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The carrion connection: Marine mammal carcasses provide an indirect subsidy to insectivorous birds

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ABSTRACT

The transfer of energy from nutrient subsidies across ecological boundaries can link the dynamics of adjacent ecosystems. At the interface between land and sea, beach-cast marine mammal carcasses are a large and nutrient-rich food source available to shoreline scavengers. In addition to subsidizing scavengers directly, marine mammal carrion may also indirectly subsidize terrestrial animals by increasing prey abundance. As part of an ongoing study using camera traps to monitor marine mammal carrion along the California coast, I documented a Black Phoebe (*Sayornis nigricans*) utilizing a California sea lion (*Zalophus californianus*) carcass to forage for scavenging invertebrates. Given the widespread distribution of pinniped rookeries and terrestrial insectivores, it is likely that insectivores prey upon invertebrate scavengers of pinniped carrion in many locations where they co-occur.

1. Main text

Food webs are increasingly being studied at the landscape level, where the dynamics of adjacent ecosystems are linked by the transfer of nutrients, energy, and materials across ecological boundaries (Polis et al., 1997). These uni- or bi-directional flows, known as "spatial subsidies," can drive strong and complex effects in recipient ecosystems (Subalusky and Post, 2019). At the interface between land and sea, marine subsidies to terrestrial ecosystems can take the form of spawning fishes, seabird guano, macroalgal wrack deposition, marine mammal carcasses, and others. Documented effects of marine subsidies in terrestrial food webs are numerous and context-dependent, including fertilization of primary producers (Spiller et al., 2010), changes in consumer body size (Richardson et al., 2019) and abundance, and alterations in food web structure and stability (Polis et al., 2004, Roffler et al., 2023).

Beach-cast marine mammal carcasses are the largest and most nutrient-rich parcels of carrion available to terrestrial scavengers in coastal ecosystems (Laidre et al., 2018). As such, marine mammal carrion is exploited by a diverse suite of invertebrate and vertebrate scavengers including carnivores (Hyndes et al., 2022), reptiles (Wikelski and Wrege, 2000), and many species of birds. Beyond providing direct subsidies to terrestrial consumers via scavenging, marine mammal carrion may also indirectly subsidize terrestrial consumers by driving numerical increases in prey availability. In this short communication, I describe a novel cross-ecosystem linkage in which I documented an insectivorous flycatcher—the Black Phoebe (*Sayornis nigricans*; hereafter phoebe)—utilizing a marine mammal carcass to forage for invertebrate scavengers.

As part of an ongoing study monitoring assemblages of vertebrate scavengers that consume marine mammal carrion along the California coast, I deployed a motion-triggered camera trap (Browning Strike Force HD Pro X) two meters away from a California sea lion (*Zalophus californianus*) carcass stranded above the high tide line at UC Santa Cruz's Año Nuevo Reserve (37.12178, −122.33787). The opportunistically encountered carcass was in advanced stages of decomposition throughout the deployment (Geraci and Lounsbury, 1993). The camera was in place from December 4–11, 2022, and was programmed to record 20 s videos of scavengers when triggered. Phoebes were recorded foraging on and in the immediate vicinity (i.e. within 0.5 m) of the carcass on a daily basis until December 10th, when the carcass was buried in sand by Northern elephant seals (*Mirounga angustirostris*) (Fig. 1). On two occasions, a phoebe was recorded removing invertebrate scavengers directly from the carcass (16:03 on 5 Dec. 2022 and 9:06 on 6 Dec. 2022; Video 1, Video 2). Phoebes have been documented at only one of three carcasses monitored to date, so future camera trapping efforts are required to provide insight into the relative frequency of this foraging behavior and its associations with pinniped rookeries, habitat features, and specific levels of carcass decomposition.

Phoebes are aerial insectivores that occasionally consume non-flying

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Fig. 1. Black Phoebe perched on a California sea lion carcass.

arthropods, small fish, and berries (Wolf, 2020). An abundant flycatcher along beaches and coastal bluffs of the California coast (Wolf, 2020), it is possible that phoebes may regularly prey upon invertebrate scavengers of marine mammal carrion in sites where they co-occur. Apart from one investigation which hypothesized that Antarctic Terns (*Sterna vittata*) consume necrophagous invertebrates from decomposing seal carcasses (Jażdżewska, 2009), to my knowledge this is the first published direct observation of marine mammal carrion indirectly subsidizing a terrestrial vertebrate via the consumption of invertebrate scavengers. In a similar ecological pathway, Catenazzi et al. (2009) documented high carbon and nitrogen isotope values of *Chinchippus peruvianus* solifuges (Arachnida) near a South American sea lion colony in Peru, suggesting that arthropod scavengers of pinniped carcasses are likely important dietary items for *C. peruvianus*.

While marine mammal carcasses are rarely considered an important form of marine subsidy to terrestrial ecosystems, marine mammal aggregations in space and time can lead to "hot spots" and "hot moments" of cross-ecosystem nutrient transfer (Subalusky and Post, 2019). This is particularly true in areas near pinniped rookeries, which serve as important sites of carrion deposition in the form of carcasses and afterbirth (Quaggiotto et al., 2018). Because Año Nuevo Reserve hosts rookeries of two pinniped species, northern elephant seals and California sea lions, pinniped carrion may subsidize terrestrial consumers at an elevated rate in this and ecologically similar locales (Reid et al., 2018). Given the widespread distribution of pinniped rookeries and terrestrial insectivores, it is likely that insectivores prey upon invertebrate scavengers of marine mammal carrion in many locations.

Pinniped-derived marine subsidies to terrestrial ecosystems can take the form of feces, carrion, and active predation by land-based predators. These subsidies can enter terrestrial food webs at all trophic levels—from primary producers (McLoughlin et al., 2016) to insects, birds (Hayward et al., 2010), small mammals (Catenazzi and Donnelly, 2008), and top predators (Stander, 2019). Rookeries therefore present unique opportunities to investigate the effects of marine resource inputs on terrestrial ecosystem dynamics at multiple levels, such as changes in consumer space use and fitness, multitrophic interactions, and ecosystem-level nutrient cycling. Future research efforts should focus on both direct and indirect effects elicited by these pinniped-derived subsidies, including indirect subsidies to terrestrial insectivores foraging for carrion-scavenging invertebrates.

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Declaration of Competing Interest

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