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Review

Ecology of Fear: Acclimation and Adaptations to Hunting by Humans

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Abstract: Humans greatly influence the ecosystems they live in and the lives of a wide range of taxa they share space with. Specifically, human hunting and harvesting has resulted in many species acclimating via diverse behavioral responses, often quite rapidly. This review provides insights into how hunting and harvesting can elicit behavioral changes. These responses emerge from a species' previous and evolving ability to assess risk imposed by hunters and respond accordingly; a predator–prey game thus ensues, where both players may change tactics over time. If hunting is persistent, and does not result in the taxa's extirpation, species are expected to develop adaptations to cope with hunting via natural selection by undergoing shifts in morphology and behavior. This review summarizes the various ways that human hunting intentionally and incidentally alters such evolutionary changes. These changes in turn can influence other species interactions and whole ecosystems. Additionally, alterations in behaviors can provide useful indicators for conservation and evolutionarily enlightened management strategies, and humans should use them to gain insights into our own socio-economic circumstances.

Keywords: behavioral responses; culling; fear; indicators; non-consumptive effects; predation risk; rapid evolution; wildlife management

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1. Introduction

The contrast was striking. A 1989 visit to the Gazelle Peninsula of the Island of New Britain, Papua New Guinea, provided just fleeting glimpses of parrots in the wild: A flash of green—perhaps a rainbow lorikeet (*Trichoglossus moluccanus*)? A flash of white—a sulfur-crested cockatoo (*Cacatua galerita*)? Both were seen at great distances flying high, fast and away. The best view of such birds was in Rabaul's outdoor market where some were in cages, and others in just feather adornments for sale, all acquired by skilled trappers and hunters pursuing their livelihood [1,2]. Now, switch to a few days later in Cairns, Australia; viewed from a park bench, there were dozens of noisy rainbow lorikeets packed in a nearby tree. Additionally, two sulfur-crested cockatoos foraged on the ground just meters away. There was no need for binoculars, patience or observation blinds. This was birdwatching made easy. Why the stark contrast in birdwatching experiences? The answer was a fear of humans, high in the Gazelle Peninsula and low in Cairns. The same bird species exhibited phenomenally different ecologies driven by the presence or lack of intense human hunting [3,4].

Clearly, species can be driven into extinction by intense hunting. Examples in recent centuries include the Great Auk, the Dodo, and the Passenger Pigeon. Some species may persist only in refuges from hunting, such as the Javan Rhinoceros, which today is found only in the Ujung Kulon National Park in Java. Because the remnant population is protected from hunting, ironically, there is unlikely to be selection that could improve survival in the face of hunting, outside the park.

In response to hunting or harvesting, some species will eventually acclimate or adapt via diverse behavioral responses—if they do not go extinct first. Such escape behaviors may simply be part of the species' current repertoire reflecting past selection pressure. The behavioral responses could emerge from a pre-existing ability to assess risk from humans and respond accordingly. Furthermore, if hunting is persistent and does not result in the prey's extirpation, then adaptations via natural selection acting on heritable variation may follow. The hunted population may evolve traits to directly avoid mortality, or to indirectly exploit and avoid changed opportunities and hazards resulting from altered population sizes or population structures. Over a long-enough timescale, hunting will cause any persistent yet continually exploited population to first acclimate via plasticity and then adapt. In human-dominated landscapes, phenotypic traits (both plastic and genetic responses) of wild populations change at a faster rate when those populations are hunted and harvested by humans [5,6]. Human-hunted systems showed phenotypic changes 300% quicker than natural systems and 50% quicker than human-driven (though not hunted) systems [6]. The question does not concern whether this will occur, but how much and how quickly it will occur.

Here, we review and provide conceptual frameworks for how hunting and harvesting species (1) elicit behavioral changes in the prey, (2) induce subsequent evolutionary changes, (3) drive indirect and emergent properties influencing other species interactions or whole ecosystems, (4) can have useful behavioral indicators for conservation and management, (5) can inform behaviorally and evolutionarily enlightened management strategies, and (6) provide a mirror into our own socio-economic circumstances. Understanding human effects on the evolution and behavior of hunted and harvested species becomes critical for sustainability. As we shall discuss below, harvesting through hunting and fishing involves diverse motives and cultural and regulatory contexts, all of which can vary locally and globally in time and space.

2. The Hunters: Motives and Forms of Hunting and Harvesting

Humans have harvested animals for millennia, with our own evolution linked to hunting. Just like any predator that intentionally seeks to capture prey, a predator–prey behavioral game ensues that may result in longer lasting inter-generational coevolution. What is special about humans as predators—besides our own self-obsession as a species—is (1) the rapidity with which we have crafted technologies to become more lethal and diverse in our hunting repertoires, (2) the degree to which we induce incidental and unintentional mortality to other species, leading to novel selection pressures, and (3) the expanding role of social norms, bioethics, hunting and management rules, and, dare we say, the fickleness of humans in determining the extent to which we hunt other animals. Among a number of species worldwide, it is notable how, for species like the Canada goose (*Branta canadensis*) and beaver (*Castor fiber* and *C. canadensis*), humans have gone from being their greatest predator to their benefactor in <100 years [7,8]. Humans have become a new apex 'super-predator' and represent a main source of risk for wild populations [9,10]. Motives for hunting can include desires for fun, money, and revenge [11]. All of these can change rapidly, because of a wide variety of social, economic, and cultural forces.

