Coyote (*Canis latrans*) use of marine resources in coastal California: A new behavior relative to their recent ancestors

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Abstract

Coyotes (*Canis latrans*) are known to consume marine foods, but the importance and persistence of marine subsidies to coyotes is unknown. Recent access to a marine subsidy, especially if gained following apex predator loss, may facilitate coyote expansion along coastal routes and amplify the effects of mesopredator release. Our goal was to quantify and contextualize past and present marine resource use by coyotes on the central coast of California via stable isotope analysis. We measured $\delta^{13}C$ and $\delta^{15}N$ values in coyotes, their competitors, and their food resources at two modern sites, seven archaeological sites spanning in age from ~3000 to 750 BP, and from historical (AD 1893–1992) coyote and grizzly bear hair and bone sourced from coastal counties. We found evidence for marine resource use by modern coastal California coyotes at one site, Año Nuevo, which hosts a mainland northern elephant seal (*Mirounga angustirostris*) breeding colony. Seals and sea lions account for ~20% of Año Nuevo coyote diet throughout the year and this marine subsidy likely positively impacts coyote population size. Isotopic data suggest that neither historic nor prehistoric coyotes consumed marine-derived foods, even at sites near ancient mainland seal rookeries. Marine resource use by some contemporary California coyotes is a novel behavior relative to their recent ancestors. We hypothesize that human alteration of the environment through extirpation of the California grizzly bear and the more recent protection of marine mammals likely enabled this behavioral shift.

Introduction

The transfer of energy and resources from ocean (Polis and Hurd, 1996) to land can have profound consequences for coastal terrestrial ecosystems (Rose and Polis, 1998; Spiller et al., 2010). One avenue for energy transfer is the consumption of marine foods by terrestrial animals, a phenomenon that is quite common and significant; Carlton and Hodder (2003) reviewed 135 records of marine resource use by 45 different terrestrial mammal species on every continent except Antarctica. Marine resource use is generally sporadic and opportunistic; however, marine subsidies can also significantly contribute to the maintenance (e.g. Roth, 2003) and/or expansion (Killengreen et al., 2011) of predator populations. The recent population increase and range expansion of mesopredators has largely been attributed to top-down release following the widespread loss of apex predators (Prugh et al, 2009; Ripple et al., 2013; Ritchie and Johnson, 2009). But bottom-up effects, including anthropogenic and/or marine resource subsidies, can also contribute to (Killengreen et al., 2011; Polis and Hurd, 1996), attenuate (Elmhagen and Rushton, 2007; Polis and Hurd, 1996; Rose and Polis, 1998; Spiller et al., 2010), or possibly even amplify top-down effects.

Coyotes (*Canis latrans*) have a rapidly expanding North and Central American range (Chubbs and Phillips, 2005; Fener et al., 2005; Hidalgo-Mihart et al., 2006; Mendez-Carvajal and Moreno, 2014) and a significant body of research now attributes coyote expansion predominantly to wolf extirpation (e.g. Berger and Gese, 2007; Peterson, 1996; Ripple et al., 2013; Thurber and Peterson, 1991). Coyotes have also been shown to benefit from

anthropogenic (Fedriani et al., 2001; Newsome et al., 2015) and marine subsidies (Rose and Polis, 1998; Schwarcz, 1991), and they can have cascading impacts on other predators and prey (Crooks and Soulé, 1999). On the central coast of California, coyotes have been observed consuming marine resources, but the importance of these resources to their diets is unknown. If this marine subsidy has a recent onset, it may be facilitating coyote expansion along coastal routes. Furthermore, if access to a marine subsidy was only gained following the removal of a competitor, a new marine subsidy could intensify the effects of mesopredator release.

Here we aim to quantify the current marine subsidy to coyotes and evaluate its spatial and temporal coverage. Our goals are (1) to characterize the extent and importance of a marine subsidy to modern coyotes on the central California coast and (2) to determine whether this marine subsidy is recent or has roots deeper in

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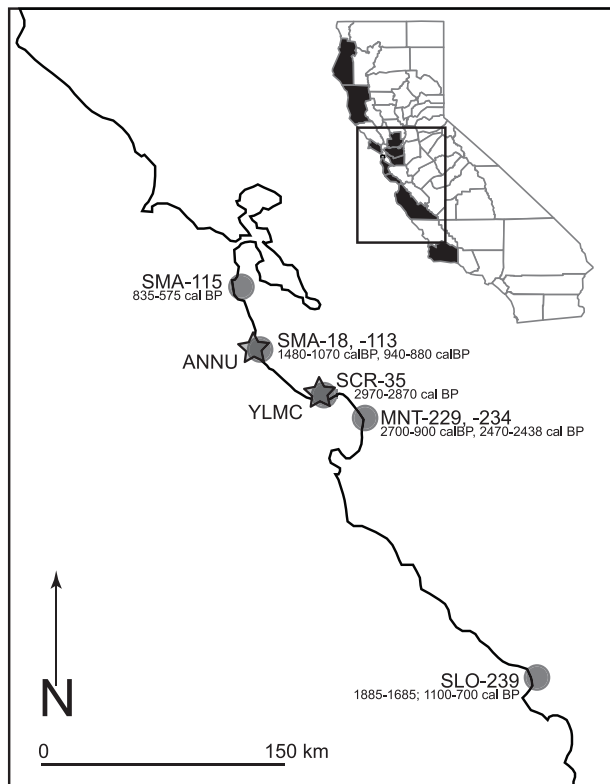
Figure 1. Map of the central California coast illustrating sampling localities: seven archaeological sites used in this study (gray circles) and two modern scat transects (stars with black outlines; ANNU: Año Nuevo, YLMC: Younger Lagoon/Moore Creek). Dates of occupation for the archaeological sites are listed below the site codes: Montara State Beach (CA-SMA-115; Hylkema 1991), Año Nuevo (CA-SMA-18; Hylkema et al., 2006; Newsome et al., 2007), Quiroste Valley (CA-SMA-113; Gifford-Gonzalez, 2011), Davenport (CA-SCR-35; Newsome et al., 2007), Moss Landing (CA-MNT-229; Dietz et al., 1988; Jones, 2002; CA-MNT-234; Newsome et al., 2007), and Morro Bay (CA-SLO-239, Jones et al., 2017). Details regarding the fauna at these archaeological sites are described in the Supplementary Text available online. Coastal counties from which we analyzed historical specimens are shaded in black.

the Holocene. We use coyotes as a test case to examine the possible interplay between top-down (apex predator loss) and bottom-up (resource subsidy) effects on mesopredator expansion. The central California coast is an ideal region to investigate the past and present magnitude of a marine subsidy to coyotes. Not only is the marine environment highly productive, offering numerous opportunities for the delivery of subsidies to adjacent terrestrial communities, but humans have occupied this part of the coast for thousands of years, allowing for the accumulation of subfossil assemblages in archaeological middens.

