PNAS COMMENTARY

Wolves, otters, ungulates, and a promising path for ecology

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We know that animals are picky eaters, but how picky are they? The question might seem whimsical, but it is one of the core challenges in trying to forecast Anthropocene ecological dynamics. Dietary flexibility in response to environmental change has profound implications for food webs and population persistence and, hence, for biodiversity and community stability. For consumers, flexible foraging reduces reliance on any one food, increasing the odds of survival when a favored food becomes rare. For prey, a flexible predator can be a blessing or a curse. On the one hand, intermittent prey switching can relax top–down pressure and create windows for population recovery (1). On the other hand, alternative prey can prevent predator populations from cycling and thus sustain pressure on small populations (apparent competition; (2)) or else cause at-risk species to crowd into the same safe spaces (actual competition; (3)).

Despite the importance of dietary plasticity, empirical understanding is weak. One reason is that it is difficult to monitor the foods eaten by free-ranging animals (4). Another is that the regents of ecology have tended to celebrate grand theoretical generalizations while despairing of the "messy detail" (5) in field data. Insider lingo even has a set of veiled put-downs for research deemed too parochial: *descriptive*, *reductionist*, *case study*, *natural history*. But what if the messy details are actually the key to understanding anything at all (6)? And what if the technical advances now enabling ecologists to confront that messiness (4, 7) can propel the field past its longstanding hang-ups (5)?

Whatever the answers to those questions are, "next-generation natural history" (7) is supplying enough insight—often into species we thought we knew well—to drown any prejudice against empirical detail. Drone surveillance captures killer whales (*Orcinus orca*) systematically hunting down great white sharks (*Carcharodon carcharias*), and satellite tags show how the sharks skedaddle (8). DNA barcoding proves that many ostensible generalist species are in fact flocks of different, specialist species (9, 10). DNA metabarcoding reveals both unexpected dietary breadth within species (11) and unexpected dietary differentiation among them (12, 13). While these and other recent discoveries challenge assumptions about food-web structure, functional redundancy, and foraging behavior, few studies have yet linked them to population dynamics. In PNAS, Roffler et al. (14) do just that, using an ingenious blend of approaches to show how a surprising interaction between two keystone species, one terrestrial and one marine, sustained an island predator population and caused the extirpation of its formerly predominant prey.

An earlier study by Roffler et al. (11) used DNA metabarcoding to characterize the diets of wolves (*Canis lupus*) at 12 sites across southeastern Alaska. Wolves are thought to specialize, and perhaps depend on, ungulates such as deer, elk, and moose. Indeed, ungulates accounted for the majority of wolf diets at most sites. But the survey also found >50 other species of vertebrate prey—birds, bears, rodents, fish, mustelids, and even toads—many of which were previously unrecorded. Nor do wolves stop at vertebrates; one loner in Idaho ate enough grasshoppers to meet 10% of its daily nutritional demand (15). Among the sites studied by Roffler et al. (11), one stood out. On Pleasant Island, a 50-km^2 wilderness south of Glacier Bay National Park, wolves hardly ate any ungulates. Instead, they subsisted mainly on marine mammals, with one species—sea otter (*Enhydra lutris*)—accounting for ~60% of their diet.

Alaskan sea otters are the archetypal keystone species, controlling nearshore ecosystems by regulating sea urchin populations, which otherwise obliterate kelp forests (16). After nearly being driven extinct by the fur trade, otters were protected and proliferated in the Aleutian Islands. They reached Glacier Bay in the 1990s and proliferated there, too, with an estimated population of ~8,000 by 2018. Predation on sea otters by killer whales and sharks is not uncommon and has contributed to local population declines along the Pacific coast (17, 18). Elsewhere, high otter densities, coupled with their habit of hauling out on shore to rest, suggest the potential for predation by terrestrial carnivores, but there has been little evidence that these events are more than incidental (11, 19).

In their new study, Roffler et al. (14) reconstruct the timeline and ecological impacts of wolf-on-otter predation at Pleasant Island (Fig. 1). Wolves landed in 2013, presumably across one of the narrow channels from the nearby Gustavus headland. In 2015, wolf scats contained ~98% deer DNA (*Odocoileus hemionus sitkensis*). By 2018, this proportion had dropped to 0%, while the sea otter fraction increased from ~2% to a steady ~70%, with seals, birds, and fish making up the remainder. The authors quantified this shift through metabarcoding of wolf scats and stable-isotope analysis of wolf hairs (sea otters are distinct from deer in both $\delta^{13}C$ and $\delta^{15}N$), augmented by camera-trap footage of predation events.

