ARTICLE

Coastal and Marine Ecology

Leaving more than footprints: Anthropogenic nutrient subsidies to a protected area

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Abstract

Mobile animals that traverse ecosystem boundaries can fundamentally reshape environments by providing critical nutrient and energy inputs to the ecosystems they inhabit. In particular, aggregations of seabirds often transform coastal and island ecosystems through large amounts of nutrient-rich guano deposition. Anthropogenically driven losses of these subsidies can occur through changes in abundance of mobile species, including seabirds, and have been shown to drive whole-scale ecosystem state change on islands. However, even though many species that forage on anthropogenic food sources are highly mobile and may thus play important roles in moving nutrients from urban systems to otherwise conserved ecosystems, the impacts of anthropogenic supplements on spatial subsidies have been largely ignored. Here we examine the effects of large nesting colonies of Western Gulls (*Larus occidentalis*), a generalist carnivore known to forage on human refuse, on the Channel Islands of California. Specifically, we explore how their foraging on human subsidies may change nutrient deposition patterns at their relatively remote and protected breeding islands. We equipped gulls with GPS loggers to assess the frequency of urban foraging, and we partnered this tracking data with bird density data to estimate the rate of wild and urban-derived guano deposition on two different islands. Consistent with research on other gull species, we found high (up to 40%) but island-specific rates of urban foraging, resulting between 66 and 93 kg ha^{-1} of guano in these two sites during the breeding season, a level greater than half the amount of fertilizer applied annually in typical commercial agricultural settings and likely the primary source of nitrogen and phosphorus inputs to this system. Specifically, we estimate that 27 kg ha^{-1} year^{-1} of nutrient-rich guano is shuttled to these otherwise isolated islands from anthropogenic sources. This research highlights the large shadow (i.e., footprint) that human activity can cast on even remote ecosystems by driving significant nutrient enrichment through impacts on animal behavior and connectivity.

INTRODUCTION

Nutrient transfer by mobile animals can link many seemingly disparate systems and have significant effects on ecosystem functioning (Subalusky & Post, 2019). For example, bears' movement of salmon-derived nutrients to riparian forests changes forest growth and composition (Helfield & Naiman, 2001; Hilderbrand et al., 1999); hippopotami alter water chemistry and shape biodiversity in rivers through defecation of terrestrially derived food sources (Stears et al., 2018); and large whales' transport of nutrients from ocean depths to the surface may change global patterns of ocean productivity (Roman & McCarthy, 2010). As mobile animals that traverse ecosystem boundaries and form large nesting aggregations, seabirds provide important nutrients to their nesting and roosting grounds by depositing nutrient-rich guano sourced from their distant foraging grounds (Caut et al., 2012; Ellis et al., 2006; Wootton, 1991). In areas where nutrient input from other sources is often minimal, seabird colonies have been found to profoundly influence productivity and community structure via the cascading effects of bird-derived nutrient subsidies (Ellis, 2005; Fukami et al., 2006; Otero et al., 2018; Young, McCauley, Dunbar, et al., 2010). In many cases, the impacts of cross-ecosystem subsidies can dwarf internal nutrient cycling budgets, such that disruptions of subsidy linkages can even trigger whole system state changes (Croll et al., 2005).

It has been well established that human activities, such as introduction of invasive species that prey on seabirds or habitat modification, often disrupt allochthonous nutrient inputs to ecosystems by reducing guano deposition (Croll et al., 2005; Fukami et al., 2006). Indeed, work comparing seabird and anadromous fish movement from the Pleistocene to the present suggests that the total transfer of nutrients by these taxa is now often severely depleted, with nutrient transfer from sea to land estimated at less than 4% of its prehuman levels (Doughty et al., 2016). However, in areas where seabirds have shifted toward readily exploiting anthropogenic food sources, nutrient budgets of surrounding ecosystems may instead become increasingly subsidized by humans, with potentially similar, but largely unexplored, ecosystem-level consequences.

Humans have influenced and subsidized global nutrient budgets dramatically: nitrogen inputs to terrestrial ecosystems have increased with a rise in fertilizer use and cultivation of nitrogen-fixing crops (Vitousek et al., 1997), a rise in emissions and atmospheric deposition poses

threats to biodiversity across the globe (Phoenix et al., 2006), and eutrophication remains an imminent threat to many vulnerable marine and freshwater ecosystems (Deegan et al., 2012; Diaz & Rosenberg, 2008; Peñuelas et al., 2013; Silbiger et al., 2018; Vitousek et al., 1997). In an Anthropocene era of urban expansion and global change (Grimm et al., 2008; Seto et al., 2012), few areas remain protected from direct human pressures (Venter et al., 2016). For example, roe deer may transport nutrients from fertilized fields to forest patches in Europe, significantly altering forest nutrient budgets (Abbas et al., 2012), and geese feeding in croplands can deposit high amounts of nutrients in wetlands (Kitchell et al., 1999). As far as humans increasing nutrient movement into otherwise protected areas by subsidizing animal diets, this remains a relatively unexamined eutrophication threat to remote or protected ecosystems.

The ability of seabirds, particularly gulls (*Larus* spp.), to readily supplement their diet by visiting human refuse sites and consuming anthropogenically derived food sources has been well documented (Ackerman et al., 2018; Blight et al., 2015; Fuirst et al., 2018; Langley et al., 2021; Navarro et al., 2016; Shaffer et al., 2017). As seabirds are a taxon of conservation concern (Croxall et al., 2012), the effects of anthropogenic diet subsidies (i.e., human refuse, fishery discards, and agricultural crops) on seabird populations' reproductive output, body condition, and health have garnered considerable attention (Annett & Pierotti, 1999; Auman et al., 2008; Duhem et al., 2008; Navarro et al., 2017; Ramírez et al., 2012; Weiser & Powell, 2010). However, the effects of anthropogenic diet subsidies on wildlife and surrounding ecosystems are varied (Oro et al., 2013). For example, food subsidies can often increase reproductive output and elevate population densities of a subsidized species (Plaza & Lambertucci, 2017). These population increases may result in reduced populations of sympatric species through spillover predation or competition (Ripple et al., 2013; Votier et al., 2010; West et al., 2016), a decoupling of standing predator–prey relationships (Rodewald et al., 2011), increases in nutrient outputs to surrounding ecosystems (Wilson et al., 2004), and shifts in plant communities (Vidal et al., 2000; Wal et al., 2008). The importance of seabird nutrient inputs to the ecosystems they nest on is well-documented, as is the increasing reach of urbanization and availability of anthropogenic food sources; however, understanding the effects of the coupling of these two phenomena remains in its infancy.