Behavioral games adjust over time as the strategies of hunters adjust to circumstances, technologies, and changes in the behaviors and other characteristics of the hunted prey. Sometimes, humans adjust faster than their quarry. The Blitzkrieg hypothesis suggests the megafaunal extinction in the late Quaternary was driven by human predation and prey naivete to the colonizing humans [12,13]. Humans were able to spread across land masses, responding to the hunted's behavior, following the prey's gradient of fear and adjusting harvest methods accordingly. Those prey that survived did so by becoming fearful of humans and adjusting their own behaviors. Furthermore, these prey responses, in turn, influenced the hunters' actions, setting off a two-player game of hunters versus the hunted. This game was first recorded 43.9 thousand years ago in an elaborate rock art panel in a limestone cave in Leang Bulu'Sipong, Sulawesi, Indonesia. The art depicts several therianthropes, which were mythological part-human part-animal figures hunting wild pigs and dwarf bovids [14]. Historical paintings and more current photographic evidence demonstrate a wide variety of human predation and subsequent influences on wildlife (Figure 1).

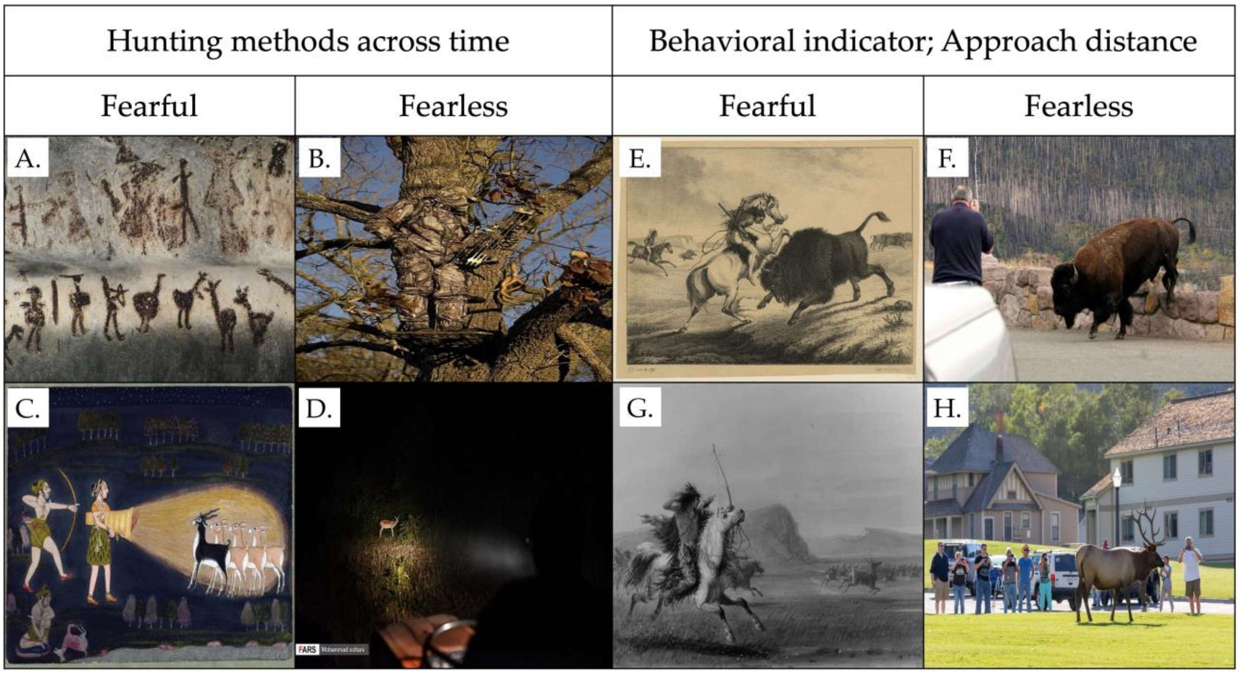

Figure 1. Contrasting examples of different hunting methods across time (left section; photo columns 1 and 2) and the behavioral indicator, approach distance (right section; photo columns 3 and 4), that either elicit fear (photo columns 1 and 3) or demonstrate fearlessness (photo columns 2 and 4). (**A**) A cave painting in the Magura Cave in North-Western Bulgaria depicting scenes of hunters pursuing cervid-like species with bows (Wikimedia Commons); (**B**) a person, wearing camouflaged clothing and in a deer stand, waiting for game with a crossbow (Wikimedia Commons); (**C**) 18th century art depicting the Bhil Ghantabhera hunting method, in which a bell is rung and an oil lamp is lit through a concave basket to illuminate the animal and hide the hunter (Walters Art Museum); (**D**) a depiction of spotlighting, usually from a vehicle, which is illegal on public land in the USA but allowed on some private land (Fars Media Corporation); (**E**) a print of Native American hunters pursuing bison from horseback, by artist A. Kollner (Library of Congress); (**F**) a bison jumping over a wall while being photographed by a tourist in 2005 at Yellowstone National Park, USA (NPS/Arnie Spencer); (**G**) a painting, circa 1860, of a Native American person hunting elk on horseback, with the animals retreating, by artist A. Miller (Walters Art Museum); (**H**) a group of tourists approaching a large bull elk in 2014 at Yellowstone National Park, USA (NPS/Neal Herbert).

