



Recovery of a marine keystone predator transforms terrestrial predator–prey dynamics

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Sea otters (*Enhydra lutris*) and wolves (*Canis lupus*) are two apex predators with strong and cascading effects on ecosystem structure and function. After decades of recovery from near extirpation, their ranges now overlap, allowing sea otters and wolves to interact for the first time in the scientific record. We intensively studied wolves during 2015 to 2021 in an island system colonized by sea otters in the 2000s and by wolves in 2013. After wolf colonization, we quantified shifts in foraging behavior with DNA metabarcoding of 689 wolf scats and stable isotope analyses, both revealing a dietary switch from Sitka black-tailed deer (*Odocoileus hemionus*), the terrestrial in situ primary prey, to sea otters. Here we show an unexpected result of the reintroduction and restoration of sea otters, which became an abundant marine subsidy for wolves following population recovery. The availability of sea otters allowed wolves to persist and continue to reproduce, subsequently nearly eliminating deer. Genotypes from 390 wolf scats and telemetry data from 13 wolves confirmed island fidelity constituting one of the highest known wolf population densities and upending standardly accepted wolf density predictions based on ungulate abundance. Whereas marine subsidies in other systems are generally derived from lower trophic levels, here an apex nearshore predator became a key prey species and linked nearshore and terrestrial food webs in a recently deglaciated and rapidly changing ecosystem. These results underscore that species restoration may serve as an unanticipated nutrient pathway for recipient ecosystems even resulting in cross-boundary subsidy cascades.

apparent competition | food webs | marine subsidies | predator–prey interactions

A widely recognized ecological phenomenon is the connection of ostensibly distinct systems through the transboundary movement of resources (1). Allochthonous subsidies such as marine resources commonly increase productivity of terrestrial systems through the transport of nutrients by physical or biotic agents, or through movement of organisms (1, 2), and may directly or indirectly affect terrestrial food webs and population dynamics (1, 3). The effect of allochthonous subsidies from a donor system depends upon characteristics of the consumer and the focal habitat; more mobile and generalist consumers inhabiting permeable ecosystem boundaries or landscapes with a higher edge to area ratio may receive increased subsidies (1, 4, 5). The magnitude and the timing of the availability of marine subsidies is also influential to predator–prey dynamics. Seasonal availability may result in prey switching, or temporarily satiate predators, easing pressure on resident prey (i.e., apparent mutualism) (6), whereas consistent availability is likely to decouple predator density from local prey availability, resulting in increased predation pressure on resident terrestrial prey (i.e., apparent competition, refs. 3, 7, and 8).

Marine subsidies to large mammalian predators have the potential to be particularly influential given the strong effect apex predators have on their herbivore prey with consequences for vegetation structure and composition. Although wolves (*Canis lupus*) are considered to be obligate ungulate predators (9) with population densities consistently linked to ungulate density (9, 10), they display a high degree of dietary plasticity and consume a variety of alternative prey (10) including marine resources (11–15). If marine resources are abundant and predictable in space and time, and do not present a risk to obtain, they may allow canid populations to persist despite low abundance of primary prey, which may in effect uncouple their numerical response from ungulate abundance (16–18) leading to apparent competition through increased ungulate predation (19).

Sea otters were once nearly extirpated throughout their North Pacific range but have rapidly recovered in some areas due to reintroduction efforts and legal protection (20, 21). These conservation successes have been hailed not only for recovering an endangered species, but also for restoring a keystone species interaction in nearshore communities (22). Sea otters play an important role as predators of marine invertebrates such that their absence leads to the proliferation of sea urchins, which eliminate kelp forests with concomitant declines in biodiversity (23). Where sea otters recover, they can become extremely

Significance

While there has been much effort to understand how sea otter recovery transforms nearshore ecosystems, the effects on terrestrial systems have remained uninvestigated. We documented a transboundary food web interaction resulting from the recolonization of sea otters in Icy Strait, Alaska, which provided an ample marine subsidy to island wolves, and subsequently caused extirpation of a terrestrial ungulate. This defies former predictions of predator–prey dynamics which do not account for increasingly abundant and predictable subsidies such that occur on the forefront of the sea otter recovery wave. Although disruption of terrestrial consumer–resource dynamics was previously unforeseen, it hints at both the possibility that these interactions occurred historically and could also become more widespread as sea otters continue to rebound.

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abundant. For example, after translocation from the Aleutian Islands in the 1960s, sea otters reached the southern fjord entrance to Glacier Bay National Park in the late 1980s and have continued to expand rapidly (Fig. 1A) before recently approaching local carrying capacity and a population estimate of 8,108 individuals (95% CIs = 6,374, 10,456) (Fig. 2B) in 2018 (24, 25).

We have recently discovered that this profusion of sea otters also serves as a substantial food resource for wolves in the archipelagic landscape of Southeast Alaska and particularly in areas adjacent to Glacier Bay (Fig. 1B) (26, 27) where sea otters are protected and the most abundant marine mammal (25). After decades of recovery, the ranges of wolves and sea otters now overlap allowing these species to interact for the first time in the scientific record. This presents the possibility that the ongoing recolonization of sea otters will, surprisingly, modify species interactions in terrestrial systems and would represent an unusual species interaction in which a keystone marine apex predator also serves as an important bottom-up resource to a terrestrial apex predator.

We report on a serendipitous opportunity to study sea otter-wolf-ungulate interactions focused on Pleasant Island and the adjacent mainland Gustavus Forelands on the periphery of

Glacier Bay (Fig. 1A), beginning shortly after wolves became established on Pleasant Island in 2013. From 2015 to 2020, we used two complimentary methods to profile temporal dietary patterns of wolves—DNA metabarcoding of scats and stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ ratios. We evaluated wolf dietary data in combination with population trends of wolves and ungulate prey, human harvest, and winter severity to provide insight on the factors driving predator-prey dynamics. Wolves are highly mobile and typically have a more dispersed home range than their ungulate prey, allowing them to take advantage of patchy resource distribution. To determine whether island wolves were accessing prey available in adjacent mainland systems, we assessed the spatial distribution and movement patterns of wolves by analyzing individual wolf relocation data obtained from GPS-collared wolves and wolf scats genotyped at 38 single nucleotide polymorphic markers (SNPs). In small and isolated populations, such as occur on islands, generalist predators may have large impacts on prey species even leading to local extinctions (5, 27, 28). We found that increasingly abundant marine subsidies decoupled predator-prey (i.e., wolf-ungulate) relationships, as predators switched from ungulates to marine resources. The continued annual reproduction of wolves on a primarily sea otter