In the present study, we characterize anthropogenic foraging by a generalist seabird and explore bird-derived nutrient inputs on two uninhabited protected coastal islands found along the North American west coast. Western Gulls (*Larus occidentalis*, WEGU) are large carnivorous gulls found along the North American west coast, where they readily exploit anthropogenic food sources throughout their range (Pierotti & Annett, 1995, 2001; Shaffer et al., 2017). Many Western Gulls forage in urban areas during the nesting season (Annett & Pierotti, 1989), particularly those that nest on islands that are located closer to urban areas (Shaffer et al., 2017). Santa Barbara Island (SBIS) and Anacapa Island (ANIS), part of the Channel Islands National Park (California, USA), seasonally support various nesting seabirds, including dense aggregations of nesting Western Gulls (Carter et al., 1992).

Much of work on effects of disturbance on animal nutrient transfer has relied on large-scale passive diffusion models based on coarse values such as animal home range (e.g., Doughty et al., 2016) or stable isotope data to detect the total quantity of energy transfer (e.g., Young, McCauley, Dirzo, et al., 2010). However, there is increasing recognition of the potential value for integrating tools from animal movement with these other tool sets to get higher resolution information on identity and quantity of animal-mediated transfer of nutrients (Ellis-Soto et al., 2021). To this end, we utilize a combination of GPS loggers and stable isotope analysis to determine foraging patterns of breeding birds and collected soil samples to assess nutrient concentrations. Specifically, we investigate (1) the extent to which breeding gulls across both islands feed on anthropogenic food sources, (2) shifts in soil nutrients before and after the gull breeding season, and (3) the proportion of gull-derived nutrient inputs that are likely being subsidized by anthropogenic foraging. We hypothesize that anthropogenic subsidies may be a major component of island nutrient cycles, particularly for islands closer to mainland urban areas. Our study highlights how anthropogenic subsidies may be modulating nutrient inputs to a protected island ecosystem.

METHODS

Study sites

This study was conducted on ANIS and SBIS, the two smallest of the Channel Islands off the coast of Southern California (United States). ANIS is composed of three islets with a total area of 2.9 km^2 and is 20 km from the mainland (Schoenherr et al., 2003). SBIS has an area of 2.6 km^2 and is 61 km from the mainland (Schoenherr et al., 2003). Both islands are currently managed as part of the Channel

Islands National Park and host large breeding colonies of various seabird species, including Western Gulls (Carter et al., 1992). ANIS and SBIS are both dominated by nitrogen-limited annual grasslands and island sage scrub; they receive low annual precipitation, which occurs primarily during the winter months (nonbreeding season of seabirds). As they are both uplifted islands, they receive few marine wrack subsidies to island soil and have no springs or streams that would supply a flow of nutrients (Halvorson, 1992; Halvorson et al., 1988; Schoenherr et al., 2003; Subalusky & Post, 2019; Vitousek et al., 1997).

Nutrient sources and soil nutrients

We assessed nutrient sources and sampled soil on ANIS and SBIS in 2019 to test for concentrations of available nitrogen and phosphorus, as these soil characteristics are associated with nutrient deposition in seabird colonies (Ellis, 2005; Young, McCauley, Dunbar, et al., 2010). Sampling locations were evenly distributed across the two islands and were selected based on nesting Western Gull densities from previous breeding seasons (personal communication with National Park Service) to approximate an equal distribution of high and low bird density sites at each island. Eight sites were sampled on East ANIS, with a minimum distance of 100 m between sites, and 11 sites were sampled throughout SBIS, with a minimum distance of 200 m between sites (Appendix S1: Figure S1).

Nutrient sources

We measured seabird density and the presence of nitrogen-fixing plants to account for different drivers of nutrient concentrations at each site. For measuring seabird density, we conducted nest counts (five 10 m × 4 m belt transects) at each site in August 2019. We conducted five vegetation surveys using quadrats (1 m × 1 m) at each site to assess the presence and percent cover of nitrogen-fixing plant species (family: Fabaceae) that could be driving nitrogen inputs to study site soil. Quadrats were arranged with one quadrat in the center of the survey site and one quadrat each at 5 m north, south, east, and west from the center quadrat.

Soil nutrients

At each site on each island, we collected four random samples of topsoil (10 cm) within a 200-m^2 area at two separate time points: early in the nesting season when gulls are establishing territories and starting to build

nests ("early breeding season," April 2019), and once most chicks had hatched ("late breeding season," July/August 2019). Soil samples were dried at the field site, homogenized (by site), and sieved (<2 mm) upon return to lab facilities at UC Santa Barbara. Soil samples were then evaluated for concentrations of available nitrogen (NO_3-N and NH_4-N) (cadmium reduction method; Dahnke & Johnson, 1990) and phosphorus (Mehlich, 1984) at Brookside Laboratories (New Bremen, OH, USA).

Statistical analysis

We used linear mixed-effects models fit by maximum likelihood to explain variations in phosphorus, ammonia, and nitrate across islands, between sampling periods, and with varying gull density. Full models were specified for each soil nutrient using the lme4 package (Bates et al., 2015) with nutrient concentration as a response variable; island, sampling period (early or late breeding season), nest count, and the interaction of all variables were fixed effects, and site was a random effect (Appendix S1: Table S1). Best-fit models were selected according to small-samples corrected Akaike information criterion (AIC_c) using the package MuMIn (Barton, 2020). All computations were done in R using R Studio and the tidyverse package (R Core Team, 2020; RStudio Team, 2020; Wickham et al., 2019).

Foraging behavior

We studied Western gull foraging behavior during the 2016 incubation period (April–May). Feather and blood samples were collected from 137 adult gulls (84 on ANIS and 53 on SBIS) for stable isotope analysis, and a subset of 52 birds was equipped with GPS trackers. All sampled and tracked birds were captured from nests containing 2–3 eggs with a snare carpet or single foot snare. Birds that were sampled but not tracked were only captured once and sampled for feathers (two breast feathers and two underwing coverts) and blood (between 0.5 and 2.0 ml of blood from the brachial vein) for stable isotope analysis. We also measured body mass with a spring balance (±20 g), and culmen, tarsus, and skull lengths using calipers (±0.1 mm). Nine of the sampled gulls regurgitated when captured, and these opportunistic diet samples were also collected in the field.

A total of 52 gulls (31 on ANIS and 21 on SBIS) were equipped with a GPS logger (igotU GT-120, Mobile Action Technology) that recorded a GPS location every 30–60 s with an accuracy of 2–4 m. Upon initial capture, a logger was attached to the bird's three central tail feathers using Tesa adhesive tape (Tesa Tape, Charlotte, NC, USA). The GPS loggers were removed from their original plastic casing to decrease total mass and then encased in waterproof heat-shrink tubing. Loggers were deployed for a minimum of 24 h before attempting recovery using the capture methods mentioned above. GPS loggers were recovered from 26 gulls on ANIS (83%) and 17 gulls on SBIS (80%). Although loggers were recovered as quickly as 24 h later, mean deployment was an average of 60+ hours per bird, and total deployment time was limited by tracker battery life (total of 2778 h of tracking data). Most gulls conducted a single foraging excursion per day (as observed in Cimino et al., 2022; Shaffer et al., 2017). In addition to removing the GPS logger upon recapture, we conducted the sampling protocol for feathers, blood, and morphometric data described above. All blood samples were kept cold, and blood was centrifuged within 2 h of collection and then kept frozen in liquid nitrogen until it returned to the laboratory at UC Santa Barbara.