We present carbon and nitrogen isotope data from coyotes, their competitors, and their potential food resources collected from two present-day coastal sites, seven coastal archaeological sites spanning periods of occupation from ~3000 to 750 BP, and from historical coyote and grizzly bears from coastal California counties (Figure 1). Año Nuevo State Park (San Mateo County, CA) presently supports a dense seasonal concentration of California sea lions (*Zalophus californianus*) as well as a breeding colony of northern elephant seals (*Mirounga angustirostris*) that was established in the 1960s (Le Boeuf and Panken, 1977). Mainland rookery sites such as these likely provide terrestrial predators and scavengers easy access to living and dead seal pups, both of which are possible coyote food sources (Steiger et al., 1989; Way and Horton, 2004). Younger Lagoon Reserve,

while also a protected area along the coast, lacks a seal rookery. Looking to the archaeological sites, a preponderance of evidence points to the existence of mainland northern fur seal (*Callorhinus ursinus*) rookeries coincident with ancient human occupation at Moss Landing, CA (CA-MNT-234 and CA-MNT-229; Burton et al., 2001; Gifford-Gonzalez, 2011; Milliken et al., 1999) as well as at Año Nuevo, CA (CA-SMA-18; Gifford-Gonzalez et al., 2006; Hylkema, 2002), allowing for a comparison between past and present sites with very similar resource availabilities. In contrast with northern elephant seals, *C. ursinus* typically comes ashore to pup and breed between June and October (Riedman, 1990), with some hints of a longer span of maternal attendance in prehistoric populations (Newsome et al., 2007). By comparing modern and prehistoric coyote diets in coastal California at sites with and without seal rookeries, we show that marine resource use by some present-day coyotes is a new behavior relative to their recent ancestors. We argue that reduced competition with both grizzly bears and humans likely enabled this behavioral shift, which suggests that the top-down effect of mesopredator release could be amplified by the bottom-up effect of a newly gained resource subsidy.

Methods

Approach

Stable isotope analysis is an ideal approach for assessing the relative importance of marine and terrestrial resources to past and present coyote diets. The $\delta^{13}C$ and $\delta^{15}N$ values of animal tissues and scat reflect the isotopic composition of an animal's diet, offset by characteristic diet-to-tissue isotopic discrimination factors in both carbon and nitrogen, which can vary depending on the tissue being analyzed (reviewed by Koch, 2007). Marine ecosystems are isotopically distinct from terrestrial ecosystems in part because of baseline differences in the isotopic composition of primary producers; in many regions, including coastal California, marine primary producers are enriched in both ^{13}C and ^{15}N relative to terrestrial plants (Newsome et al., 2010). Furthermore, marine food chains are generally longer than terrestrial food chains, leading to greater trophic enrichments in the heavier isotopes. Apex predators in marine systems thus have $\delta^{15}N$ values in the range of +16 to +19 ‰, while terrestrial apex predator $\delta^{15}N$ values range between +7 to +12 ‰. Coastal California is dominated by C_3 plants (Suits et al., 2005), consequently, its coastal terrestrial food webs are characterized by relatively low $\delta^{13}C$ values, ranging from −22 to −28 ‰, while marine-sourced materials tend to have higher values. Consumers relying on a mixture of marine and terrestrial resources will have $\delta^{13}C$ and $\delta^{15}N$ values between these end members.

Modern sample collection and analysis

Between May 2011 and August 2013, we collected mammalian mesopredator scats quarterly along coast-to-inland transects at Año Nuevo ($n = 346$, 37.1188ºN, 122.3066ºW; Figure 1) and about 20 miles to the south at Younger Lagoon/Moore Creek ($n = 169$, 36.9510ºN, 122.0665ºW). Because it is difficult to accurately distinguish among mammalian mesopredator scats by morphology alone, we focused our efforts on a subset of scats that were DNA-verified to species in collaboration with Wildlife Genetics International (WGI) (Reid, 2015). We submitted cotton swabs of the exterior of the scats, which WGI processed as tissue using QIAGEN DNeasy Blood and Tissue Kits. For the species test, WGI performed two variants of a sequence-based analysis of the mitochondrial 16S rRNA gene (Johnson and O'Brien, 1997) using primers that amplify across all mammals or preferentially across Carnivora sequences; results were compared to a reference collection of > 125 mammalian species. From this subset, we identified

29 scats from Año Nuevo and 13 scats from Younger Lagoon as coyote based on mtDNA evidence and/or the presence of coyote guard hairs (Miotto et al., 2007). To increase our sample size, we then used a quadratic discriminant function predictive morphometric model (Reid, 2015) to identify additional scats in our collection as coyote with > 60% probability (15 from Younger Lagoon, 5 from Año Nuevo). Our scat dataset additionally includes DNA-verified gray fox scats (*Urocyon cinereoargenteus, n* = 27; all from Año Nuevo) and bobcat scats (*Lynx rufus, n* = 62; 9 from Younger Lagoon, 53 from Año Nuevo). To enable comparison between the isotopic values of different coyote tissue types, we also opportunistically obtained bone collagen samples from two road kill coyotes collected on CA Hwy 1 adjacent to Año Nuevo as well as two road kill individuals collected adjacent to Younger Lagoon Reserve (California Fish and Game permit SC-11995).

We used the results of our previous work on coyote scat contents (Reid and Koch, 2017) to identify coyote food sources for isotopic characterization, including marine mammals, deer, small mammals, berries, arthropods, reptiles, birds, anthropogenic foods, and other mammalian mesopredators. When possible, we sourced local isotopic data for these food items from the literature, but we also opportunistically collected berry and insect samples along the transects and sampled hair from live-trapped small mammals at Año Nuevo. We followed the guidelines of the American Society of Mammalogists (Sikes and Gannon, 2011) for all of our work with animals, which was approved by the UC Santa Cruz Institutional Animal Care and Use Committee (permits Kochp1105 and Kochp1211).