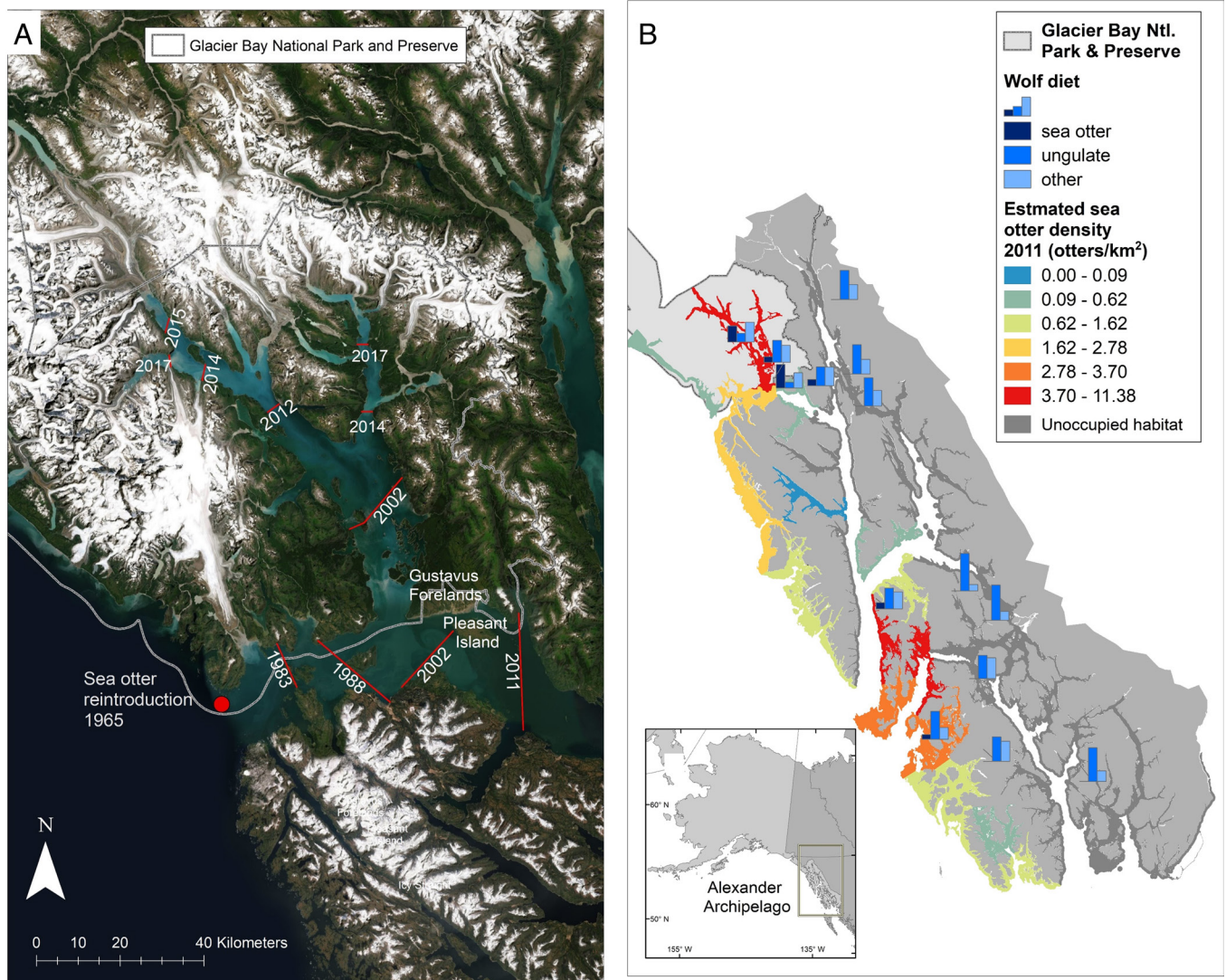


Fig. 1. Study area. (A) Temporal sequence of sea otter colonization of Glacier Bay National Park and Preserve and Pleasant Island in Icy Strait, Alaska, USA. (B) Sea otter consumption by wolves occurred in areas with the highest estimated sea otter densities (21, 24), but the relative frequency of sea otter in wolf scats was highest in Glacier Bay and Pleasant Island (26, 28).

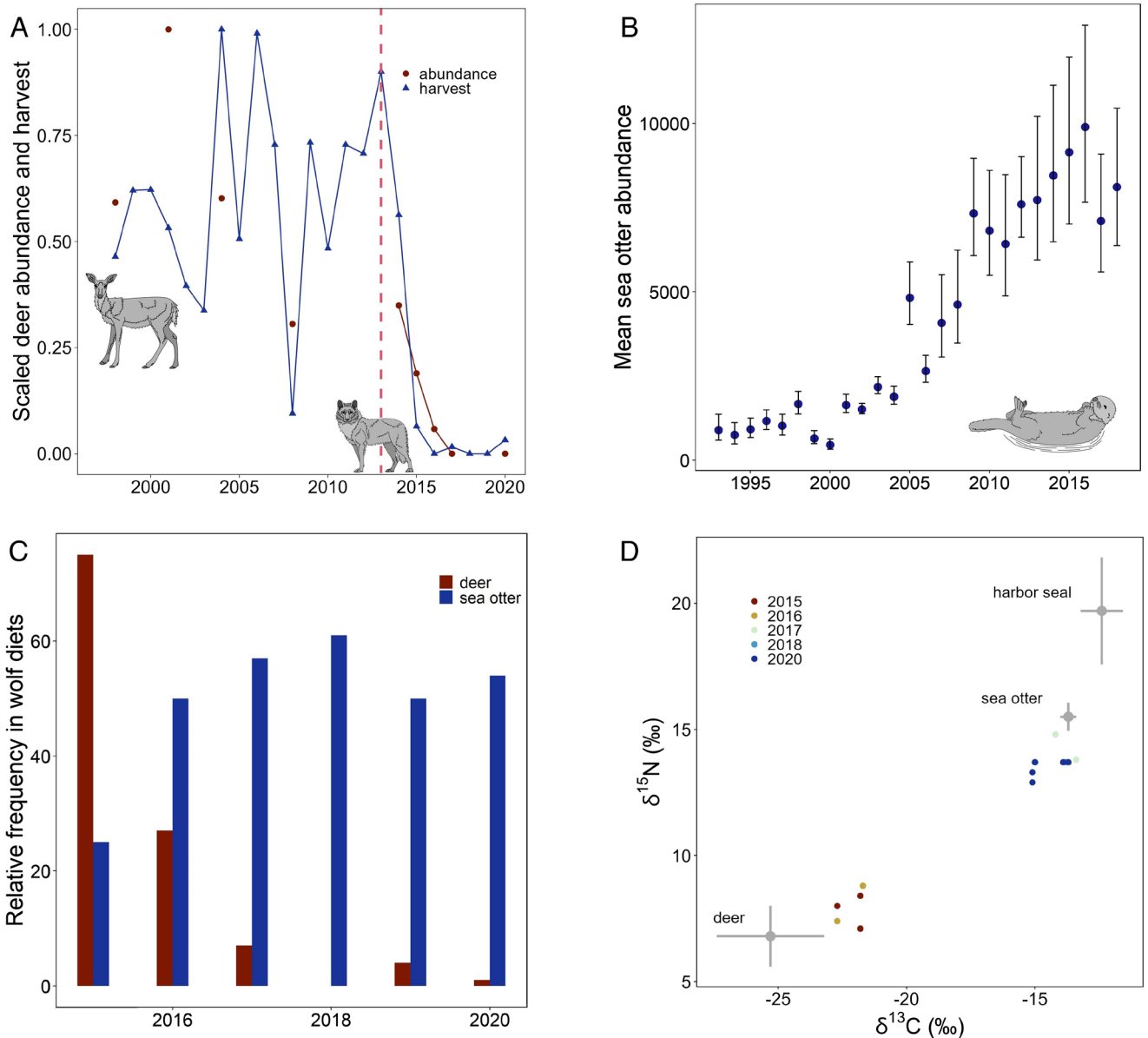


Fig. 2. Prey population and wolf diet trends. (A) Sitka black-tailed deer abundance and harvest declined on Pleasant Island after wolves became established in 2013. (B) Annual population estimates of sea otters (with 95% credible intervals) in Glacier Bay have increased dramatically since re-establishment. (C) The proportion of sea otters in Pleasant Island wolf diets increased as the proportion of deer decreased, measured by the relative frequency of occurrence of prey identified in scats (D) Isopleth of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for Pleasant Island wolf hair indicates increasing relative importance of marine resources in comparison to terrestrial resources coinciding temporally with declines in deer abundance.