Tracking data analysis

All tracking data were postprocessed and analyzed according to the methods described in Shaffer et al. (2017). In brief, erroneous locations were removed using an iterative speed filter, and foraging trips were identified as any trip where a gull traveled farther than 1 km from the island for durations that exceeded 30 min. Foraging excursions were further characterized by calculating the total distance traveled, maximum range, and duration of each foraging trip. In addition, we determined foraging trip destinations (mainland/urban or pelagic and intertidal) and proportion of time spent away from the island. All trip destinations were evaluated by comparing whether a gull visited the mainland or remained at sea using high-resolution coastline data (Global Self-consistent, Hierarchical, High-resolution Shoreline Database; gshhs v.2.3.5). If a foraging trip crossed over onto land, destinations were further evaluated by plotting tracks over Google Earth (Google Earth Pro v.7.1.7.2600) to pinpoint specific destinations that gulls visited within urban areas and/or shoreline. We also determined the frequency of urban foraging trips as a proportion of the total number of trips conducted by each gull and whether foraging by each bird was mixed (some trips to urban areas, some to natural areas), wholly urban (all trips to urban areas), or marine (all trips to natural areas). All track analyses were performed using purpose-built routines and functions in the Mapping and Machine Learning and Statistics toolboxes in MATLAB R2016b (MathWorks, Natick, MA, USA).

Stable isotope analysis

We conducted stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ isotope ratios in feather and blood samples to explore potential foraging differences between the two islands and across the breeding and nonbreeding season, as stable isotope values can be useful indicators of diet. For seabirds foraging in marine environments, $\delta^{15}N$ values reflect foraging trophic level, where higher $\delta^{15}N$ values indicate a higher trophic level, and $\delta^{13}C$ values indicate food source, where enriched $\delta^{13}C$ indicates inshore food sources and lower values indicate offshore food sources (Hobson et al., 1994). In the case of seabirds foraging in marine and terrestrial environments, lower $\delta^{15}N$ values have been used to indicate increases in urban foraging (Blight et al., 2015; Lenzi et al., 2019; Osterback et al., 2015). Furthermore, isotopic signature of human food has been estimated using human hair samples from Southern California (e.g., Larson et al., 2020) and is very low in $\delta^{15}N$ values. Additionally, $\delta^{13}C$ values can be used to differentiate between anthropogenic diets and natural diets, where higher $\delta^{13}C$ values are indicative of a C_4 photosynthetic pathway, which is common in US corn-based food systems and distinct from the lower $\delta^{13}C$ values of natural vegetation, which primarily have C_3 photosynthetic pathways (Jahren & Kraft, 2008). In cases of wildlife foraging in terrestrial and marine systems, marine foraging $\delta^{13}C$ values are intermediate between those of C_3 and C_4 terrestrial foraging values, making it somewhat more difficult to distinguish between marine and anthropogenic foraging via carbon isotope values (Kelly, 2000).

We used isotopic signatures from gull plasma to infer diet during the breeding season, as the integration rate for plasma is high and isotope ratios represent a feeding period of ~3 days (Hobson, 2005). We also used isotopic signatures from feathers to infer longer time periods, as feathers have a much slower integration rate and isotopic ratios reflect diet at the time of feather growth after a molting period (Hobson, 2005; Hobson & Clark, 1992). For Western Gulls, molting occurs twice a year in the early fall and late winter and lasts at least 2 months; thus, feather isotopic ratios represent the nonbreeding season and the very early and late portions of the breeding season, or a year-round diet (Howell & Corben, 2000; McCaskie, 1983). Prior to isotopic analysis, plasma was freeze-dried, homogenized, and ~0.5 mg was loaded into tin capsules. Feathers from each gull were first cleaned of surface lipids and contaminants using a 2:1 chloroform and methanol solution, followed by two methanol rinses, dried, cut into small fragments, and ~0.5 mg were loaded into tin capsules. Tin capsules were sent to the University of California, Davis Stable Isotope Facility for analysis. Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Cheshire, UK). We created isotopic biplots ($\delta^{13}C$ and $\delta^{15}N$) to visualize the differences in isotopic space for the breeding season (plasma) and year-round (feather) diets of the two colonies. Additionally, we compared mean isotopic values of plasma and feather tissue across colonies using a Wilcoxon rank-sum test and generated Bayesian standard ellipses (40% confidence level) for each colony and tissue (feather or plasma) using the SIBER package in R to estimate isotopic niche space (Jackson et al., 2011; R Core Team, 2020). We compared the size of the ellipses by fitting Bayesian models adjusted for small sample sizes (SEAc) and calculated overlap in ellipse area between the two colonies, which can be used to determine overlap in diets and niche space (Eurich et al., 2019). All computations were conducted using R Studio and the tidyverse package (RStudio Team, 2020; Wickham et al., 2019).

Guano deposition estimates

We estimated the amount of guano being deposited onto the island soil by Western Gulls on ANIS and SBIS during the breeding season using tracking data, known fecal deposition rates, and known breeding population size for the two islands (Table 1).

The time spent by Western Gulls on their nesting grounds varies throughout the breeding season, so we differentiated estimated guano deposition between the incubation period and first 5 days of brooding (d_i) and the chick-rearing phase (d_r), as adults spend a significant amount of time at the nest during incubation and early brooding (Shaffer et al., 2017), but reduce this time allocation during chick rearing (Pierotti & Annett, 1995). We estimated the average amount of time (t_i) gulls spent on the island over a 24-h period during incubation and early brooding using tracking data. Throughout the chick-rearing period, adult Western Gulls are thought to decrease their time at the nest to less than 50% of the day, so we used 40% of the day (sensu Pierotti & Annett, 1995) as the value for time spent on the island during the chick-rearing period (t_r). As we were unable to determine the fecal deposition rate (f) for Western Gulls, we used the known fecal deposition rate of *Larus argentatus*, a similarly sized congener, to approximate deposition by Western Gulls (Portnoy, 1990). Fecal deposition (D_c) onto each island was then calculated as:

$$D_c = \frac{n_c[(d_i \times t_i \times f) + (d_r \times t_r \times f)]}{a},$$

where n_c represents the number of breeding adults at each colony (National Park Service, 2016), a represents the area

TABLE 1 Variables used for estimating guano deposition by Western Gulls on Anacapa Island (ANIS) and Santa Barbara Island (SBIS).

