

HUMAN IMPACTS

The unique ecology of human predators

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Paradigms of sustainable exploitation focus on population dynamics of prey and yields to humanity but ignore the behavior of humans as predators. We compared patterns of predation by contemporary hunters and fishers with those of other predators that compete over shared prey (terrestrial mammals and marine fishes). Our global survey (2125 estimates of annual finite exploitation rate) revealed that humans kill adult prey, the reproductive capital of populations, at much higher median rates than other predators (up to 14 times higher), with particularly intense exploitation of terrestrial carnivores and fishes. Given this competitive dominance, impacts on predators, and other unique predatory behavior, we suggest that humans function as an unsustainable “super predator,” which—unless additionally constrained by managers—will continue to alter ecological and evolutionary processes globally.

Humans have diverged from other predators in behavior and influence. Geographic expansion, exploitation of naïve prey, killing technology, symbioses with dogs, and rapid population growth, among other factors, have long imposed profound impacts—including widespread extinction and restructuring of food webs and ecosystems—in terrestrial and marine systems (1–3). Despite contributions from the “sustainable exploitation” paradigm (4), contemporary humans can rapidly drive prey declines (5–7), degrade ecosystems (8, 9), and impose evolutionary change in prey (10, 11). Owing to long-term coevolutionary relationships that generally limit exploitation rates, especially on adult prey, these are extreme outcomes that nonhuman predators seldom impose. Meanwhile, whether present and future exploitation can be considered sustainable is hotly contested, especially in fisheries. Debate has been largely restricted to elements of the sustainable exploitation model, namely, a model of prey abundance and yields to humanity (e.g., 12, 13).

Here, we approach the notion of sustainable exploitation differently by asking whether humans—extreme in their impacts—are extreme in their predatory behavior (14, 15). Previous work has variously estimated exploitation by humans, nonhuman predators, or both, but systematic comparisons have focused on specific taxa or regions, have lumped all predators together, have been reconstructed indirectly, and/or did not include age classes (e.g., 14, 16, 17). We address these limitations with data spanning wildlife, tropical wild meat, and fisheries systems (data files

S1 and S2). We examine variation in annual finite exploitation rates of marine fishes from every ocean ($n = 1494$ estimates, 282 species from 110 communities) and terrestrial mammals from every continent except Antarctica (631 estimates, 117 species from 179 communities) (fig. S1 and tables S1 and S2) by predator type (humans versus nonhuman), ecosystem (marine versus terrestrial), region, and trophic level. We focus on adult prey because hunters and fishers overwhelmingly target adults (18). We complement this quantitative assessment by identifying additionally unique predatory behaviors by humans that (i) facilitate the large differences in exploitation rates we detect and (ii) elicit the manifold consequences of humanity’s predatory hegemony.

Differences in exploitation rates between hunters and terrestrial predators varied among comparisons. Globally and pooled across trophic levels, exploitation rates by hunters (median = 0.06) did not differ from those of carnivores [median = 0.05; Wilcoxon test $W = 46076$, $P_{\text{adj}(2)} = 0.11$] (Fig. 1A and figs. S2A and S3A). A paired comparison over shared prey within the same community, however, revealed that hunters exploit at higher rates than the highest-exploiting terrestrial predator [paired Wilcoxon test $V = 929$, $P_{\text{adj}(2)} = 0.03$] (fig. S3B). Additionally, a similar paired comparison showed that the median proportion of mortality (an independent metric) caused by hunters (0.35) was 1.9 times that (0.19) caused by all other predators combined (paired Wilcoxon test $V = 1605$, $P = 0.004$) (Fig. 1B).

Trophic level and regional analyses (across taxa and areas with abundant data) revealed additional patterns. Although globally pooled comparisons showed that hunters and terrestrial predators exploited herbivores (artiodactyls) at similar rates [$W = 14751$, $P_{\text{adj}(9)} = 1.00$] (Fig. 1C), hunters in North America and Europe exploited herbivores at median rates 7.2 and 12.5 times those of hunters in Africa [both $P_{\text{adj}(9)} < 0.04$]; rates did not differ statistically between hunters

and terrestrial predators within any of the regions (fig. S4A). Globally, hunters exploited mesocarnivores [$W = 248$, $P_{\text{adj}(9)} = 0.03$] and large carnivores [$W = 181$, $P_{\text{adj}(9)} < 0.001$] at higher rates than nonhuman predators by factors of 4.3 and 9.2, respectively (Fig. 1C). Remarkably, hunters exploited large carnivores at 3.7 times the rate that they killed herbivores [$W = 2697$, $P_{\text{adj}(9)} < 0.001$] (Fig. 1C).

