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% (± 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% (± 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. 1*A*). 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. 1*B*). 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 ($\Sigma AIC\omega = 0.63$). 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 ($\Sigma AIC\omega = 0.36$), 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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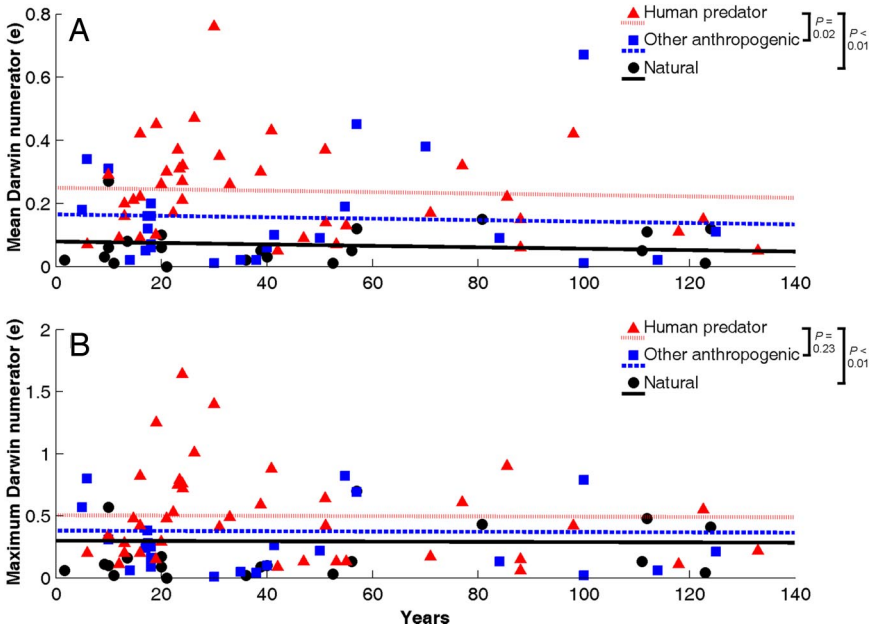

Fig. 1. Human predators outpace natural and other human-driven agents of phenotypic change. (*A*) Mean and (*B*) maximum phenotypic change (Darwin numerator) in 'natural' ($n = 20$ systems), 'other anthropogenic' ($n = 25$) and 'human predator' ($n = 40$) contexts with respect to the mean interval per study system. *Context* × *Years* interactions were not significant (both $P > 0.38$), so slopes were defined by *Years* coefficients and intercepts by *Context* coefficients. Shown are *P* values for Least Significant Difference Tests comparing marginal means between *Contexts*. One outlier datum in B (70 years, 2.57 e, other anthropogenic) not shown.

a uniquely direct and consistent human driver of change. Indirect alterations to phenotypes, like those induced by habitat modification or pollution, depend on the degrees to which 1) the environment responds to human activities and 2) affected organisms respond genetically and plastically to the perturbations. In contrast, human predators select directly on the phenotypes of populations and often adjust their effort in ways that maintain consistent strength and form of selection over time (10). Additionally, harvesting can also result in indirect selective and plastic environmental effects (e.g., increased per-capita food supply resulting from changes in density after exploitation) that can compound direct selective effects (5) and might explain the particularly rapid changes to life history traits we observed.

Regardless of the relative roles of genetic change and plasticity, such large and rapid phenotypic shifts, especially to highly exploited commercially harvested populations, have profound implications. Specifically, such alterations to phenotypes might also generate large and rapid changes in population and ecological dynamics, including those that affect population persistence (11–14). For example, because life history shifts to reproduction at smaller sizes and younger ages can reduce fecundity in many organisms, declines in harvestable biomass (15) or instability in population growth (16) might also develop rapidly in exploited prey. Additionally, the uniquely fast phenotypic changes that occur under harvest might not be mirrored by interacting organisms (i.e., predators, competitors) or by populations released from harvest. Thus, urgent questions include whether interacting species can keep pace with changes in exploited prey and how long 'phenotypic restoration' of harvested populations might require should that become a goal for population or ecosystem recovery.

Materials and Methods

We combined data from published studies that: 1) examined potential phenotypic changes in quantitative traits of harvested prey over time and, if detected, 2) concluded that harvest selection was a likely cause (17). Mean proportional change per 'system' [species in a location (4)] did not differ between the 17 studies that accounted for environmental effects (i.e., animal model, environmental covariates, probabilistic maturation reaction norms) and the 23 that did not (*t* test, $P = 0.83$). We therefore used all available data, which was comprised of 40 systems from 34 studies on 29 species (21 fish, 4 intertidal invertebrates, 2 ungulates, 2 plants). We used entire study intervals, but excluded periods of fishing moratoria and a period in one study during which natural selection overrode harvest selection (18). Data for different sexes, ages, management areas, and traits within each system generated 475 estimates of phenotypic change (see supporting information (SI) Dataset S1).

Data were extracted from tables, figures, or by author correspondence. Magnitudes (proportional changes) were calculated as:

$$m = (x_1 - x_2)/x_1$$

where x is the mean trait value at the beginning (x_1) and end (x_2) of the study (14, 17).

Rates of phenotypic change ('Darwins', or proportional change in units of e per million years) were calculated as:

$$d = (\ln x_1 - \ln x_2)/t$$

where t is time in millions of years (19, 20). Of 475 estimates, 10 were reported in original studies. For others, we used endpoint calculations (above; $n = 255$) or regressions on time series data [(20), $n = 210$]. Directionality of changes differed among traits, so we used absolute values. We did not calculate 'Haldanes', because: 1) generation times and trait standard deviations needed for the calculation (20) were usually absent, and 2) many studies tracked changes in reproductive schedules (e.g., 21), which influence generation times.

We used ANCOVA to compare 'human predator' rates to nonoverlapping cases from a database (4) on trait changes in wild vertebrate and invertebrate populations. These changes were driven by either 'natural' [$n = 20$ systems, comprised of 1549 estimates; e.g., morphological responses of Galapagos finches, *Geospiza fortis*, after episodes of drought (22)] or what we termed 'other anthropogenic' agents [$n = 25$ systems, comprised of 1023 estimates; e.g., life history responses of guppies, *Poecilia reticulata*, after introductions into novel habitats (23)]. Dependent variables for ANCOVA were mean and maximum Darwin numerator estimates per system, which represent what might typically and potentially occur in systems, respectively (4). *Years* served as a covariate to avoid the artifact of rates scaling with time (4, 19, 24, 25). We restricted ANCOVA comparisons to phenotypic (i.e., not genetic) rates in Hendry *et al.* (4) but included studies with both allochronic (evolution within populations) and synchronic (divergence among populations) designs. In both ANCOVAs, the three contexts did not differ in slopes ($P = 0.20$ and 0.29). We thus removed the interaction term to test for the effect of *Context*.

With human predator data, we used AIC_c (26) to compare candidate models ($n = 18$) comprised of *Years*, *Trait Type* (morphological versus life history), *Capture Method* (e.g., gill nets, trawls), and harvest *Mode* (commercial versus recreational/scientific) to predict the mean phenotypic change (Darwin numerator) per system. We used harvest *Mode* as a proxy for exploitation rates, which in 10 studies were greater in commercial than in recreational/scientific harvests (*t* test; $P = 0.02$). Contingency tests suggested that *Mode* was associated with *Trait Type* (*contingency coefficient* = 0.474; $P = 0.001$), making independent interpretations difficult. As a covariate in all models, *Years* showed a marginal and always nonsignificant negative trend (Fig. 1; $\Sigma AIC\omega = 0.23$).

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