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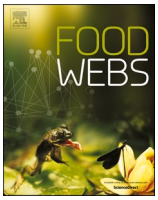

Consistent foraging on marine resources by coyotes (*Canis latrans*) on the Southern California coast

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ABSTRACT

The marine-terrestrial interface provides consumers with access to nutrient rich ocean-based resource subsidies. Coyotes, omnivorous generalists with large ranges that can span many landscape types including the coastal ecotone, might be a critical component of the intertidal food web, contributing to resource subsidy movement into the less productive adjacent coastal scrub habitat. This study utilized an array of camera traps along identified coastal game trails in two protected coastal properties in California to assess the consumption of marine fauna by coyotes in intertidal habitats. We captured coyotes consuming a variety of marine resources, including marine mammals, fish, and intertidal invertebrates. We therefore suggest that coyotes are a more consistent consumer in intertidal habitats than previously thought. We highlight the need for further research into the role of coyotes as a marine to terrestrial subsidy vector, especially under the pressure of anthropogenic change in coastal systems.

Coyotes are nearly ubiquitous across North America. They have broad diets and opportunistic foraging habits, enabling their presence in a wide range of habitats ranging from urban centers to native landscapes (Breck et al., 2019). Especially in less impacted ecosystems, coyotes may play a significant role in the concentration and movement of nutrients due to their abundance, large territories, and dietary breadth (Bekoff, 1977). While coyotes are colloquially considered terrestrial, coastal populations frequent the marine-terrestrial interface and are reported to consume a variety of marine food items (reviewed by Carlton and Hodder, 2003). Field observations of coyotes suggest they consume intertidal invertebrates including clams (Crawford, 1953) and crustaceans (Rose and Polis, 1998) as well as intertidal fish (Crawford, 1953) and seabirds (Rose and Polis, 1998). Rose and Polis (1998) examined the scat of coastal coyotes in the deserts of Baja California and found evidence of (in order of percent of diet) arthropods including crustaceans, seabirds, marine fish, marine mollusks, annelids, algae, and marine mammals. Recent stable isotope analysis of Northern California coastal coyote diet, including modern scat and historical fur and bone collagen samples, reveals that 20% of their modern diet is comprised of sea lions and elephant seals, but that this pattern has only emerged since the extirpation of the California grizzly (Reid et al., 2018). In the Gulf of California, marine resource consumption by coyotes is substantial enough to result in the increase in coastal coyote populations relative to their inland counterparts (Rose and Polis, 1998). Adjacent to Salton Sea, CA, coyotes transport marine-derived nutrients (digested fish remains) away from the marine-terrestrial boundary, potentially enriching the xeric desert ecosystem up to 3 km from the donor habitat (Brehme et al., 2009). In Southern California, coyotes have been anecdotally reported to roam the beaches in remote coastal areas, but no research has yet been conducted on their habits while in the coastal ecotone.

We implemented a large-scale assessment of terrestrial consumers in remote intertidal and coastal habitats in Southern California, using motion-triggered camera traps to capture wildlife activity on beaches. We monitored two coastal properties heavily restricted against human activity: the Vandenberg Space Force Base (VSFB) in Lompoc, CA, and the Nature Conservancy's Jack and Laura Dangermond Preserve (JLDP) in Gaviota, CA. Access to VSFB and JLDP is restricted to military personnel and approved visitors and there is minimal human infrastructure on the coastline, which allows for many wildlife species to persist relatively undisturbed. We placed forty motion-triggered cameras (Browning Recon Force Elite HP4 and Reconyx Hyperfire H600) about 0.5 m off the ground next to game trails that lead to intertidal habitats. We pointed cameras parallel to the shore to avoid them being accidentally triggered by wave movement. Cameras were set to take bursts of eight photos with a rest interval of one minute between triggers. To date, we have only analyzed photo data from April and May

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Fig. 1. A coyote carries the remnants of a pinniped carcass up the bluffs at the Vandenberg Space Force Base.