We prepared samples for isotopic analysis following published protocols. For scat samples, we analyzed the fine-grained matrix material (Reid and Koch, 2017), which we extracted by sieving and cleaned by rinsing with Milli-Q water, 0.1N HCl to remove inorganic $CaCO_3$, and again with Milli-Q. After drying and homogenizing the scat samples, we weighed ~5 mg of scat matrix into 5 mm × 9 mm tin boats for isotopic analysis. We prepared hair samples following the methods of O'Connell and Hedges (1999); samples were rinsed with Milli-Q water, immersed in petroleum ether, and sonicated for 15 min, rinsed again with Milli-Q water (five times), and dried in a 60°C oven overnight. Our collagen extraction methods followed Brown et al. (1988); bone fragments were decalcified in 0.5N HCl for ~72 h, treated in 0.1N NaOH for 24 h, lipid extracted using petroleum ether (Dobush et al., 1985), rinsed five times with Milli-Q, and freeze dried overnight. Arthropod and berry samples were repeatedly rinsed and sonicated in Milli-Q water (4× for 15 min), dried (60°C overnight), and then crushed with an agate mortar and pestle. For hair, collagen, and arthropod samples, we weighed ~0.7 mg of material into 5 mm × 9 mm tin capsules. Berry samples were weighed separately for C and N isotope analysis (~0.4 mg for carbon and ~3 mg for nitrogen) and also sealed into 5 mm × 9 mm tin capsules.

We subjected samples to Dumas combustion using a Carlo Erba 1108 elemental analyzer and then measured $\delta^{13}C$ and $\delta^{15}N$ values on a ThermoFinnigan Delta Plus XP continuous flow isotope ratio mass spectrometer at the UC Santa Cruz Stable Isotope Laboratory. Sample isotopic values were corrected using two-point normalization and adjusted for size, drift, and source stretching effects. Based on the standard deviation of 38 replicates of an in-house standard (Acetanilide), the average analytical precision was < 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$. We estimated the atomic carbon and nitrogen elemental composition of samples based on standards of known elemental composition (PUGel and Acetanilide); precision of these known compounds is better than 1%. The atomic C/N ratios in the proteinaceous tissue samples (hair and bone) fell within the ranges expected for well-preserved samples (Ambrose, 1990; O'Connell and Hedges, 1999).

We performed all data analyses in R version 3.4.1 (R Core Team, 2017). We used Hotelling's T^2-test (R-package ICSNP) to evaluate whether coyotes from Año Nuevo and Younger Lagoon have statistically different multivariate C and N isotope means. We used MixSIAR (R-package MixSIAR) (Stock and Semmons, 2016a), a Bayesian stable isotope mixing model, to estimate the proportional contributions of isotopically distinct food resources to coyote diets. We conducted Markov Chain Monte Carlo (MCMC) sampling within MixSIAR, primarily using the 'normal' setting, which included running three replicate chains (each with 100,000 draws), a burn-in of 50,000, and a thinning rate of 50. Because coyotes are omnivores and eat foods with different proportions of digestible [C] and [N], we included concentration dependence in our models to reduce bias (Phillips and Koch, 2002) and followed the recommendations of Koch and Phillips (2002) to derive digestible [C] and [N] values for coyote food sources from the USDA nutrient database. We used a multiplicative error structure in our models (Resid*Process; Stock and Semmons, 2016b) and, for Año Nuevo, we included informative priors (Moore and Semmons, 2008; Ward et al., 2010) based on previously dissected scat samples (Reid and Koch, 2017). To calculate the informative priors, we re-classified dietary items found in 12 previously fully dissected scat samples into the six isotopically distinct dietary categories presented below, determined their frequency of occurrence within the scat samples, and then scaled the prior to have a weight of 6 (a = (0.3, 0.5, 1.4, 0.3, 2.7, 0.9)), which is equal to the weight in the uninformative prior (a = (1, 1, 1, 1, 1, 1)). We used both the Gelman–Rubin diagnostic and Geweke diagnostic to assess model convergence.

To convert stable isotope values measured in a variety of tissues to coyote diet space (i.e. the muscle tissue that is digested and assimilated), we applied published organism- and tissue-specific discrimination factors (Supplementary Table 1, available online). For the Año Nuevo coyotes, we grouped dietary items a priori into six categories based on the similarity of their isotopic values: anthropogenic foods, California mouse (*Peromyscus californicus*), marine foods, plants, terrestrial herbivores, and terrestrial omnivores (Supplementary Table 2, available online; Supplementary Figure 1, available online). We used MANOVA to test for differences in multivariate means in the grouping process. For the Younger Lagoon coyotes, we separately considered two additional dietary items, vole (*Microtus californicus*) and brush mouse (*Peromyscus boylii*), the inclusion of which brought the majority of the coyote scat samples into the dietary mixing space, an important requirement for stable isotope mixing models (Phillips et al., 2014). We individually adjusted the coyote scat isotope values for discrimination by adding 1.5 ± 1.6 ‰ for $\delta^{13}C$ values and subtracting 2.3 ± 1.3 ‰ for $\delta^{15}N$ values (Reid and Koch, 2017). We also adjusted the road kill coyote collagen samples to diet using collagen-to-diet discrimination factors derived by combining coyote tissue-to-tissue apparent enrichment factors (Reid and Koch, 2017) with published hair-to-diet discrimination factors for a similar canid (Roth and Hobson, 2000), resulting in an adjustment of −2.8 ± 1.6 ‰ for $\delta^{13}C$ values and −3.5 ± 0.7 ‰ for $\delta^{15}N$ values (Reid and Koch, 2017).