Variable	Definition	Value
n_c	No. breeding birds	
ANIS		10,000
SBIS		14,000
d_i	Duration of incubation period	37 days
t_i	Average hours per day spent on island during incubation	
ANIS		20.20 h
SBIS		17.55 h
f	Defecation rate	39.4 g/day[a]
d_r	Duration of chick-rearing period	42 days
t_r	Estimated number of hours per day spent on island during chick rearing	9.6 h[b]
a	Island area	
ANIS		283 ha
SBIS		260 ha

[a]Based on the deposition rate of the congener, *Larus argentatus* (Portnoy, 1990).

[b]An approximation of 40% of day based on Pierotti and Annett (1995).

of each island (Table 1). Data from a congener suggests gull guano may be composed of 5.5% nitrogen (Bird et al., 2008), which we used to estimate the amount of nitrogen deposition. Incorporating the tracking data, we estimated what proportion of the estimated nutrient deposition occurring on each island may be subsidized by urban foraging.

RESULTS

Nutrient sources and soil nutrients

To understand potential drivers of any differences in nutrients across sites, we surveyed seabird density and nitrogen-fixing plant density. We found a higher density of nests per site at ANIS (mean $\pm$ SD: 35.12 ± 17.88 nests/200 m^2) than at SBIS (9.09 ± 5.87 nests/200 m^2). We found no nitrogen-fixing plants of the family Fabaceae in any of our vegetation survey quadrats on either island.

We observed significant differences in soil nutrients between sampling periods and between the two islands (Figure 1). For NO$_3$-N concentration, we found no significant interactions among fixed effects, and the best-fit model included only sampling period as a fixed effect with higher concentrations in the late breeding season sampling period (Figure 1, Table 2). The two next best-fit models (ΔAIC < 2) include (1) island and sampling period and

(2) nest count and sampling period as fixed effects (Appendix S1: Table S4), though there were no significant differences in NO$_3$-N among island or nest densities. All fixed effects included in our full model were significant predictors of the concentration of NH$_4$-N: these included island, sampling period, nest count, and their interactions (island $\times$ sampling period; island $\times$ nest count; nest count $\times$ sampling period), with small increases in concentration with increased nest density, higher concentrations of NH$_4$-N on SBIS, and increases in concentration in the later sampling period (Figure 1, Table 2). The two next best-fit models (ΔAIC < 2) included (1) all fixed effects but did not include any fixed-effect interactions and (2) only the sampling period as a fixed effect (Appendix S1: Table S4). Phosphorus concentration was best predicted by a model that includes island and sampling period as significant fixed effects, with a higher concentration during the later sampling period and overall higher phosphorus concentrations on SBIS (Figure 1, Table 2). The next best-fit models (ΔAIC < 2) include (1) island, sampling period, and the interaction of island and sampling period as fixed effects and (2) island, nest count, and the interaction of nest count and island as fixed effects (Appendix S1: Table S4).

Foraging behavior

We analyzed GPS logger data from 43 gulls and a total of 2778 h of tracking data throughout the course of the study. Average tracking duration (the number of hours for which the bird had a tag with an operational battery attached) and number of trips logged per bird were 60.36 ± 22.85 h and 3.23 ± 1.45 trips on ANIS and 65.09 ± 24.27 h and 6.18 ± 4.43 trips on SBIS.

We found variability in foraging behavior (defined as searching behavior for the purpose of this study) across the two colonies and between trips across individual birds. On ANIS, the mean proportion of foraging trips to urban areas was 0.41 ± 0.36, with 4 (of 26) birds conducting all their foraging in urban areas and 8 conducting all their foraging in pelagic or intertidal habitat of other Channel Islands. On SBIS, the mean proportion of foraging trips to urban areas was 0.09 ± 0.18, with no birds conducting all their foraging in urban areas and 13 (of 17) birds conducting all their foraging in pelagic or intertidal habitat of other Channel Islands (Figure 2). No birds from either island conducted trips to intertidal habitat on the mainland.

Regurgitations that occurred during handling ($n = 9$) indicated that gulls had consumed a variety of marine food items, including barnacles, crabs, fish, squid, and kill, and anthropogenic items like chicken, hot dogs, tacos, and other processed produce and meats.
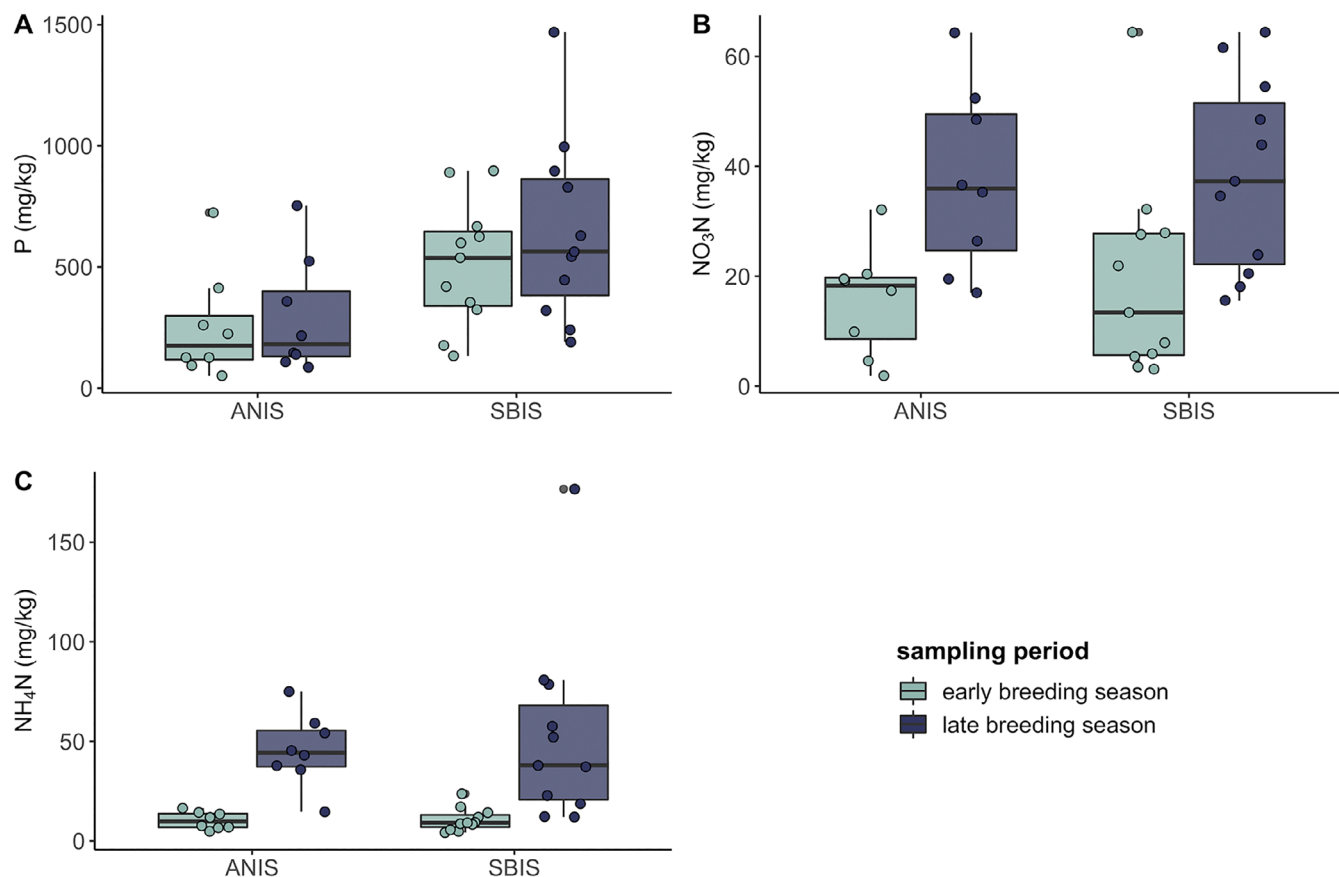
FIGURE 1 Concentrations of phosphorus (A), nitrate (B), and ammonia (C) at Anacapa Island (ANIS) and Santa Barbara Island (SBIS) in the early and late stages of the Western Gull breeding season.