Fisheries exploited adult prey at higher rates than any other of the planet’s predators (Fig. 1A and fig. S2B). Among nonhuman predators across all oceans, 50% of exploitation rates were less than 1% of annual adult biomass. In contrast, fisheries exploited more than 10% of adult biomass in 62% of cases. Overall, the median fishing rate (0.14) was 14.1 times the take (0.01) by marine predators [$W = 83614$, $P_{\text{adj}(2)} < 0.001$] (fig. S3A). In paired comparisons, median fisheries exploitation (0.17) was 3.1 times the median rate (0.06) by the highest exploiting marine predator of the same prey [$V = 382$, $P_{\text{adj}(2)} = 0.02$] (fig. S3B). At all trophic levels, humans killed fishes at higher rates than marine predators [all $P_{\text{adj}(9)} < 0.04$] (Fig. 1D), but there were no differences in take by each predator across trophic levels [all $P_{\text{adj}(9)} \geq 0.5$]. Pooling all trophic levels, the median rate of Atlantic fisheries exploitation (0.20) was 2.9 times that of Pacific fisheries [median = 0.07, $W = 6633$, $P_{\text{adj}(4)} < 0.001$] (fig. S4B).

Although our varied data set could impose biases in both directions (supplementary text), we reveal striking differences in exploitation rates between nonhuman predators and contemporary humans, particularly fishers and carnivore hunters. Interactions between human and natural systems likely underlie patterns. For example, global seafood markets, industrial processing, relatively high fecundity among fishes, and schooling behavior could, in part, explain the particularly high fisheries take, whereas gape limitation by piscivores and a generally species-rich marine environment might explain why marine predator rates are comparatively low. Higher human densities and reduced fish biomass (from longer exploitation) likely explain higher fishing rates in the Atlantic versus Pacific oceans. Moreover, motivations to kill typically inedible carnivores for trophy and competitive reasons [intraguild predation; (7)] are evidently powerful and drive acutely high rates. Although, in terms of numbers, it is easy to exploit high proportions of (less abundant) carnivore populations, the implications remain profound (below). In addition, whereas declines in tropical wild meat (5) might predict an opposite pattern, lower hunting rates of African herbivores could relate to simpler technology, less reporting, and/or longer adaptation to human predation.

Whereas sociopolitical factors can explain why humans repeatedly overexploit (19), cultural and technological dimensions can explain how. Human predatory behavior evolved much faster than competing predators and the defensive adaptations of prey (20). Indeed, division of labor, global trade systems, and dedicated

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recreational pursuit have equipped highly specialized individuals with advanced killing technology and fossil fuel subsidy that essentially obviate energetically expensive and formerly dangerous search, pursuit, and capture. Moreover, agri- and aquaculture, as well as an ever-increasing taxonomic and geographic niche, leave an enormous and rapidly growing human population demographically decoupled from dwindling prey. In fact, low prey abundance can drive aggressive exploitation, because of the increased economic value of rare resources (21).

Emerging evidence suggests that the consequences of dominating adult prey are considerable. For example, human preference for large ornaments and/or large body size has fundamentally altered the selective landscape for many vertebrates. Not only can this rapidly alter morphological and life-history phenotypes (11), the resulting changes can modify the reproductive potential of populations (22) and ecological in-

teractions within food webs [e.g., (23)]. In addition, owing to different behavior (e.g., age-class preferences and seasonality of exploitation), hunters likely cannot substitute for carnivores as providers of ecological services [e.g., regulation of disease and wildfire (7, 9), as well as mesopredator control (8, 24)]. Finally, less explored is the potentially substantial impact of prey biomass removal from ecosystems; global trade and sanitation systems shunt energy and nutrients from food webs of provenance to distant landfills and sewers.

These implications, the high exploitation rates that drive them, and the broadest taxonomic niche of any consumer uniquely define humans as a global “super predator.” Clearly, nonhuman predators influence prey availability to humans [e.g., (25)]. But overwhelmingly these consumers target juveniles (18), the reproductive “interest” of populations. In contrast, humans—released from limits other predators encounter—exploit the “capital” (adults) at exceptionally high rates. The im-

plications that can result are now increasingly costly to humanity (26) and add new urgency to reconsidering the concept of sustainable exploitation.