To compare isotopic niche breadths across different sites, we used SIBER (Stable Isotope Bayesian Ellipses in R) metrics (Jackson et al., 2011). These metrics are unbiased with respect to sample size and take into account uncertainty in the sampled data. We calculated the sample size standard ellipse area for each subgroup ($SEA.B_1$) and assessed whether they were significantly different by comparing their Bayesian 95% credible limits; ellipse areas are significantly different when the limits do not overlap. Given that scat integrates diet over a relatively short timescale, we also calculated the standard ellipse areas for each modern site based on seasonal averages ($SEA.B_2$) to reduce some of the short-term temporal variability. We included the road kill coyote bone
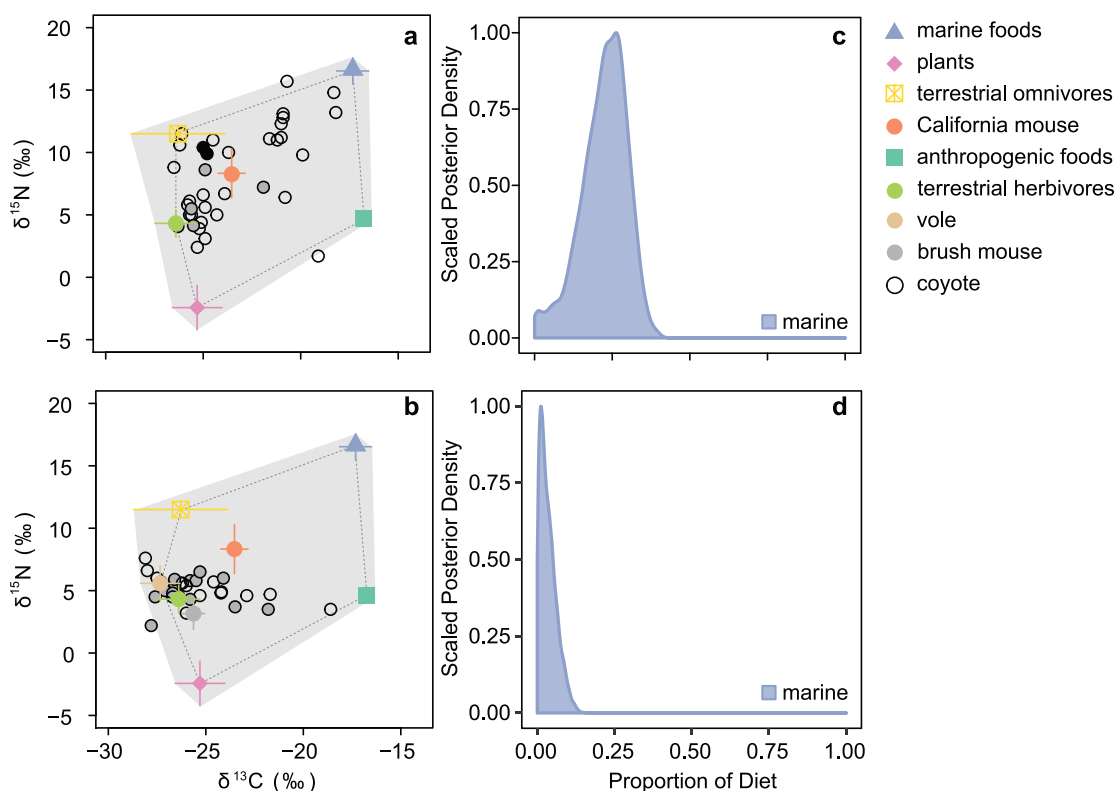
Figure 2. $\delta^{13}C$ and $\delta^{15}N$ values measured in coyote food resources and coyote scat and bone collagen at (a) Año Nuevo and (b) Younger Lagoon/Moore Creek. Coyote samples are adjusted for discrimination as described in the Methods. Coyote samples illustrated in black are measured in bone collagen, white open circles are DNA-verified scats, and those in gray are model-identified scats. The minimum convex hull of the dietary mixing space is depicted with a medium gray dashed line and the maximum convex hulls are shaded in light gray. Posterior plots of the predicted contributions of marine resources to coyote diets are shown for (c) Año Nuevo and (d) Younger Lagoon/Moore Creek.

collagen values in these calculations as individual points after adjusting collagen-to-scat (–4.3 ± 2.7 ‰ for $\delta^{13}C$ and −0.9 ± 1.3 ‰ for $\delta^{15}N$ (Reid and Koch, 2017)).

Subfossil and historical sample collection and analysis

To evaluate marine resource use by past coyotes, we sampled historical (AD 1893–1992) coyote fur and bone collagen specimens from coastal California counties ($n = 15$) and subfossil coyote bone collagen samples from seven coastal archaeological sites ($n = 28$; Figure 1, Supplementary Table 3, available online). When available, we also sampled bone collagen from potential competitors (grizzly bears, *Ursus arctos*; bobcats; and mountain lions, *Puma concolor*) and possible prey (ruminants, small mammals, pinnipeds, fish) from the same archaeological sites (Supplementary Tables 2 and 3, available online). These samples were acquired from the UC Santa Cruz Monterey Bay Archaeology Archives, Moss Landing Marine Lab, and the California Academy of Sciences. Subfossil and historical collagen and hair samples were prepared and analyzed in the same manner as modern samples. We did not consider wolves (*Canis lupus*) in this study because there was no evidence from the archaeological sites we analyzed that wolves were present on the central coast at the time the sites were occupied. While there is some historical evidence for wolves in coastal California based on written accounts of sightings between 1750 and 1850 (Schmidt, 1991), by the time of their extirpation from the state after 1901, confirmed records of wolves were confined to just San Bernardino and Lassen counties, hundreds of kilometers from the study region.

As with the modern samples, we used MixSIAR (Stock and Semmons, 2016a) to estimate the proportional contributions of

isotopically distinct food resources to past coyote diets. We ran models separately for each site. Because all isotopic values for both coyotes and their potential prey were measured in collagen, we adjusted the coyotes for discrimination using published canid collagen-to-collagen discrimination factors, subtracting 1.3 ‰ for $\delta^{13}C$ (Fox-Dobbs et al., 2007) and 2.7 ‰ for $\delta^{15}N$ (Schwarcz, 1991). These values are also quite similar to recently reported collagen-to-collagen discrimination factors for adult red foxes ($\Delta^{13}C = +1.1 \pm 1.1$ ‰ and $\Delta^{15}N = +3.2 \pm 1.8$ ‰; Krajcarz et al., 2018). We estimated isotopic values for Holocene berries by correcting modern berry data for the Suess effect (the ^{13}C-depletion of surface carbon reservoirs due to fossil fuel burning; Quay et al., 1992; Sonnerup et al., 1999) by adding 1.8 ‰ to $\delta^{13}C$ values. Previously, authors have estimated plant values for the Holocene by assuming C_3 plants had $\delta^{13}C$ and $\delta^{15}N$ values that were 5 and 3 ‰ below ungulate browsers, respectively (Newsome et al., 2004), which is advantageous because it is based on the isotope ratios of a consumer within the Holocene food web. Ungulate browsers, however, primarily consume leaves while coyotes consume fruit and/or berries and these plant tissues can differ significantly isotopically (e.g. Kolb and Evans, 2002). We therefore felt it was more appropriate to estimate berry values from modern data, despite the fact that C_3 plant isotopic values are also sensitive to environmental factors (Farquhar et al., 1989). As with the modern samples, because they are not the consumers being considered in our mixing models, we did not adjust bobcat, mountain lion, or grizzly bear isotope values for trophic discrimination.

