

COMMENTARY

Human hunters and nonhuman predators: Fundamental differences

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The article in PNAS entitled, "How constraints affect the hunter's decision to shoot a deer," (1) develops and tests an extremely useful model of the way deer hunters behave in Norway. The authors, Diekert et al. (1), find that hunters, constrained by the number of deer that they can kill, by the number of days that they can hunt, and by social norms, adjust their selectivity regarding the animals they shoot. As costs rise and constraints tighten, they become less selective in the manner predicted by an optimal stopping model (2). The analysis also recognizes that objectives (recreation, provision of meat, or deer population reduction) differ among hunters, and that such differences affect the hunters' selections of deer prey. These findings should generalize qualitatively to hunters from other nations and of other game.

Hunters and Predators: Fundamental Differences

The article spurs the reader to ponder similarities and differences between hunters (hereafter, humans) and predators (hereafter, nonhumans). This commentary focuses on some significant differences between hunters and predators, and between their effects on their prey populations.

Diekert et al. (1) observe that large carnivores, which are the natural predators in many wildlife populations, are now well below equilibrium levels in many industrial countries, and that hunters provide the predominant preying control on wildlife populations. They observe, as well, that hunters, by their selectivity and ability to kill at far above natural rates, produce far different effects on prey species than would their natural predators. However, there is a counterbalance to hunters' outsized killing capability. Humans can impose regulations on themselves (e.g., catch limits, prohibitions on taking animals of a certain size or gender, hunting seasons) and can establish and adhere to social norms. The response to such limitations is the focus of Diekert et al. (1).

Most carnivores hunt to survive; they adjust their behaviors depending on their needs and on the availability of prey. Predatory animals have highly

variable behaviors both within and among species. Lions appear lazy; they mostly sleep and rest because they can afford to do so. Snakes can be much more infrequent hunters; some eat only every 6 mo. Shrews are near-constant hunters; a few hours without eating can be fatal. Humans are in the tiny minority of species that often hunt recreationally, although our domesticated pets, dogs and particularly cats, also often kill their prey with little need for consumption.

Hunters have powers not available to predators, as mentioned; they can constrain their hunting behaviors through regulations and social norms (3). The behavior of predators, by contrast, is regulated by natural forces. Where humans are not significant participants, coevolved predator-prey populations produce equilibria. The equilibria may wander, and some populations move in cycles (4). In boreal forests, the lynx-snowshoe hare cycle, with some other predators participating, lasts roughly a decade and is an extreme example, with populations exploding and collapsing (5). Not surprisingly, lynx, just like Norwegian deer hunters, move on to less favored targets when faced with the constraint of a collapse in the hare population. Lynx, however, cannot long sustain themselves on secondary prey, and their population subsequently collapses, with emigration and losses to reproductive capability contributing.

Humans and Species Extinctions

No endangered species regulation constrains predators. However, there is virtually no known case where native predators have driven a prey species to extinction in a setting where humans played little or no role. Humans, by contrast, despite their regulatory tools, have contributed to innumerable extinctions. Humans can disrupt equilibrium patterns through their often outsized hunting capabilities, their habitat destruction, and their introductions of invasive species.

The lamented extinction of the once-multitudinous passenger pigeons is one example. Human activity greatly reduced their breeding grounds. However, the decisive exterminating factor was that those pigeons traveled in vast flocks, making them easy for humans

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Author contributions: R.Z. wrote the paper.

The author declares no conflict of interest.

See companion article on page 14450 in issue 50 of volume 113.

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to hunt even when their numbers dwindled (6). Alas, the human fervor for passenger pigeons did not give the pigeons time to evolve safer travel procedures.

A somewhat different story of cycle disruption revolves around humans' superior ability to locate their prey. Hunters, unlike the nonhuman predators, may make extra special efforts to go after trophy species, such as the "Big Five" (lion, Cape buffalo, leopard, African elephant, and rhinoceros), which then become scarce. Thus, as elephant herds collapse, as they are now doing, the price of ivory may soar. If the cost of poaching goes up more slowly than the value of ivory, the cyclical phase of depletion may accelerate rather than self-correct. This depletion raises the need for humans to hunt humans, at least in terms of tracking and arresting poachers, and thereby significantly raises the costs to elephant hunters. This observation illustrates one of the few advantages that hunters have over predators if species preservation is the concern: Humans can consciously and collectively agree to curb or redirect their hunting activities.

Heterogeneity among predators of the same species may play a significant role in natural selection. Much has been made of habitat heterogeneity in predator-prey relationships (7). Heterogeneity within a predatory species should also be considered. When prey are abundant, they are easily found. Thus, the sickly within a predatory species can survive alongside the sturdy. However, if food sources are scarce, dinner will disproportionately go to the strong and the swift. When a predatory species might be in danger due to scarcity of food, it is subject to more stringent selective pressures, which is good news for the next generation. Such a pattern is no doubt beneficial to the species' long-term survival.

The deer-hunter article by Diekert et al. (1) also stimulates readers to attend to the role of hunting from the standpoint of the prey. The survival of prey is critical to both humans and ecosystem balance, even when their natural predators have been relegated to a minor or zero role. As any prey grow scarcer, we can speculate, as more articles like the article by Diekert et al. (1) should document, on the ways they might gain a selective advantage relative to hunters. Positing that prey are important consumers of their favorite food sources, their food supply will be relatively abundant. They can spend less time foraging, an activity that tends to make them more available targets. When prey numbers are threatened by humans, a greater fraction of a prey species can

locate in more difficult terrains, further from civilization, which is another way to make them more difficult to hunt. Despite lacking great cognitive powers, prey may naturally adjust their behavior to protect themselves against hunters, as they do against predators (8).

Humans can protect a depleted prey species by adjusting their hunting behavior. Thus, social norms, regulation, or merely higher

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hunting costs lead them to turn to other species or curb hunting activity overall. A salient early success was the effort that enabled the severely threatened American alligator population to recover fully by 1987 after the Endangered Species Act had prohibited its hunt. Lynx take a different course to enable hare populations to recover; they die themselves, suffer reproductive problems, and move away.

In current times, humans seem much more capable of limiting hunting activity than they are of undoing the introductions of invasive species and the destruction of native habitats. Feral cats, introduced to locales as pets, are responsible for the extinctions of numerous bird species (9). Burmese pythons, also originally pets, now thrive in vast numbers in the Everglades. The pythons have driven populations of small animals, such as raccoons, rabbits, and foxes, down to tiny percentages of their original numbers (10). Extinction of some species, or at least local extirpation, is probable.

Humans have powers not available to animal predators, both to kill prey and to prevent such killing. Some such powers are exercised individually; others are exercised collectively. When hunters kill, their "strongly selective hunting may have unexpected ecological and evolutionary consequences" (ref. 1, p. 5). Fortunately, this article enables us to understand such selective behavior better, thus creating some potential to create policies to alter it.

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