

Human predators outpace other agents of trait change in the wild

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The observable traits of wild populations are continually shaped and reshaped by the environment and numerous agents of natural selection, including predators. In stark contrast with most predators, humans now typically exploit high proportions of prey populations and target large, reproductive-aged adults. Consequently, organisms subject to consistent and strong 'harvest selection' by fishers, hunters, and plant harvesters may be expected to show particularly rapid and dramatic changes in phenotype. However, a comparison of the rate at which phenotypic changes in exploited taxa occurs relative to other systems has never been undertaken. Here, we show that average phenotypic changes in 40 human-harvested systems are much more rapid than changes reported in studies examining not only natural ($n = 20$ systems) but also other human-driven ($n = 25$ systems) perturbations in the wild, outpacing them by >300% and 50%, respectively. Accordingly, harvested organisms show some of the most abrupt trait changes ever observed in wild populations, providing a new appreciation for how fast phenotypes are capable of changing. These changes, which include average declines of almost 20% in size-related traits and shifts in life history traits of nearly 25%, are most rapid in commercially exploited systems and, thus, have profound conservation and economic implications. Specifically, the widespread potential for transitively rapid and large effects on size- or life history-mediated ecological dynamics might imperil populations, industries, and ecosystems.

contemporary evolution | evolutionary rates | fisheries | harvest | phenotypic change

Phenotypic traits of wild populations are constantly molded by changes in the environment and by numerous agents of natural selection (1, 2). Among these myriad influences, however, modern humans have emerged as a dominant evolutionary force (3). For example, among wild vertebrates and invertebrates, and via various perturbations such as introductions into novel environments and pollution of their habitat, humans can cause more rapid phenotypic changes than can many natural agents (4).

Human predators, by exploiting at high levels and targeting fundamentally different age- and size-classes than natural predators (5–7), can generate seemingly rapid phenotypic changes in both morphological and life history traits in exploited prey (8, 9). But how might the rate of phenotypic change in exploited systems compare with other systems subject to strong directional selection? Here, we report a summary of the magnitudes of phenotypic change in 40 systems of exploited prey (fish, ungulates, invertebrates, and plants) and test whether observed changes can outpace those reported in other wild populations subject to either 'natural' or 'other anthropogenic' perturbations. We also ask what harvesting and prey characteristics elicit the most rapid of phenotypic changes in exploited systems.

Results

Data combined from 40 'human predator' systems, comprised of 475 estimates from 29 species, revealed extensive changes to the

morphology and reproductive biology of prey harvested by humans. Morphological traits (e.g., body/horn size) declined in 282 of 297 (94.9%) cases, with an average decrease of 18.3% ($\pm 13.7\%$ SD). Shifts in life history traits (e.g., reproduction at earlier ages/smaller sizes, increased reproductive investment) occurred in 173 of 178 (97.2%) cases, with an average change of 24.9% ($\pm 22.3\%$ SD).

To place these seemingly large magnitudes in the context of time interval over which they occurred, we performed a phenotypic rate comparison based on 'Darwins' (proportional change in units of e per million years). Specifically, we compared 'human predator' rates to nonoverlapping cases from a database (4) on trait changes in wild vertebrate and invertebrate populations driven by either 'natural' or what we term 'other anthropogenic' agents. Analysis of Covariance (ANCOVA) results revealed that *mean* proportional changes per system were significantly greater in human predator systems compared with both natural and other anthropogenic contexts (Fig. 1A). Estimated marginal means, which predict proportional changes for each context in the model while controlling for time interval, were greater in human predator contexts by factors of 3.4 and 1.5, respectively. *Maximum* changes per human predator system were also significantly greater than those in natural systems, but did not differ significantly from those in other anthropogenic contexts (Fig. 1B). Estimated marginal means were greater by factors of 2.6 and 1.3, respectively.

By using our human predator database only, multimodel inference suggested that harvest *Mode* was the most important predictor of phenotypic change ($\Sigma AIC_w = 0.63$). That is, commercial harvests showed greater change than recreational/scientific harvests (*Mode* only model; between-subjects effect, $P = 0.05$), consistent with expectations from higher exploitation levels observed in commercial harvest (see *Methods*). *Trait Type* was also important ($\Sigma AIC_w = 0.36$), with greater changes in life history traits compared with morphological traits (*Trait Type* only model; between-subjects effect, $P = 0.03$). *Capture Method* did not occur in top models.

Discussion

These extraordinarily high rates of trait change in exploited prey populations fundamentally alter our understanding about the tempo at which phenotypic changes in vertebrates and invertebrates can proceed in the wild. We postulate that the average pace of change is exceptionally high because harvest selection is

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