To enable direct comparison between the historical and subfossil samples, we corrected the subfossil samples for the Suess effect. We did this by fitting a spline function to the combined atmospheric $\delta^{13}C$ records from Rubino et al. (2013) and Indermühle et al. (1999) and predicting the $\delta^{13}C$ value of the atmosphere at the time each sample was collected. We then standardized
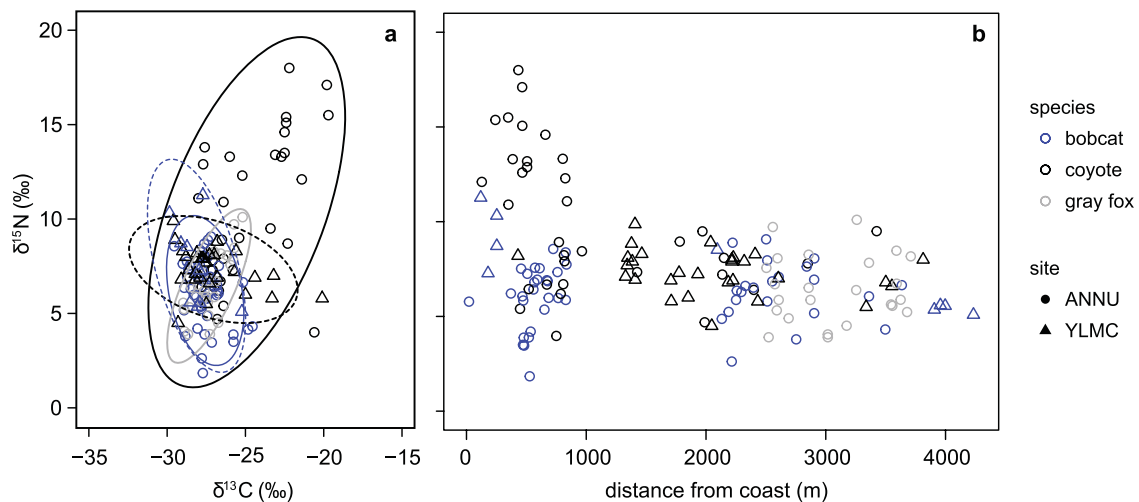
Figure 3. δ^{13}C and δ^{15}N values measured in species-verified mammalian mesopredator scats (Supplementary Table 3, available online) illustrating (a) isotopic dietary niche and (b) variation in δ^{15}N values with distance from the coast. None of the samples are adjusted for discrimination. In (a) standard ellipses depicted with a solid line correspond to samples from Año Nuevo while those depicted with dashed lines correspond to samples from Younger Lagoon/Moore Creek; there were no gray fox scats identified at Younger Lagoon/Moore Creek.

the δ^{13}C values to the time period of interest. For the historical samples, we corrected to 700 BP, which required the addition of between 0.3 ‰ for the samples from the late 1800s to 1.5 ‰ for the sample from 1991. To compare changes in isotopic niche breadth from the Holocene to present, we again used SIBER metrics (Jackson et al., 2011).

Results

Modern samples

We collected a total of 346 scats at Año Nuevo and 169 scats at Younger Lagoon/Moore Creek. The Año Nuevo coyote scats (n = 34) had a mean δ^{13}C value of −24.9 ‰ (±2.6 ‰ standard deviation (SD)) and mean δ^{15}N value of 10.4 ± 3.8 ‰ and the multivariate means were significantly different from those for Younger Lagoon coyote scats (n = 28, δ^{13}C = −27.1 ± 2.2 ‰ and δ^{15}N = 7.4 ± 1.1 ‰; $F_{2,63}$ = 11.4, p = 5.8^{-05}; Figure 2a and b; Supplementary Table 3, available online). Coyotes at Año Nuevo also had a significantly greater isotopic dietary breadth (SEA.B$_1$ = 26.7 ‰^{2}, 95% confidence interval (CI): 17.7–36.0 ‰^{2}) than those at Younger Lagoon (SEA.B$_1$ = 7.5 ‰^{2}, 95% CI: 4.9–10.4 ‰^{2}). Isotopic dietary breadth assessed from seasonal averages remained significantly higher at Año Nuevo (SEA.B$_2$ = 10.8 ‰^{2}, 95% CI: 5.2–22.4 ‰^{2}) relative to Younger Lagoon (SEA.B$_2$ = 2.2 ‰^{2}, 95% CI: 1.1–4.9 ‰^{2}). Of the 29 verified coyote scats collected at Año Nuevo, 46% contained evidence of marine resource consumption (Supplementary Table 3, available online) while none of the Younger Lagoon coyote scats contained identifiable marine material. Marine material (mainly elephant seal and sea lion hair) was furthermore present in scats collected during all seasons at Año Nuevo (Supplementary Table 3, available online). The two road kill coyote specimens from Año Nuevo similarly had isotopic values suggestive of marine resource use (δ^{13}C = −22.2 and −22.0 ‰, δ^{15}N = 13.9 and 13.4 ‰; Figure 2a, Supplementary Table 3, available online) while the two individuals collected near Younger Lagoon did not (δ^{13}C = −21.4 and −21.7 ‰, δ^{15}N = 8.3 and 10.2 ‰; Figure 2b, Supplementary Table 3, available online).

Based on the results of the isotope mixing models, pinnipeds comprised the second greatest mean dietary component (22%, 95% CI: 4–34%) for coyotes at Año Nuevo, behind terrestrial herbivores (31%, CI: 9–54%; Figure 2c, Supplementary Table 4, available online). This relatively high reliance on marine resources was corroborated by scat dissections, which similarly indicated that pinnipeds made up 22 ± 8% of coyote diet at Año Nuevo

based on the percent-by-volume of marine material in the scats (Reid and Koch, 2017). In contrast, mixing model predictions for coyote diets at Younger Lagoon suggested that pinnipeds were unimportant dietary components (4%, CI: 0–9%; Figure 2d). Instead, Younger Lagoon coyotes were predicted to have diffuse diets with various terrestrial herbivores and small mammals making up nearly equal proportions (~19% each; Supplementary Table 4, available online).