diet suggests that wolves are not currently energetically limited and that apparent competition between marine and terrestrial prey may prevent the recovery of deer.

Results

We documented shifts in wolf prey use associated with changes in prey population abundance over the course of 6 y (Fig. 2A–D). Results from DNA metabarcoding of 689 wolf scats collected during 2015 to 2021 from Pleasant Island ($n = 248$) and surrounding areas (Gustavus: $n = 401$; Glacier Bay: $n = 40$) revealed that in 2015 deer were the most prevalent diet item (75%) of Pleasant Island wolves, whereas sea otters comprised a minority (25%) of wolf diet items (SI Appendix, Table S1). However, a substantial shift in wolf foraging ecology occurred as wolves transitioned from deer to marine mammals, primarily consuming sea otters by 2017 (57% of all diet items) while the relative frequency

of deer declined to 7% (Fig. 2C and SI Appendix, Table S1). Although sea otters became the primary diet item, wolves were subsidized by a wide diversity of marine species, including six other marine mammals and fish that inhabit intertidal and near-shore zones (SI Appendix, Tables S2 and S3), where Pleasant Island wolves are often observed foraging (Figs. 3A, 4G and 5G). Wolf diet composition of all diet item groups identified with fecal metabarcoding did not vary significantly by season (summer: May to October, winter: November to April; $F = 0.603$, $P = 0.679$) nor did variation in the composition of wolf diets restricted to sea otter and deer ($F = 1.059$, $P = 0.391$) indicating that sea otters are available to wolves year-round. Because sea otters are consistently available, this may amplify the effects of wolf-mediated apparent competition between sea otters and deer, potentially leading to the extirpation of the former primary prey.

Stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in wolf hair collected from harvest, captures, and shed hair ($n = 14$; 2015 to

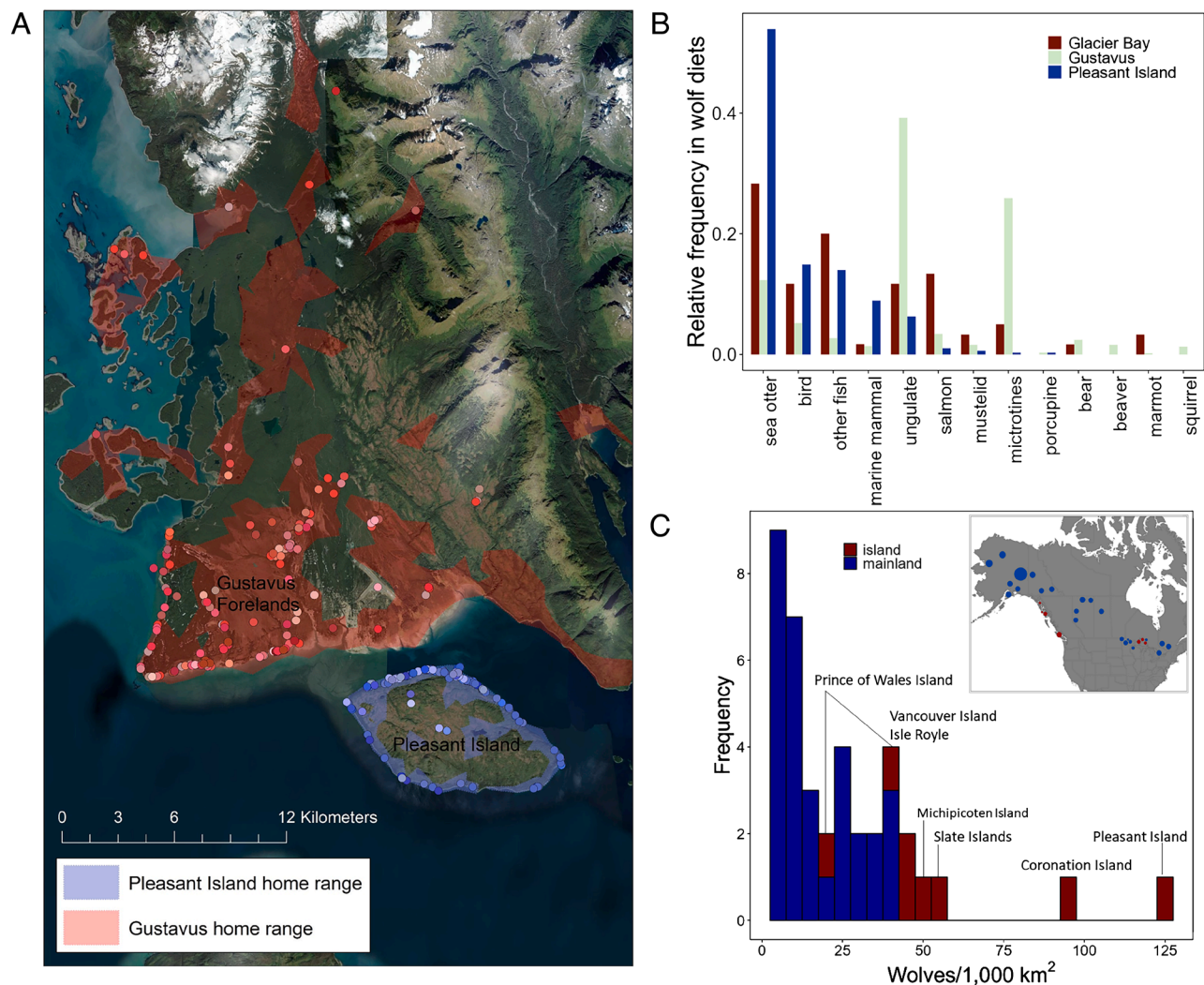


Fig. 3. Pleasant Island wolves are residents. (A) Locations of scat samples ($n = 390$) from individual wolves (Pleasant Island: $n = 19$; Gustavus, $n = 42$) identified from genotypes at 38 SNPs, and wolf pack home ranges (Pleasant Island = 21 km^2 , Gustavus = 221 km^2) from 13 GPS-collared wolves show spatial separation despite proximity. (B) Ungulates constitute a larger proportion of diets of wolves in Gustavus than on nearby Pleasant Island or in Glacier Bay (years pooled, 2015 to 2020), measured by the relative frequency of occurrence of prey identified in scats. (C) Wolf density is higher on islands than mainland populations. Wolf densities are from previously reported values and this study (*SI Appendix, Table S6*).