TABLE 2 Best-fit linear mixed models for predicting pH and concentrations of phosphorus (P), nitrate nitrogen (NO_3-N), and ammonium (NH_4-N) in soil at two *Larus occidentalis* nesting islands.

Fixed effects	NO_3-N			NH_4-N			P		
	Estimate	SE	*t*	Estimate	SE	*t*	Estimate	SE	*t*
Intercept	17.8	3.66	4.87	6.83	18.29	0.38	223.97	100.28	2.23
Nest count	...	...	...	0.1	0.47	0.21	...	...	...
Island (SBIS)	...	...	...	3.44	22.32	0.15	307.6	129.78	2.37
Sampling period (late)	20.25	4.06	4.99	11.91	25.87	0.46	95.32	34.94	2.73
Nest count × island	...	...	...	−0.06	1.29	−0.04	...	...	...
Nest count × sampling period	...	...	...	0.67	0.66	1.01	...	...	...
Island × sampling period	...	...	...	−15.83	31.56	−0.5	...	...	...
Nest count × island × sampling period	...	...	...	4.46	1.82	2.45	...	...	...

Note: Variance and SD values, respectively, for the random effect of site are nitrate nitrogen: 97.74, 9.89; ammonium: 0, 0; and phosphorus: 72,207, 268.7.
Abbreviation: SBIS, Santa Barbara Island.

Stable isotope analysis

We collected samples for stable isotope analysis from 137 Western Gulls across both colonies (Appendix S1: Table S6). There was a significant island population difference between $\delta^{15}N$ and $\delta^{13}C$ values of plasma samples from ANIS and SBIS ($\delta^{15}N$: $W = 380.5$, $p < 0.005$; $\delta^{13}C$: $W = 1161$, $p < 0.005$), but no significant difference between values of feather samples from the two islands ($\delta^{15}N$: $W = 1918.5$, $p = 0.3$; $\delta^{13}C$: $W = 1945$, $p < 0.4$).
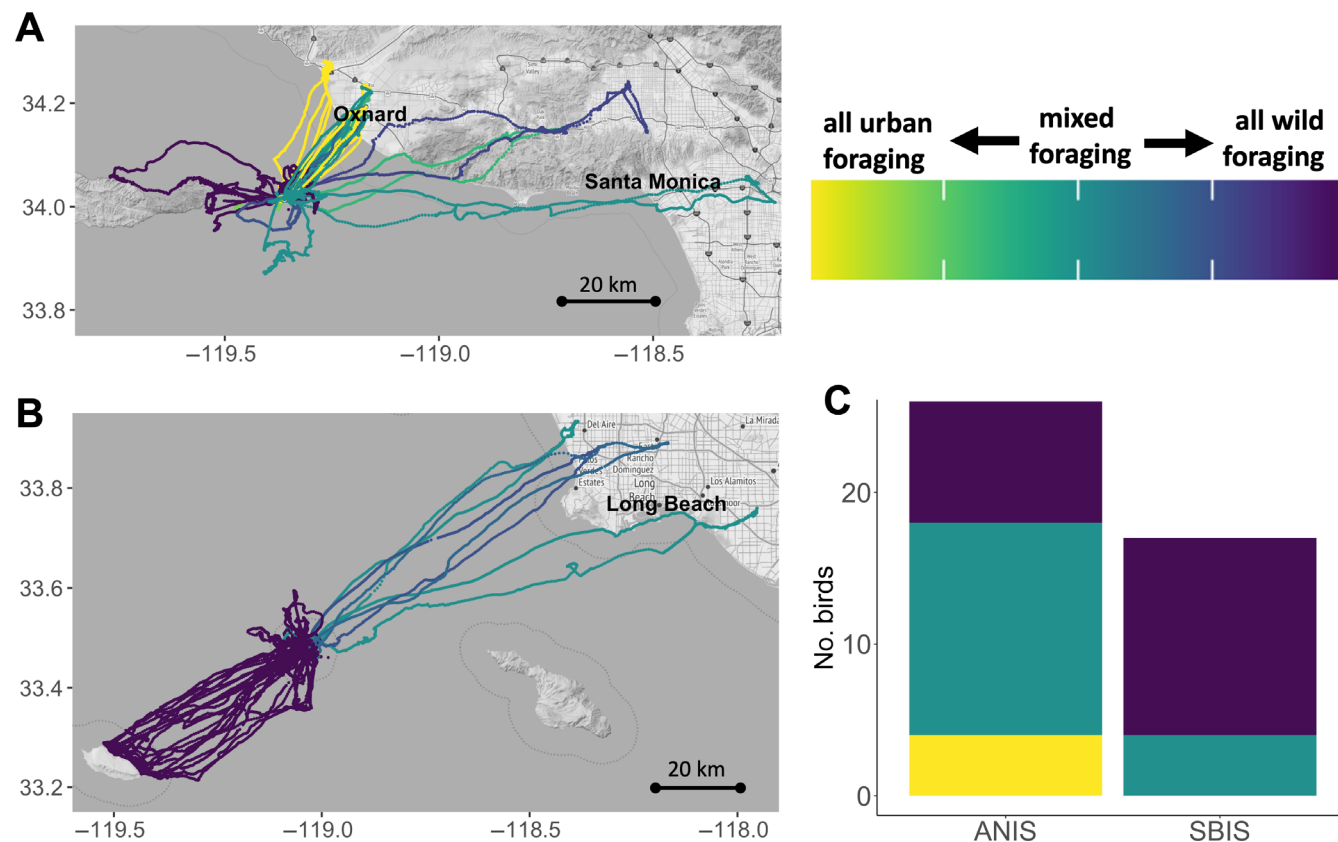
FIGURE 2 Foraging and movement behavior of 43 *Larus occidentalis* nesting on (A) Anacapa Island (ANIS) and (B) Santa Barbara Island (SBIS). Color of track denotes frequency of anthropogenic foraging (proportion of foraging trips to mainland out of all foraging trips observed) by each individual bird, where light yellow tracks denote higher frequency of anthropogenic foraging and dark purple tracks denote a more marine-sourced diet. Individual birds are classified and counted according to their foraging behavior (C): all urban foraging, a mix of urban and wild foraging, and all wild foraging.