Motives for hunting can be intentional or incidental, which does not so much matter to the prey if they become killed either way. To the hunters, however, there can be different reasons for enacting both types of hunting. Intentional hunting involves hunting animals for sustenance, management or sport. When hunters are seeking out a prey, they can assess that prey's behavioral responses and use it to their hunting advantage. For example, hunters would exploit prey naivety, as seen with the extirpation of American bison (*Bison bison*) across North America in the 19th century from humans overhunting [15]. Indigenous people that hunted in relatively low population densities and using traditional methods (though most were quick to integrate horses for increased mobility and proximity) were superseded by settler immigrants with firearms whose range and lethality increased rapidly across the 19th century. First, hunting with bow and arrow, and then the introduction and evolution of firearms intensified hunting pressure, wiping out herds and nearly exterminating the American bison.

Hunters also learn to exploit prey behaviors by creating evolutionary mismatches, where escape behaviors honed over generations to evade non-human predators can be used to the advantage of humans. Evidence in North America shows sophisticated infrastructures such as cairns and other chutes for driving and concentrating bison, including cliff jumping [16]. Native Americans coordinated relay or persistence hunting, in which hunters on horses would chase deer species, pronghorn (*Antilocapra americana*) or other game, until the animal was too tired and could easily be killed. Hunters can also exploit social behaviors by attracting prey with mating calls, the calls of conspecifics or decoys, e.g., in duck hunting. By way of anecdote, a colleague and expert hunter patiently attracted the attention of a female turkey using his hand-crafted male turkey call. After eliciting the response call of the female turkey, he stealthily advanced towards her call, only to discover an equally fooled and surprised hunter who had been skillfully making the female’s call [17].

Another important consideration for intentional hunting concerns whether hunting is for food, products, sport or luxury items. This matters. If it is for food or products, then hunting pressure may decline as the hunted population becomes more wary or sparse in number. Return on effort becomes a critical component driving the hunter’s motives. If prey acclimate or evolve better means for surviving, then the entire population of prey benefits from lowered hunting pressure. The opposite, however, may occur if hunting is carried out for sport or luxury goods. In this case, rarity leads to value. To the sports hunter, hunting may heighten interest or a sense of accomplishment. Different cultures may value animal objects or products differently. However, if such objects have cultural or luxury associations, then they provide the possessor with social capital rather than nutrition. They become more valuable with rarity. If such rare or endangered species do acclimate and evolve escape behaviors or traits, this may actually result in heightened hunting effort whether legal or illegal.

Hunting can also be incidental, which includes humans inadvertently harvesting or capturing animals in their intentional hunting (fishing and trapping) or incidental human activity (habitat alteration). In certain scenarios, humans can go out seeking ‘species A’ and happen upon ‘species B’, which is an easier to catch or more desired species. This incidental mortality includes killing animals in vehicle collisions or catching non-targeted species as bycatch, such as in fishing nets. At the individual level, threats to fish and marine mammals include incidental entanglement in fishing gear [18] and vessel collisions [19]. Mass injury [20] and mortality [21] of other species within the ecosystem can follow. Between 2003 and 2004, an estimated ten billon juvenile sea scallop died from fishing operations in the mid-Atlantic, disturbing their temperature equilibrium—scallops were being pulled to the surface and then returned to the sea floor [21].

Incidental hunting can lead to both direct lethal effects such as the selective removal of certain individuals by age, sex and size, and indirect effects such as altered behavior. Traits that make an animal more vulnerable to capture or killing can be selectively removed from the population. Animals that survive capture and killing may learn to avoid specific areas or alter their behavior to reduce predation. Even in the absence of lethality, indirect effects on the hunted can be strong and result in phenotypic trait changes that lower fitness. When behaviors have a genetic basis, this can then be passed on to future generations and lead to evolutionary shifts in behavior. Figure 2 displays two examples of intentional and incidental hunting and the behavioral responses that ensue.