2020) corroborated the large dietary shift of Pleasant Island wolves from terrestrial resources in 2015 to 2016 to marine resources by 2017. Specifically, the mean proportion of deer in wolf diets plummeted from 84.8% (95% credible interval 68.9–1) in 2015 and 89.7% (95% credible interval 69.4–1) in 2016 to 0.8% (95% credible interval 0–0.110) in 2017 (Fig. 2D and *SI Appendix, Fig. S1 and Table S4*). The contribution of deer to wolf diets remained low (1.8 to 10.6%) during 2017 to 2020, concurrent with a dramatic increase of sea otter consumption (Fig. 2D and *SI Appendix, Fig. S1 and Table S4*). Sea otters were the primary diet source with mean dietary proportion of 86.5 to 97 between 2017 to 2020 (Fig. 2D and *SI Appendix, Table S4*).

This dietary shift of wolves coincided with a precipitous crash in deer abundance. Deer abundance is estimated throughout Southeast Alaska with deer pellet transect surveys which have been conducted on Pleasant Island since 1991 and indicated relatively high densities of deer until 2015 (Fig. 2A, mean number of pellet groups per plot range = 0.72 to 1.96) (26, 28). Deer pellet counts were positively correlated with hunter harvest rates ($r = 0.74$, $t = 2.905$, $P = 0.023$), thus providing proxy information during years when pellet counts were not conducted. Between 2015 and 2016, the number of deer pellet groups surveyed declined by 72%

(26, 28). After reaching a population high of 13 wolves during the summer of 2017 (Fig. 2A and *SI Appendix, Table S5*), zero deer pellets were detected during the 2018 and 2021 surveys for the first time in the nearly 30-y monitoring program (Fig. 2A) (29, 30). Further, annual deer harvest by hunters (2006 to 2013 mean = 23, SD = 19.4) declined by an order of magnitude (2014 to 2019 mean = 1.2, SD = 1.6) providing further evidence for the population decline. Pleasant Island has been occupied by deer for approximately 100 y (30, 31) and although wolves have been sporadically reported, a pack was not established until 2013. We investigated alternative hypotheses for the decline of deer on Pleasant Island including hunter harvest and winter severity. Although high total snowfall during the winter of 2006 to 2007 initiated a decline in deer abundance recorded in both pellet group surveys and deer harvest metrics, the deer population recovered before declining precipitously after the colonization of wolves in 2013 (Fig. 2A) despite favorable snow conditions since 2015 (*SI Appendix, Fig. S2*). Further, we parameterized a stage-structured matrix population model for female deer and projected the deer population in scenarios without harvest or predation, with harvest, and with predation, which suggested that the predicted number of female deer killed by wolves would be expected to produce the

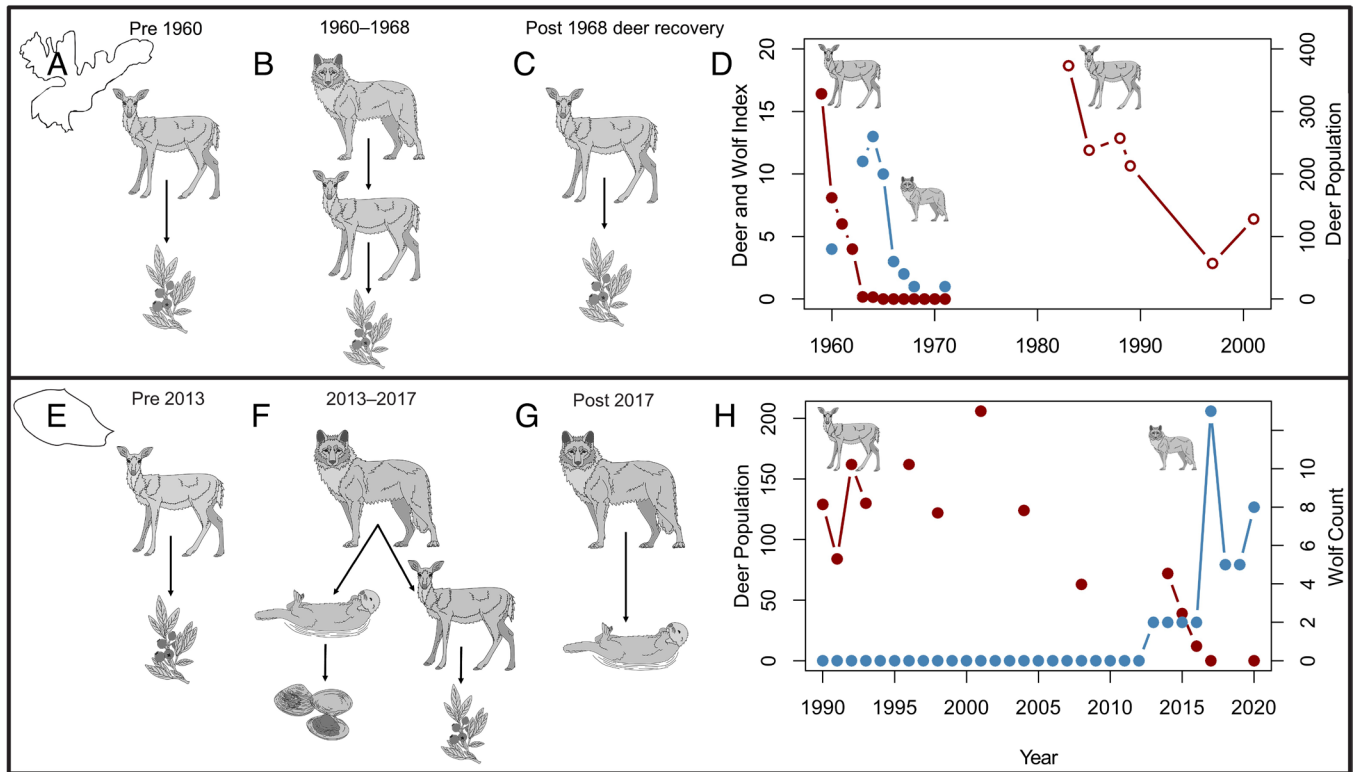


Fig. 4. Marine subsidies alter predator–prey interactions after wolf introduction and colonization. (A) prior to 1960, Coronation Island deer were abundant (29, 37). (B) Four wolves were experimentally introduced in 1960 and increased to 13 by 1964. Deer were the dominant wolf prey during 1961 to 1965 but declined as consumption of alternate prey and wolf cannibalism increased. By 1968 only one wolf remained on the island (29, 37). (C) During the 1980s wolves were absent, but deer rebounded to nearly 400 (26, 28). (D) Observed time series of deer (filled red circles—observations per person-day) and wolf abundance (filled blue circles—minimum counts) from 1960 to 2001 (26, 28) (29, 37) followed by the estimated deer population from pellet group survey data (red open circles). (E) Deer were also abundant on Pleasant Island prior to the 2013 wolf colonization. (F) Wolves reached high abundance ($n = 13$) by 2017 and deer became rare. (G) The increase in abundance and range expansion of sea otters provided a marine-derived alternate prey to subsidize wolves, sustaining high abundance and consistent reproduction. (H) Deer population from pellet group surveys (red) and minimum wolf population size based on direct observations (blue) from 1990 to 2020 indicates that deer are maintained at very low density.

observed timing and magnitude of population decline observed (*SI Appendix, Figs. S2–S4*). Despite the near absence of ungulates, wolves continued to occupy Pleasant Island with the annual minimum count (determined using multiple complimentary methods including observations, trail camera images, and DNA recapture) ranging between 2 and 13 during 2013 to 2021 (*SI Appendix, Table S5*).

