and Mexican eras (1770–1846). Spanish-speaking settlers established a chain of missions from San Diego to Sonoma, with cattle herds that grew from 300 head in 1778

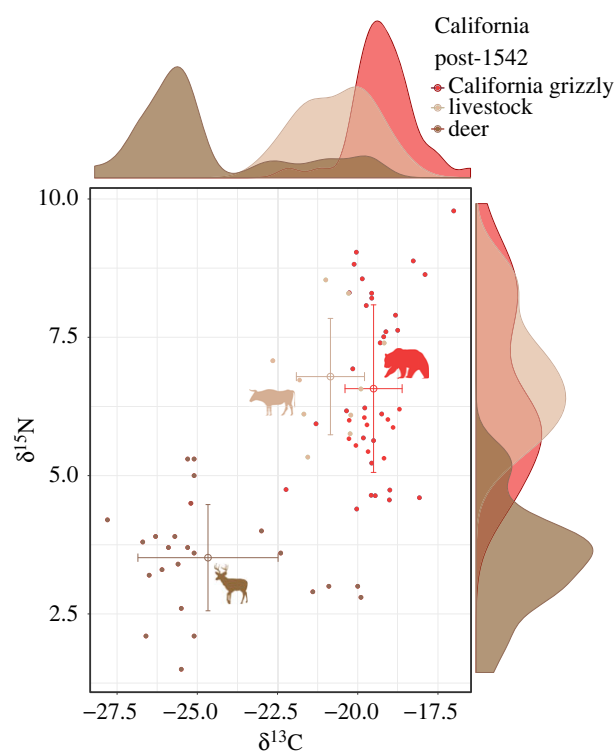


Figure 3. Biplot of stable isotope values for individual livestock (tan), deer (brown) and grizzlies (red) in the post-1542 period, as well as their means \pm 1 s.d. (produced using the R package `tRophicPosition` [36]). Also shown in the margins are the distributions of $\delta^{15}\text{N}$ (right) and $\delta^{13}\text{C}$ (top) values for these three groups. All plots account for Suess corrections. Symbols courtesy of Phylopic (<http://phylopic.org>).

to at least 400 000 head by 1821 [69,70]. By 1846, California's ranchos were producing thousands of cow hides and other livestock products [71]. Carcasses abandoned on the range and in outdoor abattoirs attracted grizzlies, but Spanish and Mexican ranchers largely tolerated them, only capturing grizzlies for bear and bull fights or dispatching those that presented a clear threat [12,18].

Following the Gold Rush and California statehood in 1850, demand for agricultural products skyrocketed and new legal systems facilitated a vast livestock empire [71]. Changes in California's vegetation, including the spread of Eurasian forbs and grasses and decline of oak woodlands [69,72], may have forced some grizzlies to switch to ungulate prey, as has been hypothesized by historians [68] and documented for extant bears in poor mast years [73]. For example, in Yellowstone the collapse of cutthroat trout populations and loss of whitebark pine nuts to white pine blister rust (*Cronartium ribicola*) and mountain pine beetles (*Dendroctonus ponderosae*), forced grizzlies to shift to other foods, including elk calves [74]. Our results suggest that California grizzlies adapted to the changing environmental conditions of the state by using food subsidies such as livestock, and that it was the specific socioecological context of California that led to the subspecies' extinction (figure 3). For example, contemporary brown bears in Hokkaido, Japan decreased their consumption of meat in response to agricultural development that reduced their terrestrial prey base and the construction of dams that blocked migrating salmon [75]. In Hokkaido, however, brown bears persisted. In California, Anglo-American settlers