Along the δ^{15}N axis, the mean value for plasma samples from ANIS (13.94 ± 1.82) was 1.28 (‰) lower than plasma samples from SBIS gulls (15.22 ± 1.44), which may be indicative of higher trophic level/marine foraging by nesting SBIS gulls; however, there was substantial overlap between the two islands (Appendix S1: Table S6, Figure 3A). A similar, although less pronounced pattern was observed along the δ^{13}C axis, where mean value of plasma samples from ANIS gulls (−19.91 ± 0.71), was 0.47 (‰) higher than the plasma samples from SBIS gulls (−20.38 ± 0.80), indicative of more C_4/anthropogenic foraging by nesting ANIS gulls (Appendix S1: Table S6, Figure 3A). For feather samples, mean isotope values (δ^{13}C, δ^{15}N) were δ^{13}C: −17.41 ± 0.86, δ^{15}N: 12.92 ± 2.23 for ANIS gulls, and δ^{13}C: −17.3 ± 0.68, δ^{15}N: 13.25 ± 2.17 for SBIS gulls (Appendix S1: Table S6).

Plasma samples from gulls on ANIS had a higher standard ellipse area (4.08) than those on SBIS (3.75), and the area overlap of 1.61 represents 39% of the isotopic niche space occupied by ANIS gulls and 42% of that occupied by SBIS gulls (Figure 3B). For feather samples, gulls from ANIS had a higher standard ellipse area (5.71) than those

from SBIS (4.65), and had an increased overlap area of 4.52, which accounted for 77% of the isotopic niche space of ANIS gulls and 95% of that of SBIS gulls (Figure 3B).

Guano deposition estimate

Based on the tracking data, we calculated the average amount of time per day gulls spent over each island during the incubation period: 20.20 ± 3.32 h on ANIS and 17.69 ± 55 h on SBIS. Using the values referred to above for duration of the incubation and chick-rearing stages, breeding bird population, defecation rates, and island size (Table 1), we estimated a Western Gull breeding season guano deposition of 66.74 kg/ha for ANIS and 93.04 kg/ha for SBIS. From these, we estimated nitrogen deposition of 3.67 kg/ha for ANIS and 5.11 kg/ha for SBIS using estimates of nitrogen content found in gull guano. Concomitantly, we estimated that 41% of gull nutrient deposition on ANIS and 9% of gull nutrient deposition on SBIS is likely a human subsidy vectored by urban foraging gulls during the breeding season.
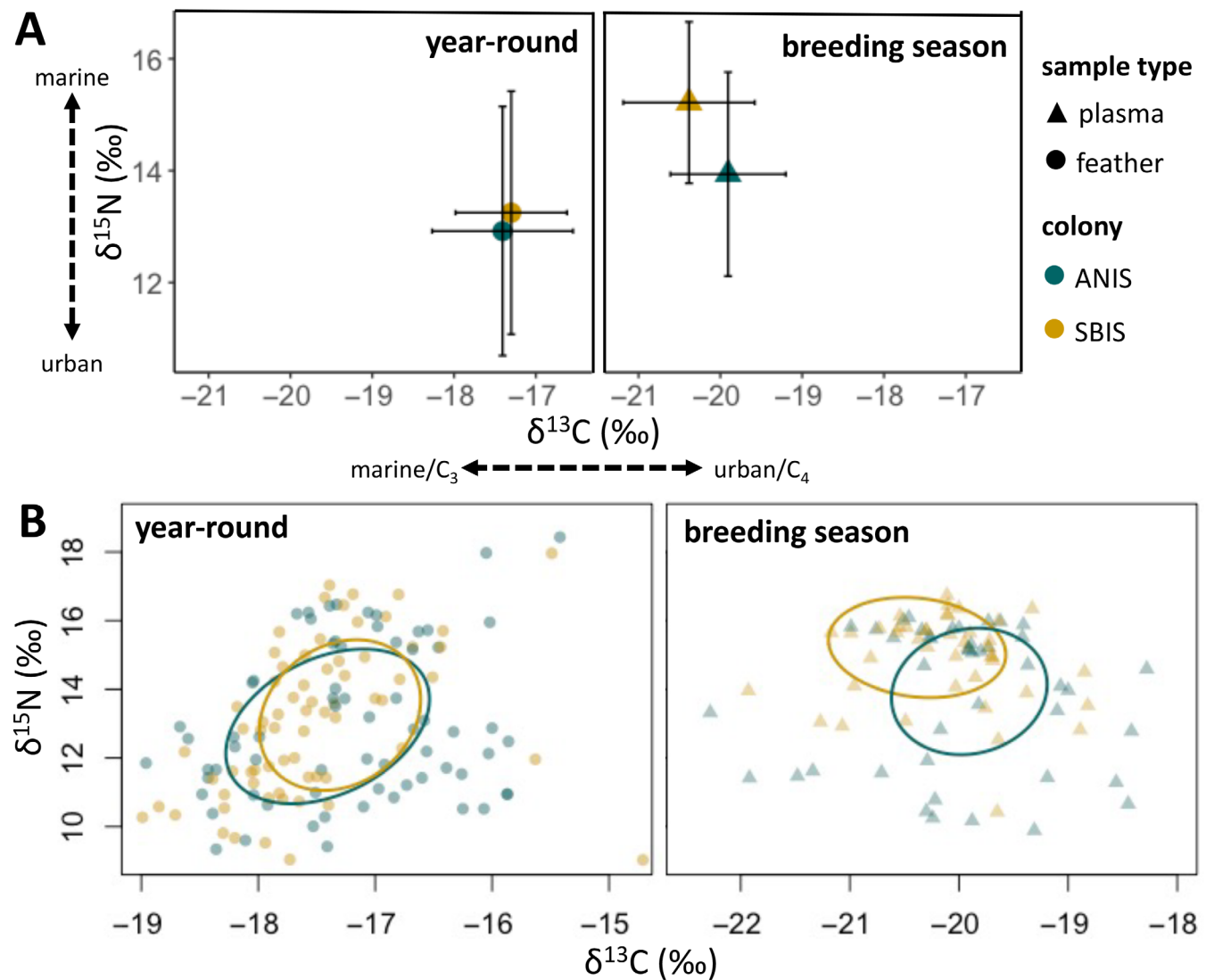
FIGURE 3 $\delta^{15}N$ and $\delta^{13}C$ (‰) signatures of plasma and feather samples collected from Western Gulls (*Larus occidentalis*) nesting on Anacapa Island (ANIS) and Santa Barbara Island (SBIS), where feather samples more closely approximate year-round diet and plasma samples approximate breeding season diet. (A) Biplot of isotopic signatures where points are group means and error bars represent standard deviations. Dashed arrows along *x*- and *y*-axes represent expected directionality of marine and urban foraging. (B) Isotopic area overlap of plasma samples and feather samples. Standardized Bayesian ellipse areas are depicted by solid lines.