Why would a canonical predator of ungulates switch to a leaner, saltier alternative? The simple answer appears to be that deer became rare after wolves invaded, forcing wolves

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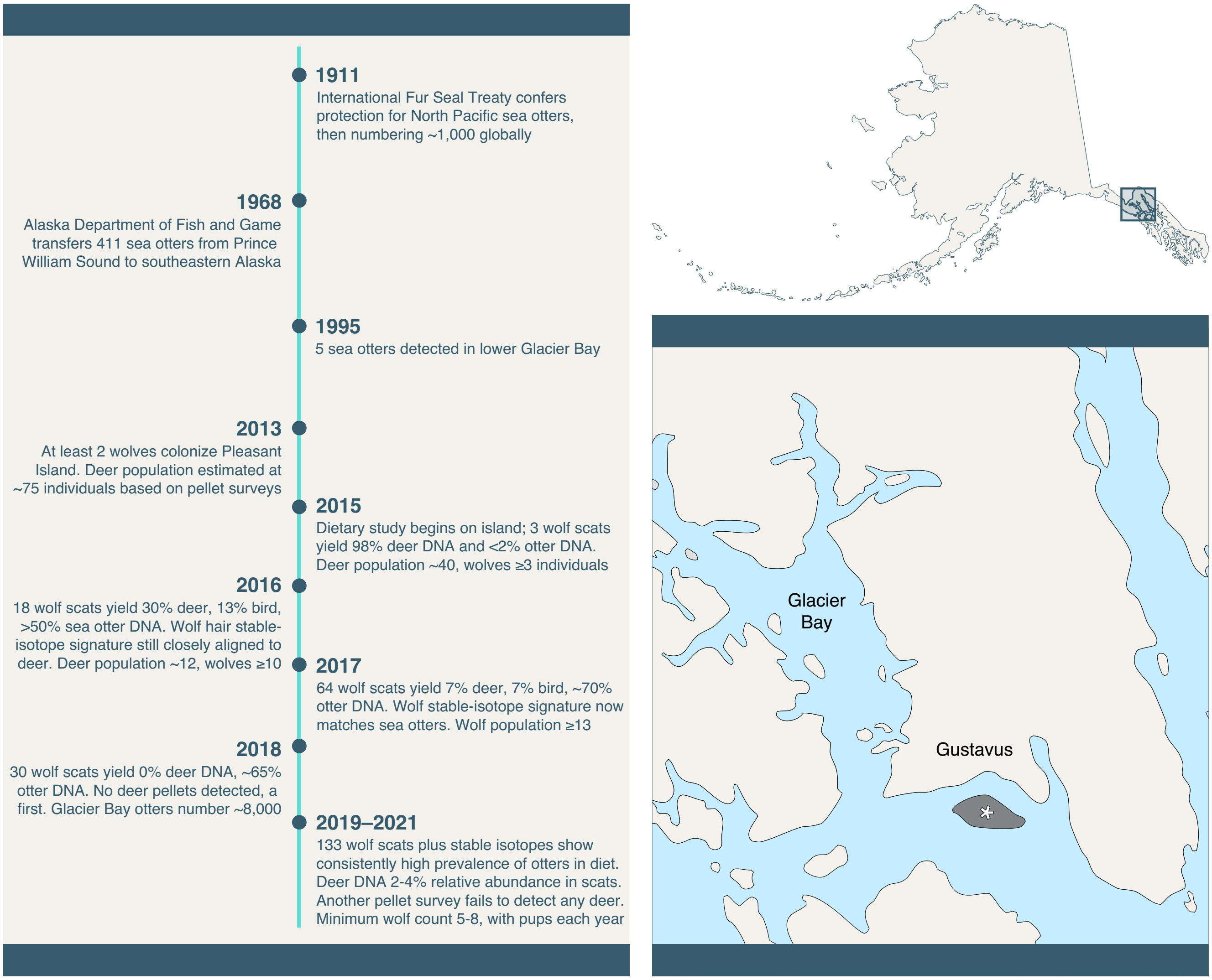

Fig. 1. Timeline of key events and findings about the three-way interaction between wolves, sea otters, and deer on Pleasant Island (starred in the detailed map, *Lower Right*) in southeastern Alaska (the box on the state map, *Upper Right*, shows the area of detail).

to broaden their diets. Censuses of deer pellets, together with reports from hunters, indicate that deer abundance on Pleasant Island was relatively stable until 2015 but then plummeted. Deer pellets decreased by 72% from 2015 to 2016; zero were detected in 2018 and then again in 2021. (Deer DNA was recovered from scats in 2019 and 2020, but at very low abundance.) While wolves were small in number (a dozen, give or take), their density was extraordinary (0.12 km^{-2}, compared to 0.02 km^{-2} on the nearby mainland)—and, crucially, was sustained even after the effective elimination of ungulate prey. Extensive telemetry and fecal genotyping of wolves on Pleasant Island and Gustavus yielded no evidence of immigration or emigration. Roffler et al. (14) conclude that wolves pushed Pleasant Island's deer to extirpation, fueled by a reliably abundant sea otter subsidy.