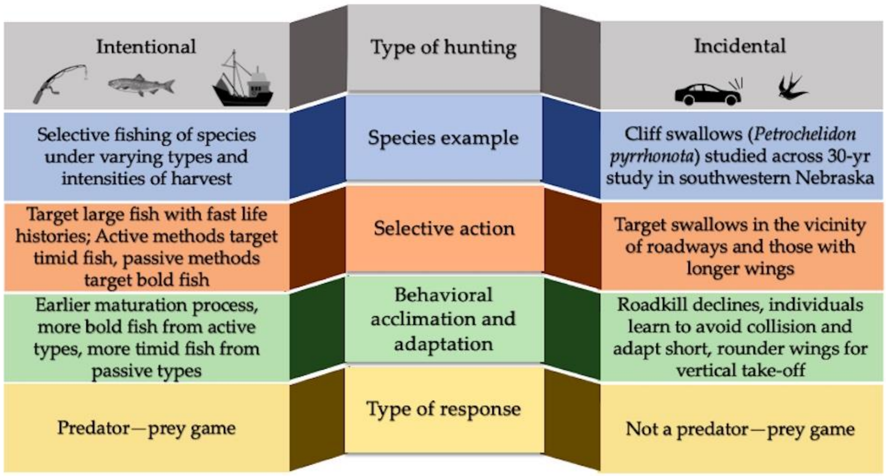

Figure 2. A schematic view of how intentional (left column) and incidental (right column) human hunting impacts the behavioral responses of different species. The intentional hunting of fish [22–24] and incidental hunting of cliff swallows [25–27] can ultimately impact future generations in similar yet contrasting ways.

Dynamics of Hunting Cultures and Regulations in Time and Space

Nature often reflects us as we impose our norms and regulations, which can change swiftly across space and time. As expected, animals respond behaviorally and then evolutionarily with the cultural and regulatory dynamics of human hunting. Depending on rates of change in how species are hunted, fished and harvested, such species may alter behaviors in near synchrony with human culture, or experience various degrees of time lags. Evolutionary changes necessarily lag changes by humans, but nonetheless can result in rapid evolution, be it hunting or simply in response to human-dominated landscapes in general [28–30]. For instance, across various European countries, hunting cultures have been hunting for subsistence, trophy, sport or culling [31–33]. When a subset of a hunted population is more vulnerable, there may be divergences in fear responses, just as trophy hunting risks selecting against the very trait desired by the hunters [34–36]. Fear responses can be rapid and occur in response to regulations such as hunting seasons, where tracks of land are opened to hunting for fixed durations. Deer hunting data from Illinois in 2012 show that in areas open to hunting, most of the kills occur in the first three days as the likelihood of shooting a deer declines precipitously (35%, 25% and 17% of the total takes occurring in days 1–3, respectively) [37]. This occurs not from population depletion but because individuals become warier or leave the area. Some cultures do not permit hunting on their land and refuse it as a moral standard [33]. In the Nyingmapa Tibetan Buddhist beliefs, Beyuls are sacred hidden valleys that have strict no-hunting restrictions [38,39]. Additionally, the Beyul people practice non-violence (e.g., Sekya) and believe there should be no hunting of animals or suffering of wildlife [39].

During the 'anthropause' or the period of reduced human activity during the COVID-19 pandemic in 2020, both human and animal behaviors changed rapidly. Despite car traffic decreasing, wildlife–vehicle collision rates in the US increased during the pandemic [40]. One contributing factor could have been human behavior such as driving faster due to the roads being less congested with traffic. From the human's perspective, wildlife became bolder. However, were wildlife actually bolder or were we just home to witness them? In Spain, the absence of humans during the early-morning rush hour coincided with an increase in urban bird detection probability [41]. Researchers in the Deccan Plateau, India, tracked the activity patterns of four highly poached mammals using camera traps during lockdown [42]. Though reduced human activity allowed wildlife to explore and increase their diurnal activities, there were decreases in forest-related law enforcement relating to poaching, thus influencing the human-induced landscape of fear [42].

3. The Hunted: Types and Efficacy of Fear Responses

Being hunted and the anticipation of being hunted, if such events are chronic, can have drastic effects on surviving individuals. As hunters adapt their own hunting methods and strategies, the hunted begin connecting cause and effect through information gained and develop a fear response. Fear is not just a human emotion; it can be readily observed among many taxa in examples of prey fleeing a predator. Fear is the conscious or unconscious perception of risk [43]. It manifests in many ways, from increased antipredator behaviors such as vigilance, immobility and aggression to avoiding risk by changing movement and habitat selection. Because prey rarely know all relevant information about human hunters, an evolutionary stable strategy for the hunted is to maintain a certain level of fear at all times [44]. Antipredator behaviors can be reactive, such as escape or flight when humans are near, or proactive traits such as standing vigilant or giving alarm calls to better detect humans and escape quicker. Fear responses are important to understand, as they can both increase and decrease prey survival [45]. Below, we organize examples of different fear responses according to the type of hunting that enables them.

Types of intentional hunting can be categorized into active and passive. Active hunting typically includes chasing and capturing a specific target. Passive hunting methods employ a sit and wait game, with the target coming to the hunter. In its most passive form, such hunting techniques can involve poisons (for fish and the control of birds and mammals seen as pests), snares and traps for all matters of terrestrial and aquatic quarries. However, it should be noted not all such methods are allowed across the globe. They are often dependent on region and land type (private or public). Such contrasting methods can greatly influence the hunted individual's response and shape more permanent phenotypic traits by selection across the prey population and species. In nature, active predators that chase their prey can cause fewer behavioral changes in prey than a passive ambush-style predation mode that often surprises prey [46,47]. African ungulates altered their space use when preyed upon by ambush-style hunters such as lions (*Panthera leo*) and leopards (*Panthera pardus*), more so than for the active chase hunters such as wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) ([48], as cited in [47]). In regard to human harvesting, these behavioral responses should lead to behavioral changes over time. Active fishing gear such as trawls and seines preferentially target timid fish with low swimming ability, thus selecting for bold individuals [22,23]. On the other hand, passive fishing gear and methods such as gill nets, traps and angling with a rod and line preferentially harvests bold, fast-growing fish, leaving more timid individuals behind, e.g., creating an emergent timidity syndrome [23,24].