Coyotes at Año Nuevo and Younger Lagoon had divergent relationships with other mammalian mesopredators (Figure 3a). At Año Nuevo, coyote scats had significantly different multivariate isotopic means from both bobcat (n = 53; δ^{13}C = −27.6 ± 1.0 ‰ and δ^{15}N = 6.2 ± 1.6 ‰; $F_{2,86}$ = 36.6, p = 3.08^{-12}) and gray fox scats (n = 27; δ^{13}C = −27.3 ± 1.1 ‰ and δ^{15}N = 6.5 ± 1.7 ‰; $F_{2,60}$ = 15.4, p = 4.01^{-6}). Coyote scats at Younger Lagoon, however, did not differ significantly from bobcat scats (n = 9; δ^{13}C = −28.1 ± 1.3 ‰ and δ^{15}N = 7.5 ± 2.3 ‰; $F_{2,36}$ = 1.18, p = 0.321) and there were no DNA-verified gray fox scats collected at Younger Lagoon. The Año Nuevo coyote scats also occupied a significantly greater isotopic niche than the other analyzed mesopredators at both Año Nuevo and Younger Lagoon (Figure 3a).

Subfossil and historical samples

Pooled subfossil and Suess-corrected historical coyote bones (n = 35) had a mean δ^{13}C value of −19.6 ‰ (± 1.1 ‰ SD) and mean δ^{15}N value of 7.5 ± 2.0 ‰ while Suess-corrected historical coyote hair samples (n = 9) had a mean δ^{13}C value of −20.7 ± 0.9 ‰ and mean δ^{15}N value of 7.9 ± 0.9 ‰ (Supplementary Table 3, available online). There was little to no evidence for marine resource use by coastal coyotes across these time periods; coyote collagen δ^{13}C and δ^{15}N values fell squarely in the range expected for an exclusively terrestrial diet at all seven archaeological sites and continued to do so into historical times (Figure 4). Isotope mixing model results also consistently indicated that marine foods were unlikely to have contributed to past coyote diets (mean contributions ⩽ 10% – although SCR-35 was an exception at 14%; Figure 4, Supplementary Table 4, available online). Direct comparison between modern Año Nuevo coyotes and those from the Moss Landing archaeological sites (MNT-229 and MNT-234), both of which were adjacent to a mainland seal rookery at the time of occupation, suggested that coastal coyote dietary breadth has expanded into the present (SEA.B$_1$ = 26.7 ‰^{2}, 95% CI: 17.7–36.0 ‰^{2} and SEA.B$_2$ = 10.8 ‰^{2}, 95% CI: 5.2–22.4 ‰^{2} at Año Nuevo
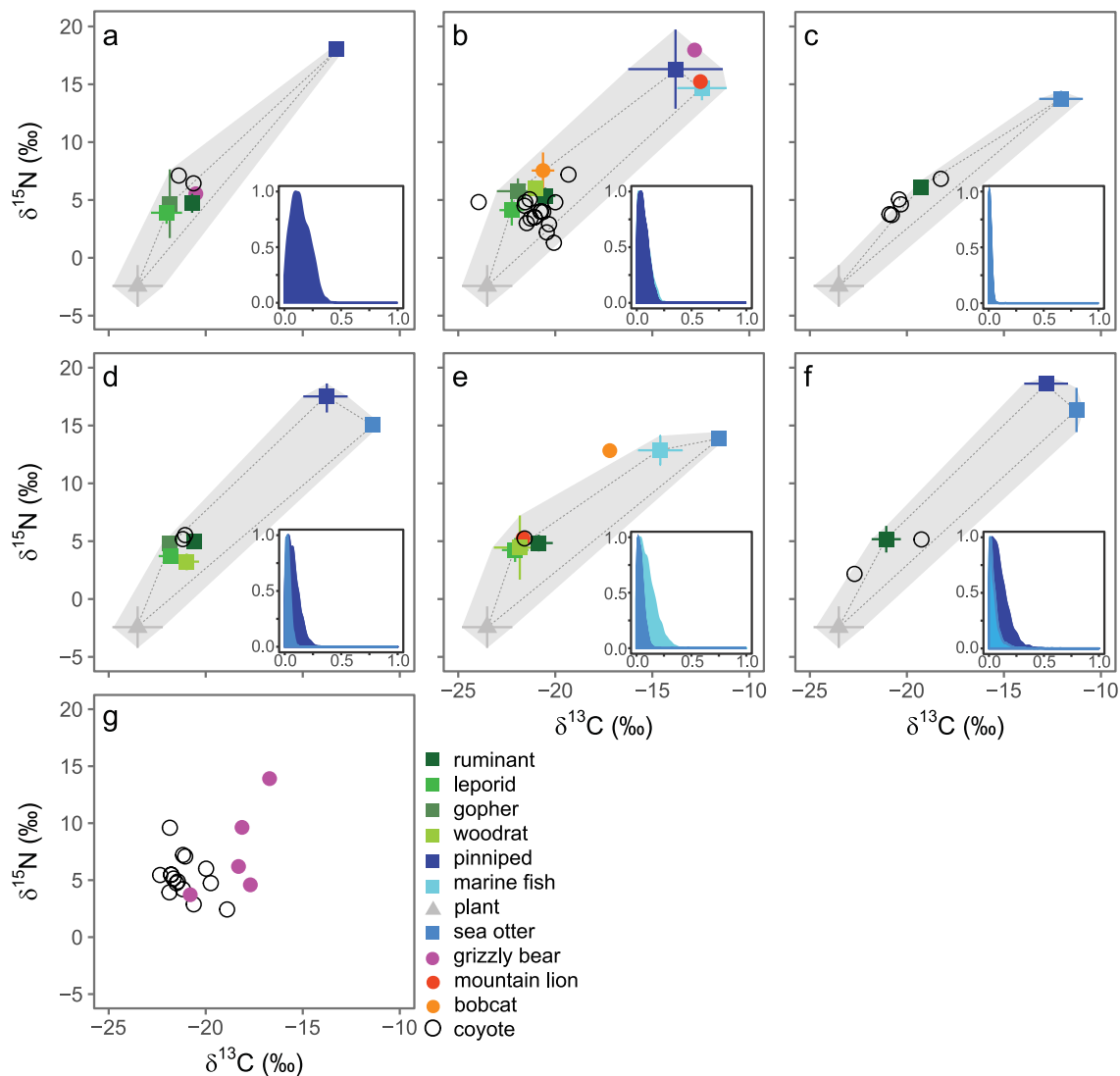
Figure 4. $\delta^{13}C$ and $\delta^{15}N$ values measured in archaeological and historical bone collagen at (a) SCR-35, (b) Moss Landing (MNT-229 and MNT-234), (c) SLO-239, (d) SMA-18, (e) SMA-113, (f) SMA-115, and (g) historical samples from coastal CA counties. Coyote values are corrected for trophic discrimination and their potential food sources are adjusted to diet space as described in the Methods (Supplementary Table 1, available online). The historical samples are Suess-corrected to 700 BP. The minimum convex hulls of the dietary mixing space are depicted with gray dashed lines and the maximum convex hulls are shaded in light gray. Insets depict the modeled proportional contribution of marine materials to coyote diets (Supplementary Table 4, available online).

today vs 4.7 ‰², 95% CI: 2.5–7.0 ‰² at the Moss Landing archaeological sites).