Although the switch to a marine diet, primarily sea otters, on Pleasant Island occurred after the deer population crash, the neighboring mainland wolf packs also frequently consumed sea otters and other marine mammals despite the availability of multiple ungulate species. Marine mammals constituted 16% of diet items overall on the Gustavus Forelands from 2015 to 2020 including primarily sea otters [13%] and harbor seals [2%]. Ungulates make up the largest proportion of all diet item groups consumed by Gustavus wolves (39%; Fig. 3B), most importantly moose (30% of diet items overall), reflecting access to a high-density moose population on the mainland (31, 32). Glacier Bay wolves have limited access to moose (Nadeau et al. 2017) and were even more subsidized by marine species including sea otters (28%), salmon (13%), and other fish species (20%; Fig. 3B), indicating marine subsidies can be very important in mainland as well as island systems, although subsidies were lower than on Pleasant Island (63% of diet items overall, including 54% sea otters).

Considering that an abundant ungulate population exists within close range (1.5 km), we questioned whether Pleasant Island might serve as an occasional hunting ground for mainland

wolf packs, or whether the wolves on Pleasant Island are resident. Wolves are highly vagile and capable of swimming among landmasses, even water crossings up to 13 km (26–28)(32, 33). To gain more information about wolf movement patterns and determine if wolves were travelling between the mainland and Pleasant Island, we captured and instrumented wolves with GPS collars on Pleasant Island ($n = 4$, 2020 to 2021) and the Gustavus Forelands ($n = 9$, 2011 to 2021). We obtained a total of 14,640 GPS locations from 13 wolves in the study area, and GPS collars recorded on average 1,331 locations (SD = 1,290) per wolf, over a time interval of 157 d/collar (SD = 111). The Gustavus wolf pack occupied a much larger annual home range as measured by two home range estimators: kernel density estimators (KDE; 487 km²), and adaptive local convex hulls (LoCoH; 221 km²) than the Pleasant Island wolf pack (KDE and clipped to low tideline = 51 km², LoCoH = 21 km², Fig. 3A). Wolf densities were conservatively estimated within KDE home ranges using the mean wolf minimum count during the study period (Pleasant Island = 6.6, Gustavus = 11.2). We also evaluated LoCoH home ranges because these estimators may more accurately depict animal home ranges when movement patterns are constrained to specific features such as islands and peninsulas. The Gustavus wolf pack occurred at similar densities (23/1,000 km²) as other wolf populations studied within Southeast Alaska (mean wolf density on Prince of Wales Island 2013 to 2019 = 21.6/1,000 km²; SD = 8.53), whereas the Pleasant Island wolf pack surpassed densities of nearly any other pack ever recorded (124/1,000 km²) (Fig. 3C and *SI Appendix, Table S6*) and constitute the first wolf pack observed to persist

with little to no ungulate prey, or even large herbivores, in their diet. The Pleasant Island wolf pack LoCoH spatial extent reflects the intensive use of the intertidal and beach zone depicting foraging patterns aimed toward acquiring marine resources, rather than terrestrial resources which would be found in the interior portions of the island (Figs. 3A and 4G). Despite the proximity of Pleasant Island to the Gustavus mainland, no movements among territories were documented. Of the nine GPS-collared Gustavus wolves, three dispersed from their natal range to other areas on the mainland, but none travelled to Pleasant Island, either temporarily or permanently, and Pleasant Island wolves did not leave the island.

To further investigate the spatial distribution and pack membership of individual wolves, we genotyped 576 wolf scats (Pleasant Island: $n = 244$; Gustavus: $n = 332$) collected during 2015 to 2020 to determine whether any wolves were physically present in both study areas indicating movement between island and mainland systems. After removing scat samples that failed to amplify, we successfully genotyped 390 scats (Pleasant Island: $n = 152$; Gustavus: $n = 238$) and identified 19 individual wolves (12 females and 7 males) from Pleasant Island and 42 individual wolves (16 females and 26 males) from Gustavus (SI Appendix, Table S7). None of the wolves that were individually identified with SNP genotypes from georeferenced scat samples were detected outside of the pack home range where they were collected further substantiating the lack of wolf movement between Pleasant Island and Gustavus (Fig. 3A and SI Appendix, Table S7). Therefore, even though these neighboring wolf pack territories are only physically separated by a narrow body of water, we did not document movements between them from the wolves identified with noninvasive genetic sampling or GPS collar data indicating Pleasant Island wolves are resident and subsidized nearly entirely by marine resources acquired from an area much smaller than a typical wolf pack home range in the Alaskan Alexander Archipelago (KDE, $n = 13$, mean = 332 km^2 , SD = 177 km^2).

Discussion

Over four decades of research in North America suggests wolf abundance is only meaningfully limited by the availability of ungulate prey as indicated by the strong positive relationship between wolf densities and ungulate biomass (9, 10); indeed, deer are the most abundant and widespread large terrestrial mammal in this ecosystem, and wolves have demonstrated a high degree of deer specialization (26, 33)(27, 34). However, our results demonstrate that marine subsidies from the recovery of sea otters have decoupled the relationship between ungulates and wolves. Sea otters are not only keystone predators in nearshore ecosystems (22, 23), but also provide a strong linkage between nearshore and terrestrial food webs by providing a critical bottom-up resource that releases wolves from nutritional limitations associated with declines in ungulate biomass.

Not only have Pleasant Island wolves defied predictions of a die-off or abandonment of the island but have persisted for 8 y and produced pups annually during 2018 to 2021 (including one litter of five pups observed in September 2020; SI Appendix, Table S5), indicating that a diet based on sea otters was provisioning them sufficiently to maintain a stable population although reduced for the transient high observed shortly after colonization and before the deer population crash. The resulting decline in deer is consistent with previous research demonstrating that under certain conditions wolves are capable of dramatically reducing ungulate populations, but rarely independently without the debilitating contributions of severe weather on ungulate body condition

or mobility (34–36), or in small and isolated populations such as on islands (36–38)(29, 37, 38). Island systems may provide avenues for strong species interactions such as apparent competition due to relative geographic isolation, which denies terrestrial prey refugia from predation and deters recolonization, and from marine resources subsidizing predators and incurring a numerical response (1, 2, 7, 16).