3.1. Responses from Active Hunting (Chase and Capture)

Active hunting such as chasing and pursuing an animal can influence behavioral responses such as shifting space and time use, increasing approach distances, changing herd dynamics and expanding the range of human cues. In ungulates, active methods, when chronic, can displace animals from specific areas, thus reducing the impact of those hunting methods [47]. White-tailed deer (*Odocoileus virginianus*) adapt behavioral strategies to the hunting period through reduced movement and space use (micro-ranges) [49]. Even before the actual hunt, during the scouting period, deer responded, as long as humans were present. Additionally, it has been reported that ungulates in hunted areas have greater flight responses than animals in non-hunted areas [50]. In Alberta, Canada, elk (*Cervus canadensis*) populations on public lands with hunting and motor activities had increased levels of vigilance and decreased feeding times near roads compared to those in the national park [51]. Behavioral responses also vary in terms of hunting intensity and duration. In areas of high hunting intensity and longevity such as southern Germany, roe deer (*Capreolus capreolus*) that are hunted year-round displayed stronger spatial avoidance of humans. In areas of lower hunting intensity and longevity, such as the USA, which imposes short hunting seasons and bag limits, white-tailed deer displayed more temporal avoidance, maintaining activities at sites and avoiding threats temporally (i.e., time latency) [52].

In ungulate game species, hunting seasons and even just human presence can elicit changes in behavior such as higher vigilance and reduced foraging (e.g., elk [51]), lower exploration and distances traveled (e.g., white-tailed deer [49]) and switching space use to safer habitats (as seen in red deer (*Cervus elaphus*) [53] and white-tailed deer [54]). In hunted reptiles like the Japanese moccasin snake (*Gloydius blomhoffi*), a venomous species intensely hunted for medicine and food, fear responses included increased flight distances from approaching humans and more defensive behaviors than those in non-hunted populations [55]. Non-hunted species can indirectly be affected by human hunting as well. Northern bobwhites (*Colinus virginianus*) are ground dwelling quails, and while they are not hunted directly, they can experience indirect exposure to hunting events that include discharged firearms, pointing dogs, horses and vehicles of hunters. Observations made after such hunting events showed that bobwhites within the hunting area had increased foraging frequency and decreased foraging durations and areas in which they foraged [56].

Human hunting pressures also influence a wide array of social behaviors and structures, such as parental care, territoriality, reproductive behavior, group size, mating systems and intraspecific competition [57]. A meta-analysis by Verdade (1996) details social behavior changes among various classes of vertebrates due to human hunting and harvesting [57]. In female Paraguayan caiman (*Caiman yacare*), decreased maternal behaviors such as frequency of nest attendance were observed at sites exposed to intense hunting [58]. This led to increased nest predation and resulted in lower egg survivorship, thus influencing the reptile's overall reproductive success. The interruption of reproductive behaviors of the passenger pigeon (*Ectopistes migratorius*) is also an example [59]. The pigeon became extinct in 1914 mainly due to intensive human hunting coupled with the breakdown of social behaviors such as colony size and breeding rate.

3.2. Responses from Passive Hunting (Sit and Wait)

Passive hunting, such as sitting and waiting for an animal to succumb to snares, nets, poisons or baits, can influence the degree of neophobia, avoidance behaviors and social learning. The hunted can begin recognizing cues left by hunters and change their movement patterns accordingly, as seen in the highly olfactory coyote. In a northern California, USA, population of coyotes (*Canis latrans*), juveniles were found to be more vulnerable to being captured by stationary devices likely due to their lack of experience and the increased time spent in unfamiliar areas [60]. Alpha coyotes in a protected population, also in northern California, used their strong scent cues and showed extreme avoidance of human activity and objects such as camera stations [61]. Beta or transient coyotes did not respond to human activity [61]. In a multispecies mesocarnviore camera trap study, masking human scent did not affect detection rates even for species that can be hunted or trapped [62]. White-tailed deer in Oklahoma, USA, altered their behavior temporally to avoid detection by rifle hunters, with a decreased observability of animals during the hunting season [63]. Risk avoidance behaviors can increase chances of escaping predation but also result in missed foraging opportunities. An animal should therefore change their fear response proportionally to the severity and intensity of the threat, as proposed by the risk allocation hypothesis [64].

4. Hunting as a Selective Force: Evolutionary Changes to Populations and Species

Rapid evolutionary changes have been linked to different anthropogenic sources of selection such as the introduction of invasive species, habitat urbanization and degradation, climate change and exploitation [65]. Exploitation through selective harvesting in particular has had a dramatic influence in driving adaptations and evolutionary change [65,66]. Hunting creates strong selective forces that start with variations in behavioral responses that allow species to acclimate first to increased predation pressures. However, a change in activity budget towards anti-predator behaviors and away from non-urgent reproductive and foraging behaviors can have major implications on future population and species demographics. Across vertebrates, selective dynamics of hunting can also shape phenotypic traits, which can go on to reduce the frequency of those desired traits and change population dynamics.