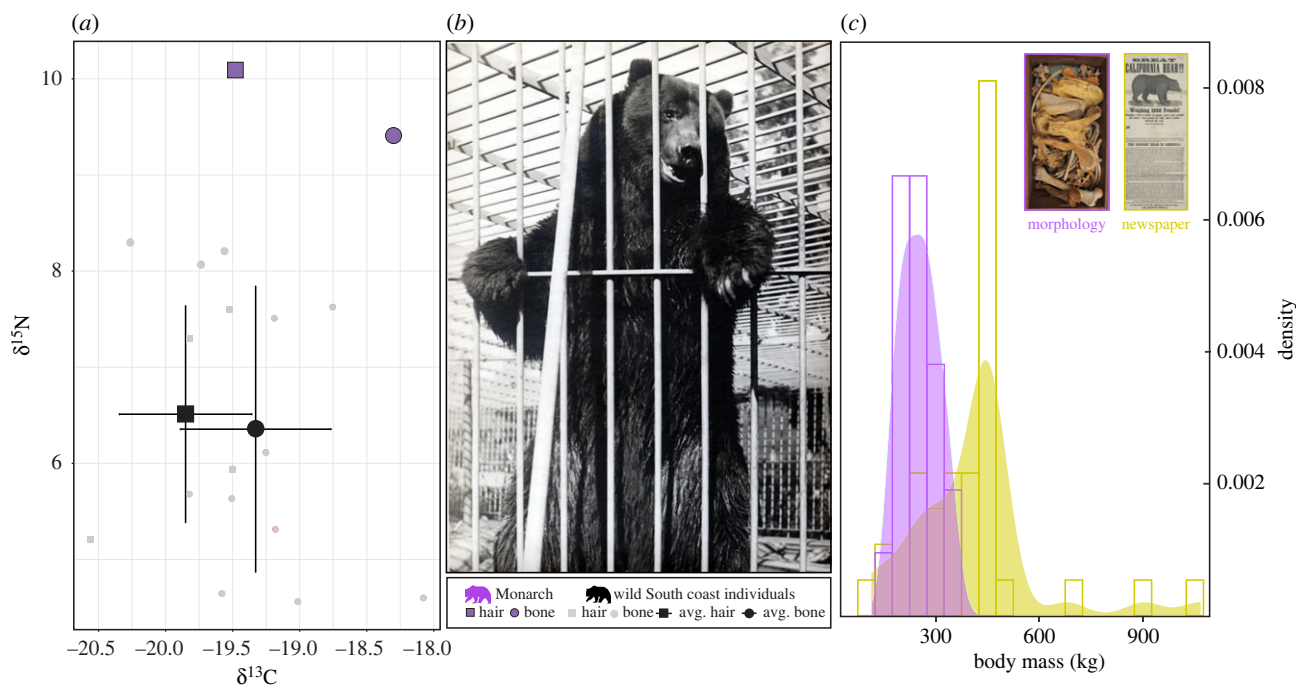


Figure 4. (a) Stable isotope values of Monarch's hair (purple square) and bone (purple circle) compared with average hair (black square) and bone (black circle) values (mean \pm 1 s.d.) and individual data (grey dots) obtained from grizzlies from California's South Coast post-1542. (b) Monarch, in captivity at the San Francisco Woodward Gardens Zoo, C. Hart Merriam Pictorial Collection (Bancroft Library). (c) Kernel estimates and histograms showing the frequency distributions of the body mass (kilogram) of California grizzlies estimated using morphologically based regression equations and reports in historical newspapers and archives from [12]. At the top of c are images of Monarch's skeleton (left) and an advertisement for a California grizzly exhibit (right, Bancroft Library).

hunted, poisoned and trapped grizzlies in response to descriptions such as one Kern County account alleging that a grizzly had killed a flock of two hundred sheep [12,17]. This animosity sparked a campaign of persecution that was eventually written into a state law (Stats. 1876, chap 3s1) which provided a bounty for grizzlies killed in certain counties.

(d) The post-gold rush transformation of California

The story of post-Gold Rush California exemplifies the complex, interconnected pattern of ecological change that can lead to, and result from, defaunation [76]. Grey wolves (*Canis lupus*), jaguars (*Panthera onca*) and wolverines (*Gulo gulo*) were extirpated [77], pronghorn (*Antilocapra americana*) disappeared from their southern range [78], and condors precipitously declined [21,79]. Among California's large carnivores, only black bears (*Ursus americanus*) were more herbivorous than grizzlies and have persisted to the present day, reaching 20 000–40 000 individuals across the state [40]. Coyotes and condors are not considered large carnivores, but both occupied the same changing ecosystems and used some of the same food resources as grizzlies. We found that most grizzlies from California's Central Coast had lower nitrogen values than coyotes and were thus not excluding coyotes from marine resources [24]. Compared to the pre-European period, both coyotes and condors, like grizzlies, increased their consumption of terrestrial animal protein, probably often in the form of livestock carrion [21,24,80]. Overall, our isotopic study of the grizzly joins others in the literature in documenting how the social and ecological changes that reverberated through California's ecosystems, beginning around 1769, had a homogenizing effect, causing the diets of higher trophic-level consumers to become more similar.

(e) The story of monarch, the last captive California grizzly

'Monarch' was captured north of Los Angeles in 1889 as part of a publicity stunt by publishing magnate William Randolph Hearst. He was then moved to San Francisco where he lived until he was euthanized in 1911. Zookeepers, believing that grizzlies required a rich, meat-heavy diet, fed him 'raw beef, apples, biscuits and other articles' [12]. When he finally died, after 22 years in captivity, Monarch weighed 1127 lbs (511.2 kg), more than twice the size of the average California grizzly in our sample. He had an $\delta^{15}\text{N}$ value that was 3‰ higher than those of other grizzly bears from his Southern California home region, and he suffered osteoarthritic pathologies caused by chronic obesity (figure 4a,b). Although Monarch lived a different life from the other bears in our study, his plight illustrates how misconceptions altered not only his individual body, but also shaped the fate of the California grizzly.

5. Conclusion

This multidisciplinary study highlights the value of combining different methodologies and types of evidence to better contextualize past human–wildlife relationships. We found that California's historical record misrepresented the ecology of grizzlies, depicting them as unusually massive and carnivorous animals. Yet this same historical record provided an accurate representation of the attitudes, values and beliefs about wildlife that prevailed among subsequent waves of European and American settlers in California, whose actions led to the extinction of the subspecies. These data add to a growing global understanding of the sources of

human–wildlife conflict while also serving to inform reintroduction discourses today [14,15].

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All original data generated by this research is available within the electronic supplementary material Data File (Excel file) and all associated analyses, graphs and results can be found in the main text or the electronic supplementary material. A three-dimensional scan of a grizzly bear specimen from the La Brea Tar Pits (HC 133) is available on Morphosource: <https://www.morphosource.org/concern/media/000548035>.

Supplementary material is available online [81].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.M.M.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; A.J.A.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, writing—review and editing; K.C.B.: conceptualization, data curation, investigation, methodology, writing—review and editing; B.T.C.: data curation, investigation; M.H.-M.: data curation, writing—review and editing; Z.S.W.: data curation, writing—review and editing; H.M.P.: data curation, formal analysis, investigation, methodology, writing—review and editing; J.R.S.: methodology, resources; S.D.C.: conceptualization, data curation,

formal analysis, investigation, methodology, supervision, visualization, writing—original draft, writing—review and editing; P.S.A.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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