Fig. 2. A coyote carries the entire carcass of a Brown pelican off the beach at the Jack and Laura Dangermond Preserve. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2022, but include notable images and observations spanning the entire dataset (April 2022 to June 2023).

During April and May 2022 we captured 281 photo-bursts of coyotes in the coastal ecotone, of which 24 included coyotes actively foraging. We recorded four coyotes carrying or consuming carcasses of marine animals during that time. Coyotes were the most commonly detected terrestrial animal at all 40 camera trap sites. Other terrestrial species observed consuming marine food items included deer (*Odecoileus hemionus*), feral pigs (*Sus scrofa*), black bears (*Ursus americanus*), Beechey's ground squirrels (*Otospermophilus beecheyi*), turkey vultures (*Cathartes aura*), and unidentifiable rodents. Our footage supports findings by Reid et al. (2018) that suggest that some coastal coyotes prey on pinnipeds (Fig. 1). However, Reid et al. (2018) only found evidence of pinniped consumption by a population of coyotes that had access to a pinniped rookery, while we observed coyotes predating on live pinnipeds, as well as scavenging dead ones, in areas where no active rookeries

Fig. 3. A coyote drags the body of a large dead pelican up a sand dune at the Jack and Laura Dangermond Preserve. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 4. A coyote holds a small fish in its mouth on the beach at the Jack and Laura Dangermond Preserve.

were present. Additionally, we provide new evidence of coyotes predating on seabirds (Figs. 2-3), marine fish (Fig. 4), and marine invertebrates (Fig. 5) on the California coast. The footage from these cameras also contains, to our knowledge, the first evidence of coyotes foraging on gumboot chitons (*Cryptochiton stelleri*), a large mollusk common in kelp forest and low-rocky intertidal food webs. Furthermore, we captured several instances of coyotes moving the carcasses of seabirds, including brown pelicans (*Pelicanus* sp.) and cormorants (*Urile penicillatus, Nannopterum auritum*), inland. Consistent foraging activity on marine food items by coyotes links terrestrial and intertidal trophic networks, suggesting that coyotes are a more important consumer in California intertidal habitats than previously estimated. We therefore propose the inclusion of coyotes as a node in the California intertidal food web.

Given their abundance along the California coast, we hypothesize that coyotes are a crucial vector for marine-derived allochthonous

Fig. 5. A lactating female coyote holds the body of a dead gumboot chiton in her mouth at the Vandenberg Space Force Base.

nutrient subsidies from the highly productive nearshore marine upwelling zone to the relatively low-productivity coastal scrub habitat. We regularly observed coyotes dragging the carcasses of seabirds, pinnipeds, fish, crustaceans, and mollusks, often leaving concentrated quantities of bones, exoskeletons, and shells at the tops of coastal bluffs or in coastal sage scrub habitat. In other cases where animals vector nutrient subsidies, similar accumulations of debris can create nutrient hot spots, which can have important downstream effects on recipient ecosystems (Subalusky and Post, 2019).

It is important to note that published instances of coyotes consuming marine prey items, including those reported here, have occurred in areas of low human density. Human activity impedes the natural movement and behavior of wildlife. Coyotes in particular favor anthropogenic subsidies in human-disturbed landscapes, while simultaneously increasing their range sizes and nocturnal activity (Bucklin, 2020; Tigas et al., 2002; Timm et al., 2004). Therefore, anthropogenic activity could disrupt coyote consumption of coastal fauna, impeding their function as a vector for marine to terrestrial subsidies (Aguilera et al., 2020; Bishop et al., 2017). As a result, coastal sage scrublands in California could be impacted by disturbance-induced changes in coyote behavior even if the habitat itself remains intact. Further use of the camera trap data from this project will involve determining whether coyote use of the coastal ecotone is reliant on low levels of human activity, and will focus on the potential anthropogenic effects on nutrient movement by mesocarnivores in a rapidly changing coastal landscape. Future research should also consider the zoonotic disease implications of wide-ranging terrestrial predators feeding on coastal fauna, especially considering mesocarnivores like coyotes who tend to also forage in areas of high human density, increasing the likelihood of wildlife-domestic contact.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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