DISCUSSION

This study provides an initial exploration into the role that anthropogenic subsidies to seabird diets may have in mediating the nutrient budgets of two coastal islands. We found an increase in nutrient concentrations, particularly nitrogen, in sampled soil following the Western Gull nesting season, suggesting that breeding gulls are leaving a measurable nutrient footprint on the island soil (Figure 1). Increases in nitrogen and phosphorus concentrations are known to be associated with nutrient deposition by colonial seabirds, and these increased concentrations can be relevant at local and global scales (Baumberger et al., 2012; Otero et al., 2015, 2018).

Gull breeding colonies have been found to dramatically increase concentrations of phosphorus and nitrogen in island soils, lakes, and ponds across various continents (García et al., 2002; Hogg & Morton, 1983; Martín-Vélez et al., 2019; Otero et al., 2015; Portnoy, 1990; Vidal et al., 1998). Because we found no presence of legumes in any of our sites, and because high islands have limited direct input of algal wrack, nutrient inputs to the island terrestrial ecosystem are likely only arriving through aeolian dust, shore drift of algae wrack vectored inland by terrestrial invertebrates, and vectored by seabirds from their foraging grounds (Halvorson et al., 1988; Lawrence & Neff, 2009; Polis & Hurd, 1996; Subalusky & Post, 2019; Vitousek et al., 1997). Aeolian dust is likely

small in magnitude compared to estimated inputs from guano, and furthermore, it would be unlikely to vary across these spatially close islets or across these sampling periods. Thus, seabirds are likely to be the dominant source of nutrients to these sites and explain variation in nutrient profiles seen across sites and seasons.

Our estimated quantity of guano deposited on the islands annually by Western Gulls is 66.74 kg/ha for ANIS and 93.04 kg/ha for SBIS, which, when compared to commercial agriculture, represents about 50% of the average global fertilizer consumption in 2018 (136 kg of fertilizer per hectare of arable land) (FAO, 2020). Additionally, our tracking data analysis revealed that 9%–41% of nutrient input is likely derived from anthropogenic food sources (Figure 2A,B), suggesting a significant anthropogenic impact on the fundamental nutrient budget of these fully protected islets that are typically viewed as remote wilderness. This amounts to an estimated 27 kg of anthropogenically subsidized, nutrient-rich guano per hectare being deposited onto the islands during the breeding season.

Although these estimates are substantial, our estimate of guano deposition by Western Gulls is lower than other estimates of total seabird inputs on nesting islands (Smith & Johnson, 1995; Young, McCauley, Dunbar, et al., 2010). However, these previous estimates included more variation in seabird species and with larger nesting populations (Smith & Johnson, 1995, Young, McCauley, Dunbar, et al., 2010). Moreover, as we did not include guano inputs from nonbreeding gulls, juveniles, and recently hatched gull chicks in our calculation, nor inputs from gulls that frequent the islands during the nonbreeding season, our estimate of guano input likely underestimates total inputs by Western Gulls to these islands. Furthermore, our estimates were based on the defecation rate of a congener as we were unable to adequately quantify the defecation rate for Western Gulls, and future work should include estimates of defecation rates for Western Gulls. Additionally, our model did not account for gut-passage time, a parameter that would improve guano deposition estimates; however, incorporating these complexities would be an important step for future work. Finally, we were unable to determine if any of our tracked gulls foraged on fishery discards while at sea, which is another common source of anthropogenic subsidy for seabirds; therefore, inputs of anthropogenically subsidized guano are likely an underestimate as well (Bartumeus et al., 2010).

Interestingly, we found that SBIS had significantly higher concentrations of phosphorus than ANIS during each of the sampling periods (Figure 1, Appendix S1: Table S2). Differences in nutrient concentrations across islands could also be a result of dietary differences

between the two colonies of Western Gulls, as our tracking data suggest that during the incubation period, gulls on ANIS foraged in urban areas more frequently than those on SBIS (Figure 2). In two additional studies examining the nutrient content of guano in two separate populations of Herring Gulls, *L. argentatus*, gulls with diets rich in fish had higher concentrations of phosphorus and an order of magnitude less nitrogen than those that frequently consumed human refuse (Gould & Fletcher, 1978; Portnoy, 1990). Although we did not explicitly explore shifts toward higher phosphorus guano or soil in our study, our results suggest that further work elucidating the ecological consequences of shifting seabird guano quality may be relevant to conservation efforts, as increases in soil nitrogen concentration and shifts in soil stoichiometry in similar systems have resulted in increases in exotic and invasive species (Fenn et al., 2010; Vallano et al., 2012).

Population-level differences in foraging strategies between neighboring colonies during the breeding season have been previously documented for Western Gulls (Clatterbuck et al., 2021; Shaffer et al., 2017). Differences in the prevalence of urban versus marine foraging are likely explained by the distance to the mainland (Cockerham et al., 2019; Pierotti & Annett, 2001; Shaffer et al., 2017), as the distance to the nearest mainland point from ANIS is 20 km, compared to 61 km from SBIS. Although we did not track individual birds for long enough durations to assess individual specialization, we did find that some gulls exhibited preferences for wholly marine or wholly urban diets during the tracking period (Figure 2C). Differing foraging strategies between individuals could also be a result of competition among colony members over marine resources near the nesting island (Ashmole, 1963) or a result of behavior learned from parents (Annett & Pierotti, 1999). It is important to note, however, that our GPS tracks represent gull foraging only during the incubation period, and Western Gulls are known to switch dietary preferences throughout the breeding season, particularly during the chick-rearing period (Annett & Pierotti, 1989). Additionally, as we did not directly collect and analyze fecal samples from tracked individuals to compare nutrient loads in gulls that foraged in each of the environments, we cannot ascertain whether foraging differences may be driving these differences in soil nutrients.