For hunting and fishing industries, the most desired animals are harvested, reducing the frequencies of those wanted phenotypes in the surviving individuals. Harvesting and hunting usually selects for distinctive individuals with a large body size and large secondary sex characteristics. In doing so, humans select against desired heritable phenotypes and, thus, increase the frequency of less desirable traits [67]. Predators, natural or human, will select for traits that disadvantage the predator; for example, cheetahs would love nothing more than slow gazelles with short legs. When we remove the most desirable individuals, we diminish the presence of desired traits. Kangaroo island, Australia, is so named because dozens of western grey kangaroos (*Macropus foliginosus*) were harvested by sailors in the early 19th century [68]. These kangaroos had no fear of humans. Such populations over time will either experience extirpation, acclimate and adapt to the novel predation risk, or survive through a cessation of hunting [69].

Intense selective harvesting of large mammals with large weapons may lead to the evolutionary shrinkage of those weapons [34], though this has been disputed by hunting groups [70]. For example, there has been an evolution of smaller horn sizes in male bighorn sheep (*Ovis canadensis*), with a decline in horn size [71,72] and body weight [52] driven by selective trophy hunting. Mouflon (*Ovis gmelina musimon*), a wild sheep in southern France, have experienced decreased body mass and size in both sexes and reduced horn measurements in males in all age classes since the inception of unrestricted selective hunting of the largest horned males in the 1970s [73]. In South Luangwa National Park in Zambia, poaching of African elephants (*Loxodonta africana*) for their ivory across twenty years resulted in the frequency of tuskless females increasing from 10% to 38% [74]. In Canada, the reduction in the silver morph in the red fox (*Vulpes vulpes*) was an early documentation of trait frequency change from selective harvest [75].

Mortality under selective hunting by humans differs from an organisms' natural mortality in that humans non-randomly hunt for size, age or specific phenotypes, in ways differing from natural selection pressures [9]. In agricultural and aquacultural systems, the most desired animals with the most desired traits are usually selectively bred with the goal of increasing the frequency of those wanted production phenotypes [76,77]. However, these human-induced evolutionary changes may ultimately work against desired management goals by impacting future yield, as is hypothesized to be happening in fisheries [78,79]. Life history traits subject to fishing-induced evolutionary changes include body size, migration timing and age structure [66,79,80]. In commercial fishing, larger fish are usually of higher value. The selective harvesting of large Chinook salmon (*Oncorhynchus tshawytscha*) has been suggested to lead to reduced size-at-age within approximately five generations [81]. Fishery-induced evolution of maturation patterns were observed in the Yukon River, Alaska, USA, which historically had large, old-aged Chinook, though the numbers of very large fish (>90 cm) has been declining with fishing [79,82]. Northern Atlantic cod (*Gadus morhua*) fisheries resulted in a shift towards earlier maturation and smaller size because the fishes harvested were usually fast-growing, matured later and therefore were removed prior to reproducing [83].

It can be difficult to separate natural and hunting-induced selection, as they operate simultaneously. However, 50 years of data on trait dynamics of pike (*Esox lucius*) at Lake Windermere, UK, suggested opposing relationships for harvesting versus natural selection [80]. Pike from the lake, which has not experienced commercial fishing since 1921, were considered under natural selection compared to pike from an experimental fishery that used gillnets, which were considered under harvest selection. Natural selection favored larger-sized fish while harvest-induced selection acted against larger-sized fish [80].

Selective harvest of strong adults from the gene pool results in their obvious removal, which can lead to sexual maturation earlier, smaller size and lower fitness. The stage of an individual's life history in which they are harvested has major consequences on the harvest-induced evolutionary change in the remaining population, as observed in anadromous salmon species and reviewed by Hard et al., 2008. Both immature and mature fish are harvested in high-sea fisheries, whereas freshwater or estuary terminal fisheries harvest mainly mature fish during spawning migration [79]. In a meta-analysis of studies on hunted and non-hunted vertebrates, invertebrates and plant species, organisms reproduced 25% earlier under human-harvested systems [6]. Ungulate harvesting also tends to reduce adult longevity, in particular for males, and also impacts their reproductive success, thus skewing the breeding sex ratio [67,84]. More than 50% of adult male ungulate and carnivore mortality can be caused by hunting [34,85,86].

Long-term studies, such as a 30-year survey of cliff swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska, USA, can demonstrate how harvesting, even if not intentional, can result in behavioral acclimation and morphological adaptations [25]. Vehicle mortality from hitting fast moving cars, among other environmental forces, contributed to cliff swallows adapting to roads with shorter wings [25,26]. Shorter wings allow for more vertical take-off, enabling birds sitting on roads, such as cliff swallows, to better avoid oncoming vehicles [26,27]. A decline in road kill over time was also seen, and those killed on roads had longer wings [25]. Additionally, cars may have killed off the risk-taking swallows, leaving cautious birds behind [25,87]. Individuals that are bolder, more active and/or aggressive are vulnerable to being hunted and harvested, leaving timid, less bold individuals. The difference between difficult-to-catch introduced brown trout (*Salmo trutta*) and the more easily captured native North American trout has been suggested to be due to the brown trout being heavily angled in Europe prior to introduction in the USA [88]. Brown bears (*Ursus arctos*) lived longer if found further from roads, which is primarily where hunting took place [89]. Brown bears were also more active at night during the hunting season [90].