Archaeological and historical coyote competitors, including grizzly bears (*Ursus arctos californicus*), mountain lions (*Puma concolor*), and bobcats (*Lynx rufus*) displayed a broad range of isotopic values (Supplementary Table 3, available online). The grizzly bear sample from the oldest site, SCR-35, was consistent with a low trophic-level, purely terrestrial diet (Figure 4a, Sample #101892; $\delta^{13}C = -20.5$ ‰ and $\delta^{15}N = 5.5$ ‰). Both the grizzly bear and mountain lion samples from Moss Landing (MNT-234 and MNT-229), however, plotted with the pinnipeds, suggesting that they consumed a significant proportion of marine foods (Figure 4b, Sample #1242; $\delta^{13}C = -12.8$ ‰ and $\delta^{15}N = 18.0$ ‰, Sample #698; $\delta^{13}C = -12.5$ ‰ and $\delta^{15}N = 15.2$ ‰). Bobcats at Moss Landing were similar to coyotes with a mean $\delta^{13}C$ value of -20.6 ± 0.6 ‰ and mean $\delta^{15}N$ value of 7.6 ± 1.6 ‰ (Figure 4b). At SMA-113, the bobcat sample appears to reflect some degree of marine resource use (Figure 4e, Sample #2979; $\delta^{13}C = -17.2$ ‰ and $\delta^{15}N = 12.8$ ‰) while the mountain lion sample was not different from the coyotes (Sample #2389; $\delta^{13}C = -21.7$ ‰ and $\delta^{15}N = 5.2$ ‰). Of the five historical California grizzly bear samples, two exhibit isotopic values indicative of marine resource

consumption (CAS 24360 and 27342, Figure 4g), both of which were from the San Francisco Bay area and of unknown age. The remaining three historical grizzly samples had isotopic signatures suggesting purely terrestrial diets (Figure 4g).

Discussion

Our analysis reveals that marine foods are important dietary resources for modern coastal coyotes at Año Nuevo, which is adjacent to an elephant seal rookery, and not at Younger Lagoon/Moore Creek. While it is possible for high $\delta^{13}C$ values to be sourced from anthropogenic food resources derived from C_4 plants, the combination of high $\delta^{13}C$ and $\delta^{15}N$ values we observe in Año Nuevo coyotes can only be accounted for by marine resource use; the mixing models predicted that anthropogenic food resources made up only 3–4% of coyote diet at both Año Nuevo and Younger Lagoon. Scat dissections confirm that marine foods, primarily northern elephant seal and California sea lion, are the source of these high $\delta^{13}C$ and $\delta^{15}N$ values (Supplementary Table 3, available online). At Año Nuevo, marine resources are consistently available throughout the year. Peaks in harbor seal strandings in Monterey Bay coincide with their breeding season

in early spring (Nevins et al., 2011), while California sea lion stranding rates are highest in the summer/early fall (Greig et al., 2005), and elephant seals begin pupping in the winter (Le Boeuf and Panken, 1977). Año Nuevo Island is a favored haul out for sea lions and consequently dead sea lions wash up on the mainland beach with regularity (Burton and Koch, 1999). Elsewhere around Monterey Bay, marine mammal strandings are not uncommon, but are less frequent (Nevins et al., 2011). Coyotes at other coastal sites may also readily consume marine foods if given the opportunity, but opportunities at any one locality are rare. Beaches may also need to be free of human activity long enough for coyotes to be comfortable feeding on stranded carcasses too large for them to transport to a safe locale, further reducing opportunities. Año Nuevo is unique in that it is protected from human interference in addition to having abundantly available marine food resources.

Scats provide a relatively short snapshot of coyote diet, on the order of several days to weeks. Canid gut retention times are just 2–3 days (Weaver, 1993); however, the incorporation rate of epithelial cells into the scat matrix may be an order of magnitude slower (Codron et al., 2011). Isotopic turnover in bone collagen, on the other hand, takes years (e.g. Hobson and Clark, 1992) instead of days or weeks. Given the significant difference in timescales represented by these different tissues, we have adjusted our sampling (by collecting scats over a 2-year period) to ensure comparability between ancient and modern samples. Previous research suggests that 50–59 scats are required to identify principal prey occurring in > 5% of scats (Trites and Joy, 2005; Windberg and Mitchell, 1990). Our species-verified sample sizes fall below these suggested minima; however, if we consider our full sample of mesopredator scats at each site, which undoubtedly includes additional un-verified coyote scats, we see the same result – marine resources are important to mesopredator diets at Año Nuevo, but not at Younger Lagoon (Supplementary Figure 2, available online). We additionally found that $\delta^{13}C$ and $\delta^{15}N$ values measured in coyote bone collagen from two modern road kill coyotes collected near Año Nuevo were indicative of marine resource consumption (Figure 2a). These collagen isotope values corroborate our findings based on coyote scat and confirm that some individuals at Año Nuevo consistently rely on marine foods throughout their lifetimes.

In contrast to their modern counterparts, subfossil and historical coyote diets did not feature marine resources as important components (Figure 4). Even at sites where mainland northern fur seal rookeries were present (Moss Landing: MNT-234 and MNT-229 and Año Nuevo: SMA-18), it appears that coyotes were not consistently consuming marine mammals (Figure 4b and d). We used power analysis to determine the number of samples required to detect marine resource use by past coyotes, given an effect size of 1.6 (Cohen's d; based on the mean difference between $\delta^{13}C$ and $\delta^{15}N$ values of modern coyotes consuming some marine vs exclusively terrestrial foods). Assuming that significance (α) = .05 and that the power level (1 – β) = .95, 23 samples are required; our sample of 28 subfossil coyotes is above this threshold. At all but one Holocene site, the mixing models estimated marine resources to comprise ≤ 10% of coyote diet. CA-SCR-35 is the exception to this, with the two coyotes there predicted to have a 14% mean dietary proportion of marine resources (Figure 4a). We argue, however, that this estimate is likely inflated because the mixing space is incomplete. Indeed, one of the two coyote samples falls outside of the mixing space, which would be more complete if we had isotopic data for other terrestrial omnivores, insects, and additional small mammals, such as the California mouse. Although we do not have samples of contemporaneous prey with which to compare the historical coyote specimens, historical coyotes continue to display relatively low $\delta^{13}C$ and $\delta^{15}N$ values, suggesting that marine resources were not incorporated into their diets (Figure

4g). Our results imply that, relative to their recent ancestors, the consumption of marine food by modern coyotes at Año Nuevo is a novel behavior.