Notably, wolf populations can achieve very high densities on islands (Fig. 3C and SI Appendix, Table S6), but the length of their tenure has variable outcomes, from many decades to ephemeral (32, 33, 39, 40). The wolves on Isle Royle (535 km^2) endured for nearly 70 y primarily on a moose diet until disease and inbreeding rendered them unable to reproduce viable offspring without assisted migration (39). On other small (184 km^2) islands such as Michipicoten on Lake Superior, wolves that colonized the island in 2013 have persisted despite the removal of some of the resident caribou to protect this rare ungulate population. Wolf densities on Coronation ($96/1,000 \text{ km}^2$) (29, 37) and Chattham and Discovery Islands in British Columbia ($526/1,000 \text{ km}^2$) (32, 33) were extremely high (although the latter included only one wolf) yet were ephemeral. Wolves are expected to maintain residence for longer durations on larger islands because of greater access to a diversity of resources (27, 28) and because larger areas support more stable multispecies trophic interactions (38). In contrast, although the primary prey appears to be nearly extirpated, an abundant marine subsidy has permitted wolves to persist at high densities on the relatively small Pleasant Island for at least the 8 y spanning 2013 to 2021.

In a classic experiment, four wolves were transplanted to Coronation Island, a 73 km^2 island in the Southeastern portion of the Alexander Archipelago in 1960 to measure the effects of wolf predation on deer (29, 37). This island was previously unoccupied by wolves and hosted a moderately abundant deer population (5.8 to 7.8 deer/km^2 , Fig. 5A). Within 4 y, the wolf population had increased to 13 while deer declined below the predicted carrying capacity of the forage resource (Fig. 5B and D). Foreshadowing the trends of Pleasant Island, wolf scat contents indicated a dietary switch from deer to marine resources (harbor seal, invertebrates, and fish), birds, and small mammals (29, 37). Eventually the wolves began cannibalizing each other until the population was reduced to one individual by 1968 (Fig. 5D), generating the conclusion that small and isolated islands cannot sustain stable populations of both wolves and deer (33, 34), which has been used as evidence that wolves are unable to maintain high densities when faced with declining deer resources (41).

Although the fate of Pleasant Island wolves remains to be seen, some characteristics may distinguish their trajectory from other case studies. First, the Coronation Island experiment occurred after the extirpation of sea otters but prior to their recovery. The absence of this key prey species may have made the difference between the Coronation Island wolves, which crashed to one individual in only 8 y, and the Pleasant Island wolves which have persisted at high density for 8 y, five of which occurred after sea otters became their primary prey (Fig. 5D and H). Second, the abundance of available sea otter prey fostered by proximity to a protected area may surpass the quantity and quality of marine-supplemented resources in other island systems. Thus, connectivity to a productive habitat such as Glacier Bay through the spread of sea otter colonization enabled spatial subsidization of trophic dynamics (3) and spatially mediated apparent competition (5) on Pleasant Island. Third, as we have not detected a seasonal pulse in the frequency of sea otters in wolf diets, we assume they are available year-round, whereas salmon, seals and other marine mammals may be seasonally available in discrete habitat patches.



Fig. 5. Sea otters killed by wolves. Adult sea otter carcasses killed by GPS-collared wolves on Pleasant Island (A and B), and Point Gustavus (C and D), Alaska. Bite marks and hemorrhaging present on carcasses (B and D). (E) Wolf tracks and drag marks leading from ocean to the kill site. (F) Sea otter haul out site, Point Gustavus. (G) Pleasant Island and (H) Gustavus wolves patrolling the intertidal zone. Image credit ADF&G (A–E and H), B. Dihle (G), and S. Neilson (F).

The greatest remaining mystery about this indirect species interaction is how an entire wolf pack can acquire sufficient sea otters to enable its persistence. Although it is unknown what proportion of the sea otter population in Glacier Bay and Icy Strait is available to Pleasant Island wolves, the sea otters are locally abundant (Fig. 1A and 2B) such that their biomass far exceeds ungulate biomass. Sea otter carcasses found on land have been documented during 2006 to 2019 ($n = 103$) (42). The cause of death could only be determined for the minority of cases (23%). The deadliest factors were disease (i.e., endocarditis, pulmonary edema) or infections (i.e., septicemia) followed by trauma from boat strike or gunshot (42). Some carcasses were reported as emaciated, and scavenging was evident at three carcasses found on land (42). Scavenging opportunities may be driven by accelerated population growth that has pushed sea otters to their carrying capacity or beyond (24), as indicated by evidence of reductions in sea otter prey abundance (43) and a corresponding decrease in energy recovery rates from foraging bouts (42). Sea otter populations at carrying capacity could result in increased scavenging opportunities through elevated mortality via depleted body condition or increased disease prevalence. Finally, scavenging opportunities may be facilitated by wounding loss from the legal sea otter harvest by Alaska Native people (although reported wounding loss is $\leq 10\%$).

Predation is likely to occur primarily when sea otters haul out on land or in shallow water, a regular occurrence sometimes involving large groups of sea otters (44) (Fig. 4F). This strategy allows them to conserve energy but increases their vulnerability to predation as they are slow and awkward on land (44). Wolf kill sites identified from GPS-collared wolves revealed sea otters predated by wolves on Pleasant Island and Gustavus including 11 freshly killed by wolves during two 30-d investigation periods in late summer 2021 and late winter 2022 Pleasant Island (Fig. 4A–E and *SI Appendix*), and trail cameras revealed wolves dragging dead sea otters (*SI Appendix*, Fig. S5). Wolves have been observed consuming sea otter carcasses and predated sea otter pups on the Alaska Peninsula (14), including one direct observation we made of three wolves ambushing a sea otter pup at a haul-out during summer 2021. Sea otters have occasionally been hunted on land by coyotes (*Canis latrans*) and brown bears (*Ursus arctos*), and by white sharks (*Carcharodon carcharias*) and orcas (*Orcinus orca*) at sea (44, 45), but in this case, sea otters become the primary food source for a terrestrial predator.

Based on sea otter weights, consumption rates of wolves, proportions of sea otters in wolf diets, and wolf abundance in our study area, 89.6 adult sea otter carcasses would be required to support the Pleasant Island wolf pack each year on average (2015 to 2020) (*SI Appendix*). This number of sea otters represents a

small fraction of the total regional population (24, 25), and it is likely that some predation of sea otters constitutes compensatory mortality of otters succumbing to disease or starvation. Therefore, while wolf consumption of sea otters has enabled apparent competition and disruption of terrestrial food webs, the effects in the marine system are likely negligible indicating a donor-controlled shift in the recipient system (1). This example contrasts with orca predation in the Aleutians, which has changed the trajectory of the sea otter population (45).

Whether the results from Pleasant Island will be broadly applicable to wolf-ungulate dynamics in other coastal systems as sea otter populations continue to recover remains to be seen, but both the substantial consumption of sea otters on the Gustavus and Glacier Bay mainland (Fig. 3B) and our recent analysis of the biogeography of wolf foraging ecology (26, 27) throughout this archipelagic landscape suggests that sea otters are readily consumed where they have recovered (Fig. 1B). Observed qualitative changes in the understory vegetation structure of Pleasant Island also suggest the potential of cross-boundary cascading effects of marine subsidies on terrestrial producers. While we have yet to detect another wolf population that relies on sea otters as the primary prey item, future research dedicating sampling effort to coastal wolf packs within the sea otter recovery zone may uncover similar pack-level dependence on sea otters, which has the potential to transform terrestrial predator–prey dynamics in coastal systems at a regional scale.