Wolves likely had some help in crushing the deer population, which averaged roughly 125 individuals from 1990 to 2005, peaked at >200 in 2001 after a succession of low-snowfall winters, and dipped to ~60 in 2008 after a heavy winter. Above-average snowfall in the years bracketing wolf arrival, along with modest but steady hunter harvest up to 2013, may have predisposed the deer to a knockout punch from colonizing predators. Yet, the authors make a persuasive case that wolves were the overriding cause: Snowfall was mild and offtake negligible from 2014 onward, and a population model predicted that wolf kills alone were sufficient to explain the trajectory of population decline. As such, the wolf–otter–deer interaction on Pleasant Island is perhaps the most striking recorded example of apparent-competitive exclusion in the wild.

The role of sea otter resurgence in producing this outcome is further bolstered by a powerful anecdotal contrast. On Coronation Island, a comparable landmass 280 km south of Pleasant Island, four wolves were introduced in 1960. Just as on Pleasant Island, wolves increased to high density (0.96 km^{-2}), the deer population collapsed, and wolves shifted to preying on birds, rodents, and marine fauna—but not sea otters, which had not yet recovered in the area (20). Unlike on Pleasant Island, the wolf population then crashed, contributing to the perception that wolves might eat many things but ultimately need ungulates.

One hopes that research on Pleasant Island will continue to answer some of the fascinating questions raised by this study. Can a small wolf population stably persist on the sea otter/seal subsidy and assorted small snacks, or will otters learn to mitigate risk and starve the wolves? What behavioral strategies allow wolves to catch and subsist on otters, and what nutritional and fitness costs (if any) does a turf-to-surf dietary shift entail? Does loss of deer impact Pleasant Island's vegetation, creating a trophic cascade analogous to those caused by sea otters in kelp forests (16)? Evidence from other Alaskan islands suggests the likelihood of this result (21), and more data on the strength and circumstances of wolf-induced trophic cascades are needed to inform debates in the continental US (22). Herbivore exclosures, if not already established, would be an asset in measuring how current and future herbivory regimes affect plants.

"The beautiful synergy of approaches employed by Roffler et al. enabled them to document dramatic dietary plasticity in an apex predator—a totally unequivocal result."

The beautiful synergy of approaches employed by Roffler et al. (14) enabled them to document dramatic dietary plasticity in an apex predator—a totally unequivocal result—and to assess the equally dramatic population-level consequences of that shift through genetic analysis, telemetry, camera trapping, a well-parameterized model, and good old-fashioned sticky-boot work. The results provide uncommonly strong support for the theory of apparent competition, and future work may boost that support (e.g., if wolves persist and deer stay gone). The stage for these events was set by successful sea otter conservation (perhaps, once upon a time, insular wolves routinely subsisted on otters), and the results have implications for understanding the consequences of growing translocation, restoration, and rewilding efforts worldwide. Exquisite detective work combined with the charisma of the main characters—wolves and sea otters, renowned keystones of their respective realms—make for an irresistible story.

My greatest enthusiasm is not about the story but about what the work portends for ecology. A broad scan leads to serendipitous discovery of an anomaly—an ecological mutation. Discovery of the novel mutant prompts a deep dive to uncover its causes and effects. Investigators creatively fuse conventional and novel techniques to derive strong causal inference. The conclusions align with one of two theoretically plausible alternatives but also challenge dogma. That sequence could describe many of the most explosive advances across all branches of biology over the last 70 years. To me, it reads a lot like a blueprint for transcending the frustrations that have prompted decades of handwringing among ecologists. This is a great case study featuring great natural history, great enough to strip the pejorative undertone from both of those terms. Ecology has overflowing vats of untested theory, scads of mesocosm studies, and plenty of "detail-free statistical patterns" (5). One thing it needs now is a rejuvenated commitment to figuring out what is what in the real world. The seemingly messy details are often not so messy when the right tools are brought to the job.

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