The demographic consequences of hunting are usually the primary focus for management. However, considerations should be made for the strong selective forces enacting on the surviving individuals, which over time can markedly change the traits of the hunted population [34]. This may vary by hunter location (more specific hunting regulations in Europe) and culture (Indigenous vs. settler colonialists), but often, these evolutionary products are not fully considered by managers, hunters and animal harvesters [91]. Allendorf and Hard (2009) propose much needed-strategies for fisheries and wildlife managers to account for the rapid evolutionary changes expected to come from selectively removing and harvesting species [67].

5. Unintended Consequences: How Responses of Hunted Prey Change Whole Communities and Ecosystems

Human hunting can alter wildlife activity patterns, which consequently influences whole ecological communities [92] and sets off behaviorally mediated trophic cascades [93]. For example, when the age structure of a population decreases from human-induced mortality, the population itself can become more susceptible to external threats [94,95]. The unintentional consequences of hunting on non-hunted species can be an important but often overlooked component in understanding these interactions. As diurnal 'super-predators', humans can push taxa toward nocturnal activity [96,97] and reduced feeding times [10]. This can influence both predator and prey species. The Florida panther (*Felis concolor coryi*) benefits from the change in white-tailed deer behaviors during the deer hunting season. Deer respond to hunting by moving further from roads and increasing nighttime activity, which is more preferable for the carnivore [54]. Predators with increased nocturnality will need to alter their diets toward prey that are also accessible in nocturnal times, which can reshape lower trophic levels [96,98]. Prey, too, may alter their diel activity and decrease their own nocturnality so as to gain a temporal and spatial human shield against predation [99,100]. In Ethiopia, mountain nyala (*Tragelaphus buxtoni*) under predation from nocturnal spotted hyenas (*Crocuta crocuta*) moved to areas of human settlements at night, which hyenas avoid out of fear of humans [101].

6. Conservation and Management

6.1. Fear Responses as Behavioral Indicators

Fear responses can be used as behavioral indicators in conservation and management programs, as they provide quantitative and qualitative metrics on an animal's perception of its environment. Just by observing a species' behavior, it is possible to determine if they are being hunted or depredated on, or even if humans are just existing nearby. Darwin noted in his studies how vertebrates that evolved on islands without humans were tamer than were animals historically living with humans.

In Nepal, in areas where hunting bans are enforced, Himalayan tahr (*Hemitragus jemlahicus*) forage and spend more time in closer proximity to humans [102] compared to another region where blue sheep (*Pseudois nayaur*) experience hunting and forage further from humans [103]. Fear responses include anti-predator behaviors such as vigilance, alarm calls and approach distance [104]. Blue sheep also respond to the risks of nearby snow leopards (*Uncia uncia*) with increased vigilance [103]. Vigilance levels, as a sign of fear, were then used by researchers in the field to assess the whereabouts of snow leopards, resulting in six sightings of this elusive predator [105].

Often, human stakeholders will either overstate or understate the impact of hunting or poaching on a species of conservation interest. Here, behavioral indicators may provide a more honest signal of how the species perceives risk from humans. Approach distance provides a useful metric [50]. Using North American bison as an example, this approach distance likely increased with the arrival of Neolithic humans [106–108]. Presumably, this distance increased further with improved hunting techniques (bows and arrows) and later with horses and guns. While this is speculation, it is known that, initially, approach distances from bison were so short that hunting with firearms was extremely effective. However, as time went on, approach distances increased, and it was only skilled buffalo hunters with longer range rifles and the means to exploit bison herd dynamics who brought on massive kill rates. Hunted to near extinction, remnant bison populations survived and later thrived through often extreme measures such as the military managing Yellowstone National Park, USA, to prevent the poaching of the few remaining bison. What has transpired now, in the absence of hunting? Bison in Yellowstone show little fear of humans and generally ignore them, save for the yearly incidents of tourists endangering themselves by assuming that comfort around humans equates to docility. Approach distances are now zero (Figure 1). Similar approach distances occur for elk that appear to use the north entrance of the park at Mammoth Hot Springs as a refugia safe from hunting or risks from other predators such as pumas (*Puma concolor*) or wolves (*Canis lupus*).

Using already established methods of quantifying fear such as giving-up densities (GUDs), foraging surveys and anti-predator behavioral observations, we can visually map out how animals may respond to risk and move across the landscape. This has been coined the 'landscape of fear', which describes the different levels of predation risk as peaks and valleys of the landscape that reflect how prey experience predation risk in a certain area [109]. In Argentina, Speziale et al. (2008) showed how Andean condors (*Vultur gryphus*) had higher GUDs on carcasses placed near roads than those placed away from roads from which humans could harass and even poach the birds [110]. This indicated that condors avoided roads and followed optimal foraging theory, trading safety for harvesting energy. Optimal foraging theory provides a framework for how we expect prey to respond with behavioral indicators. For example, prey need an optimal level of anti-predator vigilance in response to their perceptions of where a predator is [44]. Within an optimal foraging framework, prey species can use time allocation, habitat selection and wariness as tools to manage risk [43,111].