Materials and Methods

Study Site. Glacier Bay is characterized by mountainous terrain, tidewater and grounded glaciers, and forested valleys surrounding a fjord that until 260 y ago was covered in ice. The subsequent deglaciation was the most rapid and extensive in recorded history (45) and uncovered 1,500 km² of land facilitating one of the best documented examples of terrestrial primary succession following deglaciation (46). This climate-induced landscape change has influenced changes in the distribution and abundance of marine and terrestrial mammal populations. For example, early successional vegetation communities promoted the colonization of moose into Glacier Bay by the mid-1960s and by 2006 populations reached high densities on the Gustavus Forelands of 3.9 moose/km² (30, 31). Wolves have been observed in Glacier Bay since the 1880s but have only occupied the Gustavus Forelands following moose colonization; the first wolf was harvested in 1987 but consistent harvest only occurred during 1997 to 2020 (n = 43). Climate change and subsequent deglaciation has also increased the availability of suitable habitat for sea otters (27, 28). Since arriving in Glacier Bay in the late 1980s, sea otters have expanded northward (Fig. 1A), and anthropogenic and natural causes contributed to their unparalleled growth (Fig. 2B). Glacier Bay National Park and Preserve is a marine protected area, thus both commercial fishing and subsistence and recreational hunting are prohibited thereby ensuring abundant nearshore prey for sea otters and refuge from human hunters. Sea otters have also expanded eastward throughout Icy Strait and are frequently observed in the near-shore regions of point Gustavus and around Pleasant Island (24, 25).

Sample Collection. We collected scats during early spring and late summer 2015 to 2020 on Pleasant Island (n = 294) and the Gustavus Forelands (n = 433) while conducting planned scat collection surveys and opportunistically coinciding with other wolf monitoring field work. On Pleasant Island our scat collection transect was the perimeter of the island on beaches and game trails, and in Gustavus our transect was the shoreline from the townsite to Bartlett Cove. Beginning in 2018 in Gustavus and 2020 on Pleasant Island (when we first captured and GPS-collared wolves at each site), we additionally visited wolf GPS clusters during August 15 to September 30 and February 15 to March 30 (described below), collecting scats at clusters and between sites. We collected scats in the upper fjords of Glacier Bay during summer 2018 on a boat-based collection survey (n = 52). We stored scats in Ziploc bags frozen (−20 °C), labelled with location, date, and perceived age of the scat (e.g., fresh, old) prior to analysis, until ready for sample preparation and analysis. Wolf guard hair samples were collected

opportunistically from trappers and hunters (n = 10; 2015 to 2020), or during wolf captures (n = 3; 2020), and one shed hair sample was collected while conducting ground surveys on Pleasant Island in August 2020. Hair samples were stored in a coin envelope and stored at room temperature. We collected muscle samples from fresh (<2 d) sea otter carcasses found at GPS-collared wolf kill sites in the Gustavus study area (n = 4), and from sea otters legally harvested by Alaska Native hunters (n = 2).

Molecular Scat Analyses. For the metabarcoding of prey remains in wolf scat, we used previously described procedures (26, 27) summarized below. We pooled three subsamples from each scat (total quantity = 200 mg) and used a slightly modified extraction protocol (26, 27) from the Qiagen DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany). Each extraction batch contained a blank control to identify possible cross-contamination. We used slightly modified primers (47) to amplify a ~100 bp region of the mitochondrial 12S region to identify vertebrate species consumed by wolves. We tagged each of 384 forward and reverse primers with unique matching 8 bp indices to identify individual scat samples and reduce error originating from tag jumping (48). PCR procedures were previously described (26, 27). We quantified DNA concentration of the samples using a fluorescence microplate reader with the AccuBlue dsDNA Quantitation Kit (Biotium, Hayward, CA) and normalized each sample accordingly. Following normalization, 3 μL from each sample per 96-well plate was pooled into a 0.65-mL Eppendorf tube. We used NEBNext Ultra II Library Prep Kit (New England BioLabs, USA) to adapt the pools of 384 PCR products into Illumina sequencing libraries each with a unique 6 bp library index following the manufacturer's instructions. Library pool purification, quantification, and sequencing were previously described (26, 27).

We used a bioinformatics pipeline to analyze raw sequence reads (26, 27). We clustered sequences from each sample by 100% similarity and assigned taxonomically using BLAST against 12S vertebrate sequences in GenBank and from a custom 12S database of vertebrate tissue from the Pacific Northwest maintained by the Levi Lab to fill gaps in Genbank. We assigned taxa with 100% match and high query cover (≥99%) to species level after ensuring that no other taxa in Genbank also had 100% match, and manually BLASTed against taxa that could not be assigned to species and assigned to genus or family based on percent match of related taxa. Filtering and quality control measures were carried out on taxonomically assigned sequences as previously described (26, 27). The short 12S region is highly conserved taxonomically such that wolves and coyotes, which are sympatric in our study area cannot be differentiated. To distinguish wolves from coyotes, we amplified a fragment of the mtDNA control region using a single dye-labeled forward primer paired with a reverse primer and analyzed the fragment size on an AB3730 capillary DNA sequencer (Applied Biosystems, Foster City, CA) (26, 27, 49).

Prey amplification success rate was 91%, and predator amplification success was 97%. After removing coyote scats identified from control region mtDNA (Gustavus: n = 92; Glacier Bay: n = 15), and scats that did not contain any prey DNA (n = 68), 701 scats collected were included in subsequent analyses. After filtering artefacts that typically slightly mismatched wolves or the dominant prey items, we retained ~95% of reads for downstream analysis. Overall, the scat samples contained 72 diet items (Pleasant Island: n = 38 (SI Appendix, Table S2), Gustavus: n = 51; Glacier Bay: n = 12) and had on average 17,370 diet item DNA sequences per sample (SE = 1,633). The number of diet items per scat ranged from one to seven (mean = 1.43, SD = 0.837).

Stable Isotope Analyses. Wolf hair and sea otter muscle samples were analyzed for δ¹³C and δ¹⁵N ratios to distinguish between wolf prey as marine sources have higher carbon and nitrogen signatures in relation to terrestrial sources (50). The stable isotope ratios reflect wolf assimilated diet composition during the period of growth of the hair (late spring through late fall) (13). Wolf hair samples were rinsed in 2:1 chloroform/methanol solution to remove surface contaminants and air-dried, then cut into ~2 to 3-mm pieces with surgical scissors and homogenized. The sea otter muscle samples were lipid extracted three times with 2:1 chloroform/methanol and lyophilized prior to weighing. A quantity of 0.5 to 0.6 mg of each individual wolf and sea otter sample was sealed in tin capsules for isotope analysis. The δ¹³C and δ¹⁵N values were obtained using continuous-flow isotope ratio mass spectrometry by using an elemental analyzer (Flash 2000, Thermo Fischer Scientific) combined with a ThermoDelta V^{plus} mass spectrometer interfaced with a ConFlo IV (Thermo Fischer Scientific). All laboratory work was performed by the Alaska Stable Isotope Facility at the Water & Environmental Research Center (University of Alaska Fairbanks). Stable isotope

ratios are expressed in delta (δ) notation as parts per thousand (‰) deviation from the international standards VPDB (carbon) and Air (nitrogen), and measurement precision was $\pm 0.43\%$ for $\delta^{13}\text{C}$ and $\pm 0.26\%$ for $\delta^{15}\text{N}$.