Transformation requires imposing limits of humanity's own design: cultural, economic, and institutional changes as pronounced and widespread as those that provided the advantages humans developed over prey and competitors. This includes, for example, cultivating tolerance for carnivores (7), designing catch-share programs (27), and supporting community leadership in fisheries (28). Also key could be a new definition of sustainable exploitation that focuses not on yields to humanity but rather emulates the behavior of other predators (14). Cultural, economic, and technological factors would make targeting juvenile prey challenging in many cases. Aligning exploitation rates on adults with those of competing predators, however, would provide management options between status quo exploitation and moratoria. Recent approaches to resolve controversies among fisheries scientists reveal how distant such predator-inspired management prescriptions are now. For example, although the mean “conservative” fishing rate estimated to rebuild multispecies fisheries across 10 ecosystems (0.04) is one-fourth their maximum sustainable yield rates (0.16) (13), it remains 4 times the median value we estimated among marine predators globally (0.01). Consequently, more aggressive reductions in exploitation are required to mimic nonhuman predators, which represent long-term models of sustainability (14).

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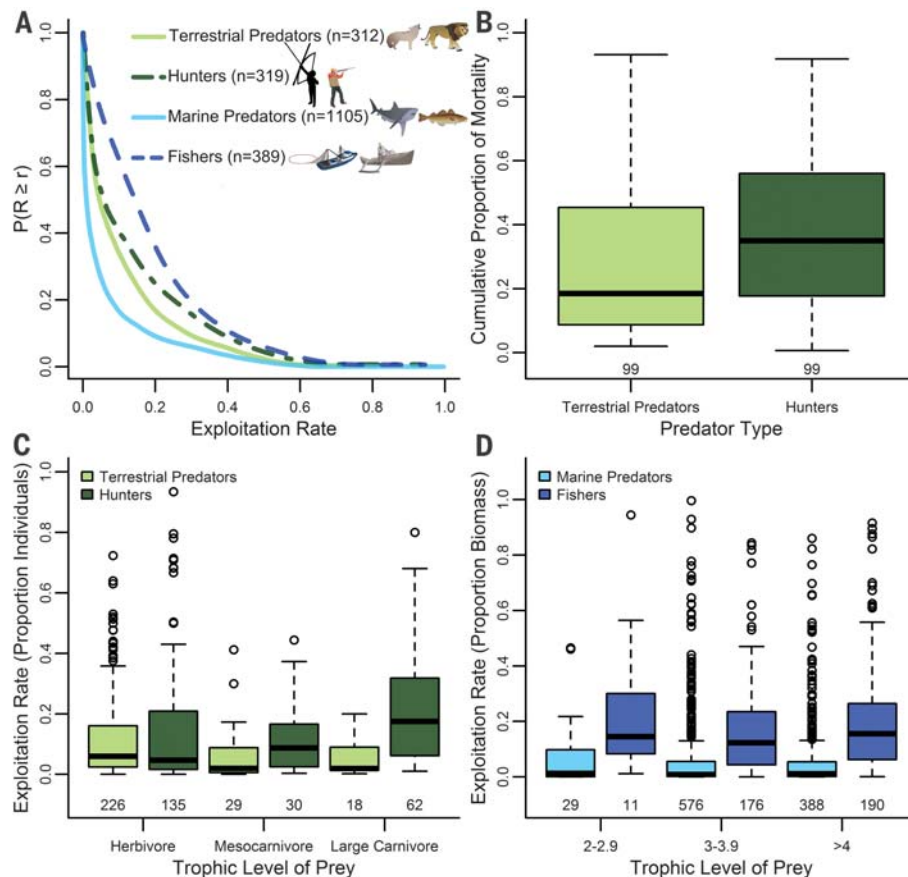


Fig. 1. Patterns of exploitation by human and nonhuman predators on adult prey. (A) Complementary cumulative distribution functions showing the probability of predators exploiting prey at a rate (R) greater than or equal to a given annual finite exploitation rate (r), on the basis of the number of available individuals in populations of terrestrial mammals) or biomass (marine fishes). (B) Proportion of annual mortality caused by hunters and all other (i.e., aggregated) terrestrial predators consuming the same prey population. (C and D) Exploitation rates of human and nonhuman predators across trophic levels in (C) terrestrial and (D) marine systems. Whiskers represent distance from upper and lower quartiles to largest and smallest nonoutliers. [Art by T. Saxby, K. Kraer, L. Van Essen-Fishman/ian.umces.edu/imagelibrary/ and K. Eberlins/123rf.com]

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SUPPLEMENTARY MATERIALS

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 Materials and Methods
 Supplementary Text
 Figs. S1 to S6
 Tables S1 to S2
 References (29, 30)

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PLANT MICROBIOME

Salicylic acid modulates colonization of the root microbiome by specific bacterial taxa

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Immune systems distinguish “self” from “nonself” to maintain homeostasis and must differentially gate access to allow colonization by potentially beneficial, nonpathogenic microbes. Plant roots grow within extremely diverse soil microbial communities but assemble a taxonomically limited root-associated microbiome. We grew isogenic *Arabidopsis thaliana* mutants with altered immune systems in a wild soil and also in recolonization experiments with a synthetic bacterial community. We established that biosynthesis of, and signaling dependent on, the foliar defense phytohormone salicylic acid is required to assemble a normal root microbiome. Salicylic acid modulates colonization of the root by specific bacterial families. Thus, plant immune signaling drives selection from the available microbial communities to sculpt the root microbiome.