Our plasma sample isotope analysis, complemented by gull behavior from the tracks, shows evidence of a difference in proportion of anthropogenic foraging between colonies, with SBIS showing higher $\delta^{15}N$ stable isotope values consistent with lower consumption of human food refuse (demonstrated elsewhere to have low $\delta^{15}N$ values) (Figure 3). However, the results of feather stable isotope

analysis indicate that these differences diminish during the nonbreeding season (Figure 3B). Without tracking individuals during the nonbreeding period, it is unclear whether the trend we observed of greater urban foraging in gulls from ANIS is maintained after the breeding period when they are not tied to a central place. However, there is evidence of Western Gull numbers increasing around refuse dumps in winter months, suggesting that Western Gulls spend more time foraging in urban environments during the nonbreeding season (Spear, 1988). Additionally, the mean feather $\delta^{15}N$ stable isotope values for both islands (SBIS: 13.25 ± 2.17, ANIS: 12.92 ± 2.23) are lower than those reported for feathers of gulls presumed to be foraging on a mixed diet of anthropogenic and marine sources, further suggesting that our samples reflect a shift towards increased urban foraging by SBIS gulls (Blight et al., 2015; Osterback et al., 2015). If the trend we observed in urban foraging between colonies is the result of colony distance to the mainland, completion of breeding and thus a departure from nesting island allow for a shift toward a more urbanized diet. It is also possible that a diet switch may be triggered by variations in oceanic productivity and marine resource availability (Cimino et al., 2022), as the Santa Barbara Channel is most productive during spring and least productive during fall and winter (Brzezinski & Washburn, 2011; Pierotti & Annett, 2001). Thus, anthropogenic foraging is likely providing important subsidies even to SBIS gulls that primarily forage in marine habitats during the breeding season. The influence of anthropogenic diet subsidies on nesting island soils may therefore reach beyond the direct deposition of guano after an urban foraging trip, but by supplementing diets of these birds during the nonbreeding season.

Our results show that there is a considerable difference in foraging preferences of Western Gulls during the incubation period between ANIS and SBIS, which could lead to differences in soil phosphorus concentrations; however, other differences between the islands could also play an important role in shaping soil nutrient profiles. For example, differences in soil types, precipitation, and topography could account for differing soil chemistry across the islands (Sims & Pierzynski, 2005; Tiessen, 2008). Differing influences of humans could also account for these differences in soil chemistry (Tiessen, 2008), as both ANIS and SBIS were historically inhabited by the Chumash and Tongva people, respectively (Perry et al., 2019; Rick, 2006), and share a more recent history of livestock ranching (Rick et al., 2014). This latter human presence resulted in overgrazing and the introduction of non-native species, which led to dramatic vegetation shifts and erosion, both of which can affect soil quality and nutrient retention (Rick et al., 2014; Tiessen, 2008). It is not certain; however,

if the histories of human presence on the islands differ enough to result in such drastic difference in soil profiles. Furthermore, both islands host colonies of other species of nesting seabirds, and guano deposition from other seabirds that nest on the islands could contribute to variation in soil chemistry as excreta from different species can vary in total phosphorus content (Carter et al., 1992; Otero et al., 2015). As Western Gulls are the most abundant nesting seabird on the islands (excluding seabirds that nest on cliff faces and thus do not contribute guano to island soil), it is not likely that other seabirds may be driving these differences in soil nutrient profiles; however, future studies should consider inputs by other seabirds (Carter et al., 1992; National Park Service, 2016).

As in much of conservation biology, this study is limited by a lack of baseline knowledge. In this case, we lack historical baselines of Western Gull population abundance. Without such data, it is impossible to know whether anthropogenic subsidies are buffering the effects of depleted natural food sources and maintaining historical levels of nutrient inputs to the islands or whether they are creating an artificially subsidized nutrient budget. However, the implications are clear for other systems where long-term population trends of commensal species are better established. For example, on the Mediterranean and Atlantic Islands, substantial increases in seabird populations subsidized by anthropogenic foraging have resulted in a greater influx of nutrients to terrestrial habitats, which has led to plant species turnover and persistence of invasive species (Baumberger et al., 2012; Otero et al., 2015; Vidal et al., 2000). Additionally, anthropogenic diet subsidies may alter not only the amount of bird-derived deposition to an island but also the quality of the guano itself. As previously described, a shift toward more urbanized diets could lead to increased nitrogen content and reduced phosphorus in guano deposited on nesting islands, which could result in increased biomass of invasive plants (Fenn et al., 2010; Gould & Fletcher, 1978; Portnoy, 1990; Vallano et al., 2012). Restoring native plant communities has been an extensive ongoing effort on the Channel Islands (Adams et al., 2009; Jacques et al., 2005); thus, any dramatic increases in nitrogen inputs will be important for ongoing management efforts.

This study has focused only on the effects of these commensal birds on nutrient budgets; however, it is likely that these birds vector many other potentially dangerous biotic and abiotic items to these protected systems. By frequenting urban areas, and more specifically landfills, gulls can concentrate contaminants, microplastics, and introduce foreign microbes to these protected areas, such as the Channel Islands National Park, in addition to contaminating watersheds and beaches frequented by humans (Cockerham et al., 2019; Converse et al., 2012;

Dolejska et al., 2007; Provencher et al., 2018). Finally, all of these effects are likely to extend beyond the island's terrestrial ecosystem. While conducting our work, we observed that many gulls defecate shortly after taking flight, which, in cases where nests are located close to the shoreline, would result in guano deposition along the intertidal and not on the island itself. Like terrestrial ecosystems, bird-derived nutrient inputs can also play an important role in shaping intertidal communities (Wootton, 1991).

Our research highlights the importance of the large shadow that human activity can cast on nutrient dynamics of even seemingly isolated and protected ecosystems. We observed a difference in the amount of urban foraging between breeding gulls on each island, with high levels of urban foraging on ANIS. Additionally, we measured an increase in nitrogen and phosphorus concentrations in the soil of both islands following the gull nesting season. Finally, we estimated the amount of nutrient deposition on the islands that may be derived from urban sources due to anthropogenic foraging by gulls. Given that whole-scale ecosystem change is known to occur with the loss of animal vectored subsidies, this work argues for more focus on potential ecosystem-scale effects of animal vectored anthropogenic subsidies in wild spaces. In areas where generalist animals are foraging in urban areas, future research should explore whether similar impacts due to anthropogenic foraging are already occurring, particularly in areas where considerable effort has been dedicated to conservation. For example, in these study sites—the ANIS and SBIS—where restoration and preservation of wilderness is a priority, it is important to clarify how these anthropogenic subsidies are altering these sensitive ecosystems (National Park Service, 2017).

Wildlife that exploits anthropogenic food sources can link urban and human-modified areas with even remote and relatively undisturbed areas. As the human footprint continues to expand, it is becoming increasingly clear that no system is out of the reach of human influence. Thus, continuing to understand how urban foraging can affect not only the species feeding on anthropogenic diets but also the ecosystems they inhabit is essential for managing ecosystems in the Anthropocene.

CONFLICT OF INTEREST
The authors have no conflict of interest to disclose.

DATA AVAILABILITY STATEMENT
Data (Guerra et al., 2022) are available from Dryad: https://doi.org/10.25349/D9J31X.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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