To quantify changes in wolf diets over time, we implemented Bayesian stable isotope mixing models using the MixSIAR package (version 3.1.10) (51) in the R statistical environment. We included biological year (May 1 to April 30) as a random factor in the mixing models to estimate the mean proportion of each diet source and Bayesian 95% credible intervals by biological year. We used the proportional diet estimates from fecal metabarcoding analyses to establish an informed prior by rescaling the occurrence per item (O/I) index value of prey items to sum the same weight as the uninformative prior (51) and only included diet sources $>5\%$ O/I to avoid overparameterizing models (52). Thus, diet sources included sea otter, deer, and harbor seal which made up 50%, 7%, and 6%, respectively, of all diet items identified in Pleasant Island wolf scat with DNA metabarcoding during 2015 to 2020. We included $\delta^{13}\text{N}$ and $\delta^{15}\text{C}$ values of wolf hair tested against the mean and SD of the three prey items (SI Appendix, Table S8). Isotopic values for deer muscle tissue and harbor seal hair were previously obtained from the same geographical region as our study area. To account for tissue-specific isotope discrimination, we corrected the isotopic values of diet items using trophic discrimination factors of 3.4 ± 0.3 SD ($\delta^{15}\text{N}$) and 2.6 ± 0.2 SD ($\delta^{13}\text{C}$) for wolf's food sources (53). All mixing models were run with three chains of 1,000,000 length thinned by 500 after a burn-in of 500,000. Model convergence was assessed with Geweke and Gelman-Rubin diagnostic values (51).

Data Analyses. We quantified wolf use of prey species by calculating indices of the relative frequency of occurrence as 1) the occurrence per feces (O/F) index (the number of occurrences of a diet item divided by the total number of scat samples) and 2) the occurrence per item (O/I) index (the number of occurrences of a diet item divided by the total number occurrences of all diet items). We included O/F for comparison to previous wolf diet studies, but restricted statistical tests to O/I indices to avoid overcounting prey items that co-occur in scats containing multiple species, and therefore, the results reported here are conservative estimates of diet composition of wolves. In addition, we calculated the relative read abundance of diet items as the proportion of prey DNA sequence reads in a scat sample divided by the total number of prey DNA sequences in that sample. We evaluated the significance of variation in diet item consumption between seasons using a permutation-based multivariate analysis of variance (PERMANOVA) (54). We generated separate Bray-Curtis dissimilarity matrices using the O/I index and ran analyses with 99,999 permutations and pairwise comparisons using Bonferroni's correction. For tests of seasonal differences of diet item groups, we used the estimated age of the scat and the date of collection to group scat samples into seasons (summer: May to September, winter: October to April). We performed PERMANOVA analyses using the `adonis2` function in the `vegan` (v. 2.6-2) R package (55).

Population Trends. We estimated the minimum counts of wolves (i.e., highest number of wolves observed at any point during the biological year [May to April]) on Pleasant Island and the Gustavus Forelands; because of dense forest canopies obscure visibility during aerial telemetry, we used a combination of methods. To obtain the best annual count for each pack we observed individuals accompanying GPS- or radio-collared wolves during aerial telemetry flights (using a Scout fixed wing airplane or a Hughes 300 helicopter), from the ground during other field work activities, and from trail camera images (Reconyx HC600). We established trail cameras in both study areas beginning during winter, 2017. We could conduct telemetry observations dependent on maintaining a sample of GPS-collared wolves (see below).

Wolf Individual Identification. We designed a panel of SNPs ($n = 38$) for individual identification of wolves based on previously published SNP positions and flanking regions in Cronin et al. (56). We designed a sex-specific primer pair

targeting 80 bp of the Y chromosome (57) to determine the sex of individual wolves. We used probability of identity values estimated in GenAlEx 6.5 (58) to determine the power of our SNP panel to distinguish between individual wolves ($\text{PID} = 5.3 \times 10^{-12}$ and $\text{PID}_{\text{sibs}} = 1.6 \times 10^{-6}$). The samples were genotyped in triplicate using multiplex amplicon sequencing. SNP primer design, optimization and genotyping protocol followed previously described methods (59).

Wolf Movement Patterns and Home Range. We captured and radiocollared wolves during 2011 to 2021 using modified padded long spring (Easy-Grip #7, Livestock Protection Company) and unpadded coil spring foothold traps (MB750, Minnesota Brand Inc.) with commercially produced lures and canid urine used as attractants. Restrained wolves were immobilized using either tiletamine HCl and zolazepam HCl, or a combination of ketamine and medetomidine. Capture and handling procedures conformed to guidelines established by the ADF&G Animal Care and Use Committee (ACUC #0043-57) and the American Society of Mammalogists (60). We captured three wolves (two female adults and one male pup) on Pleasant Island during 2020 and one wolf (female adult) in 2021 and instrumented the adults with GPS collars (Telonics GPS/Iridium model TGW-4577 4; SI Appendix, Table S9). Nine wolves (6 females and 3 males) have also been captured on the Gustavus Forelands during 2011 to 2021 and instrumented with GPS collars (TGW-4577-4 and TGW-3590; SI Appendix, Table S9). We obtained locations at 30-min intervals during a 30-d period in late summer and late winter to detect wolf kill sites, and 6-h intervals during the rest of the year from the 11 wolves captured after 2017, and at 6-h intervals for the two wolves captured in 2011 and 2016. Wolf relocations collected during the 30-min interval periods were thinned to every 6 h and occurred at the same time of day to be consistent with the 6-h location data collected during the rest of the year.

We calculated wolf pack home ranges using the 95% isopleths of the KDE with least squares cross-validation, and the 95% isopleths of the adaptive local convex hull method (61) with the maximum distance between GPS locations used as the adaptive value. We also calculated 95% minimum convex polygons (MCP) (62) to facilitate comparison to other wolf studies. Home ranges estimated by KDE and MCP methods may include areas not used by the study animals, especially when home ranges have distinct boundaries formed by areas of non-habitat. Because our study area is characterized by islands and peninsulas surrounded by ocean, we also used LoCoH estimators, which may more accurately depict animal home ranges when movement patterns are constrained to specific features (61). We performed home range analyses with the `hrh` package (63) in R 4.0.3 (R Core Team 2021). To accurately represent territorial wolf space use we excluded locations of wolves that dispersed permanently away from their natal pack home range.

Data, Materials, and Software Availability. Anonymized Illumina sequence data have been deposited in DRYAD (doi: [10.5061/dryad.zgmsbccgg](https://doi.org/10.5061/dryad.zgmsbccgg)). Some study data available (Restrictions apply to the availability of GPS location data, which were used under agreement with the Alaska Dept. of Fish and Game, so are not publicly available. With permission of ADF&G, data are available from the authors upon reasonable request).

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