Recognition of plant pathogens in leaves leads to dramatic changes in transcription, synthesis of defense phytohormones and antimicrobial compounds, and elaboration of physical barriers (1, 2). Defense phytohormones are structurally diverse plant secondary metabolites that integrate plant immune system output responses while repressing cell

growth and proliferation. Salicylic acid (SA), jasmonic acid (JA), and gaseous ethylene mediate localized and systemic plant immune responses (3, 4). Nonspecific systemic acquired resistance is mediated by SA in leaves (5). In contrast, induced systemic resistance in leaves can be triggered by specific rhizobacteria colonizing roots and is mediated by JA and ethylene (4). SA and JA act antagonistically in responses to infection by biotrophs, at least in leaves (6). The defense phytohormones control a set of overlapping signaling sectors, each contributing to the regulation of plant defense via transcriptional and biosynthetic output in leaves (7).

Accessions of *Arabidopsis thaliana* show variation in defense phytohormone profiles after infection, even though they share similar root-associated bacterial microbiota (8–10). Previous studies examined the roles of defense phytohormones in shaping the wild-type root microbiome by using single mutant lines defective in their biosynthesis or perception, or exogenous defense hormone application in combination with bacterial culturing and/or lower-resolution profiling methods. No generalizable clarity has emerged to date (11, 12). We therefore compared the bacterial root microbiome of wild-type *A. thaliana* accession Col-0 with a set of isogenic mutants

lacking biosynthesis of, and/or signaling dependent on, at least one of the following: SA, JA, and ethylene. We focused on those with multiple mutations that eliminated overlapping defense-signaling sectors (Fig. 1A and table S1) (13). We anticipated that this experimental design would reveal the contributions of plant defense phytohormones to wild-type root microbiome composition.

Through sequencing the 16S rRNA gene, we profiled bacterial communities of rhizosphere (soil directly adjacent to the root) and endophytic compartment (EC) from roots grown in a previously characterized wild soil from the University of North Carolina Mason Farm biological preserve, as well as unplanted bulk soil (figs. S1 to S4, tables S2 to S4, and supplementary materials, materials and methods 1 to 3 and 6a to 6d) (10). Sample fraction (soil, rhizosphere, or endophytic compartment) and the differentiation of endophytic samples from bulk soil and rhizosphere explained the largest proportions of variance across the bacterial communities examined (table S5) (8, 10). Endophytic bacterial communities were less diverse than bulk soil and rhizosphere communities (Fig. 1B and fig. S4), with reduced representation of Acidobacteria, Bacteroidetes, and Verrucomicrobia and enrichment of Actinobacteria and Firmicutes [analysis of variance (ANOVA), *q* value < 0.05]. Individual Proteobacteria families were either enriched or depleted in endophytic communities as compared with those of bulk soil and rhizosphere samples (fig. S5 and supplementary materials, materials and methods 6b). These results are consistent with distributions of bacterial phyla from *A. thaliana* roots grown in four wild soils (8, 10).

Plant genotype affected phylum-level bacterial root endophytic community composition [4.3 to 5.0%, canonical analysis of principal coordinates (CAP)] (Fig. 1B and supplementary materials, materials and methods 4b and 6e) (14), with both hyperimmune *cpr5* and immunocompromised quadruple *dde1 ein2 pad4 sid2* mutant communities displaying lower α -diversity indices than that of the wild type (Fig. 1B, fig. S4B, and supplementary materials, materials and methods 1b). The relative abundance of Firmicutes was lower in immunocompromised *jar1 ein2 npr1, ein2 npr1, and npr1 jar1* mutants, which all lack response to SA (Fig. 1, A and B, and table S1). Actinobacteria were less abundant in *cpr5* and *pad4* endophytic samples, whereas Proteobacteria were more abundant in *cpr5* and *jar1 ein2 npr1* (Fig. 1, A and B; fig. S8; and supplementary materials, materials and methods 4a). Only mutants that lacked all

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An anomalous and unbalanced predator

In the past century, humans have become the dominant predator across many systems. The species that we target are thus far in considerable decline; however, predators in the wild generally achieve a balance with their prey populations such that both persist. Darimont *et al.* found several specific differences between how humans and other predatory species target prey populations (see the Perspective by Worm). In marine environments, for example, we regularly prey on other predator species. These differences may contribute to our much larger ecological impact when compared with other predators.

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