What caused this shift in behavior? We hypothesize that relaxed interspecific competition with grizzly bears, humans, and dogs, or more likely a combination of these, allowed some modern coyotes to broaden their dietary niche. Brown bears in Alaska are known to limit marine resource use by wolves when they co-occur (Darimont et al., 2009). Historical evidence suggests that California grizzlies were abundant along the coast and that they consumed marine foods (Storer and Tevis, 1996), so it is possible that the extirpation of the California grizzly bear afforded coyotes the opportunity to change their diets and move into the grizzlies' former niche. Although we were only able to obtain isotopic data from two subfossil grizzly bears, the absence of dietary overlap between the grizzly (sample #1242) and mountain lion (sample #698) at Moss Landing, on one hand, and co-occurring coyotes, on the other, is in line with expectations for competitive exclusion (Figure 4b, Huey et al., 1974; Schmitt and Coyer, 1983). Given that grizzlies displayed a variety of dietary preferences into the historical period, however, it is unlikely that this is the only explanation. Humans were without question relying heavily on marine resources in the past (Bartelink, 2009; Beasley et al., 2013; Newsome et al., 2004) and the presence of their camps and dogs on the coast could have deterred coyotes. For example, Hofman et al. (2016) found that both ancient humans and their dogs consumed marine resources in high proportions in the Channel Islands off the coast of southern California; however, they found little to no evidence for marine resource use by island foxes (*Urocyon littoralis*), which was likely a consequence of interference competition with domestic dogs. In contrast to Holocene peoples, modern humans are trying to reduce exploitation of coastal resources by creating coastal parks, marine sanctuaries, and enacting wildlife protection programs, making marine resources more available to coyotes today.

Regardless the reason for modern coyote dietary niche expansion, the marine subsidy to some coastal California coyotes clearly has a recent onset. How then is this new subsidy affecting coyotes and the greater coastal ecosystem? We were not able to successfully extract nuclear DNA from our scat samples; however, two lines of indirect evidence (camera traps and scat deposition rates) suggest that the coyote density near the coast at Año Nuevo is elevated relative to further inland and relative to Younger Lagoon (Supplementary Tables 5 and 6, available online). Given that coyotes at Año Nuevo continue to consume terrestrial foods in significant proportions in addition to marine resources, theory predicts that this increased consumer density could depress local terrestrial resources (Gompper and Vanak, 2008; Polis et al., 1997; Rand and Louda, 2006; Rose and Polis, 1998). The possibility also exists that other mesopredators, such as bobcats and gray foxes, are supported in greater numbers at Año Nuevo because coyotes have shifted out of otherwise contested niche space (e.g. Gomez et al., 2010). By comparing coyote scat isotope values with those measured in DNA-verified bobcat and gray fox scats at both sites, it's apparent that coyotes at Año Nuevo have significantly greater isotopic dietary niches than the other mesopredators (Figure 3a, Supplementary Table 3, available online). It is also clear that these different mammalian mesopredators are partitioning dietary and spatial resources (Figure 3a and b). First, only coyotes at Año Nuevo appear to be consuming marine resources; this is different from the past, when we see evidence for one bobcat consuming marine foods at CA-SMA-113 (Figure 4e). Furthermore, scats found close to the coast were exclusively from bobcats and coyotes while gray fox scats were found further inland where the vegetation along the transects is characterized by mixed evergreen forest. A more detailed assessment of dietary and spatial niche partitioning by mesopredators at Año Nuevo

will be necessary to more thoroughly delineate how the marine subsidy to coyotes is impacting their competitors.

Narratives of coyote expansion have primarily invoked a combination of apex predator extirpation and deforestation as the key drivers (Hody and Kays, 2018; Ripple et al., 2013). Coyotes are also recognized as synanthropes, appearing to do well in highly modified suburban and urban environments (e.g. Gehrt et al., 2011). Our results add an additional piece to these narratives, suggesting that release from competition in coastal areas can confer the benefit of access to a resource subsidy (when it is abundantly available, as at Año Nuevo), making coastal routes potentially lucrative for range expansion. There is mounting evidence from elsewhere in North and Central America that coyotes benefit from the sea in many coastal areas (Alvarez-Castaneda and Gonzalez-Quintero, 2005; Atencio, 1994; Eckrich and Owens, 1995). For example, at the very edge of their range in Panama, where coyotes first arrived in 1995, they are observed more frequently in coastal areas than in the interior (Mendez-Carvajal and Moreno, 2014). The same is true at the other end of their expanding range in Labrador (Chubbs and Phillips, 2005). We therefore suspect that marine resources are important for coyotes along this expanding edge and may offer the means by which coyotes expand their range into South America.

We have shown that marine subsidies to coyotes in coastal California have a very recent onset and that coyotes are likely positively impacted by a marine subsidy where it occurs. Today, marine resources comprise ~20% of coyote diets at Año Nuevo, where there is an active northern elephant seal rookery and an essentially constant delivery of marine resources to land. In contrast, coyotes did not consume marine resources in significant enough proportions for us to detect at Younger Lagoon, where marine resources are scarcer. In the past, coyotes did not consume marine foods in significant proportions, even at localities adjacent to mainland eared seal rookeries, such as Moss Landing (MNT-229 and MNT-234) and Año Nuevo (SMA-18). Past peoples (Bartelink, 2009; Beasley et al., 2013; Newsome et al., 2004), their dogs (Hofman et al., 2016), and California grizzly bears (Storer and Tevis, 1996) did, however, rely on marine resources and could have prevented coyotes from gaining access to a subsidy from the sea. The onset of heavy marine resource use by coyotes at Año Nuevo appears to have been delayed until marine mammal populations began to recover following the Marine Mammal Protection Act and designation of marine sanctuaries. Finally, this newly gained access to marine resources has implications for coyote range expansion – it may be that coastal routes lacking former apex predators provide coyotes with relatively easy pathways by which to extend their territory. Further study of additional coastal coyote populations, particularly from coastal locations along their expanding edge, will clarify the importance of a marine subsidy to coyotes more broadly.

Data accessibility

All data supporting the results reported here are currently available in the supplementary material and will be archived in the Neotoma database (www.neotomadb.org).

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