The risk disturbance hypothesis suggests that prey will prefer proximity to humans if the predator attacking that prey avoids humans out of fear [99]. Nowak et al. (2016) demonstrated this with Samango monkeys (*Cercopithecus mitis*) in South Africa. They had lower GUDs when observers were present, presumably as this scares away leopards [112]. However, in an area with denser human habitation and where Samango monkeys raid gardens and crops, the monkeys directly feared the presence of humans and their domestic dogs. Leighton et al. (2010) suggest means for using scarecrows and other cues of humans to scare off predators of species of conservation interest [113].

6.2. Hunting for Fear

For species and ecosystem management, the concept of 'hunting for fear' was proposed as a way to generate behavioral responses in ungulates that minimize their ecological impacts [47]. This idea incorporates the 'ecology of fear', which considers how the responses of prey to predation can influence whole ecosystems [44], and the risk allocation hypothesis, which indicates that prey need to tradeoff time on anti-predator behaviors and their normal activity such as reproduction and foraging [64]. For hunted prey to have the strongest and longest lasting behavioral response, variable risks from humans need to be spatially predictable yet temporally unpredictable [47].

One example of humans creating a highly predictable phenology of fear is in the hunting of ungulates, which can result in reduced herd size, reduced impacts on ecosystem and spatial avoidance [114,115]. Specific hunting methodologies can produce varying behavioral effects in ungulates. Game hunting usually aims to minimize fear, with hunters camouflaging themselves and shooting from long distances or hunting seats. However, the ambush-style hunting of ungulates on foot and shooting at close range create stronger risk effects [47]. Hunting with dogs versus without may pose higher risks and therefore may evoke more pronounced behavioral changes. When reducing herd sizes to prevent damage to an ungulate's ecosystem, more culling may be required when the prey make no connection between humans than when they do. Frightened mule deer, for instance, will be more wary and forage plants less intensively [116]. Therefore, culling programs using sharp shooters at night with silencers may be less effective than active hunting on foot or with dogs.

Hunting for fear may be one of the ways through which humans co-habitat with large mammalian predators that otherwise would prey on humans. Human–wildlife conflicts loom large when the wildlife can kill us, our pets and our livestock [117]. In Kenya and Tanzania, the Masai ritual of having young men hunt a lion may instill fear into the lion population, thus allowing for children and otherwise defenseless individuals to herd livestock in areas with lions [118], as noted in a 1901 treatise [119]. The revenge killing of wildlife that threatens humans or livestock is common across numerous cultures throughout history. A study of European lynx (*Lynx lynx*) suggested that the only benefit of lynx hunting on lamb mortality was through direct culling [120]. Furthermore, revenge killing can result in unsustainable hunting and the loss of predator species [121]. Wolves in northern Minnesota, USA, were never extirpated, remained as a small population, and posed threats to livestock. Protection included an 'eye for an eye' where problem wolves were selectively (or haphazardly) hunted. Such a management strategy may have been crucial in permitting the persistence of this wolf population (because surviving wolves likely behaviorally avoided humans), and may have aided in the subsequent recovery of wolves in the Great Lakes region, USA [122]. Hunting by both humans and pumas of Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in California, USA, resulted in the deer adjusting temporal activity patterns, reducing encounter risk and facilitating their survival [123]. Interestingly, fear of humans may explain the hunting patterns of pumas in these human-dominated landscapes. Fear responses of both deer and pumas to humans may contribute to the stability and sustainability of this predator–prey system.

Even when the goal is to exterminate a pest population, hunting may backfire by causing excessive fear that renders prey hard to eradicate and hunting ineffective. Such is the case of invasive wild pigs (*Sus scrofa*) in Canada, where the Province of Ontario banned boar hunting in 2022. The regulatory amendment to their Endangered Species Act noted that "Wild pigs that are exposed to hunting pressure flee into new areas and learn to avoid humans" [124]. In a recent Associated Press article from 20 November 2023, a professor at the University of Saskatchewan, Ryan Brook, noted how the pigs were becoming increasingly wary and nocturnal [125]. Where hunting is not banned, it is ineffective, with success rates of hunters being 2–3% of the wild pig population per year despite its capacity to increase at over ten times that rate. This is an example of hunting for fear not working as intended.

7. Managing Evolving Prey: Evolutionarily Enlightened Management Strategies

Management goals are primarily related to the conservation of biodiversity and harvest rate optimization, either for a specific species or the entire ecosystem. To achieve these goals, managers need to consider the ecological and evolutionary consequences of hunting and resource management—but rarely do so. Human disturbances occur at rapid rates, and some species may experience evolutionary shifts alongside those anthropogenic effects [126,127]. In documented cases of contemporary microevolution, 86%, or 18 out of 21 cases, involved human causes [128]. Current approaches to conservation and management must be illuminated via an understanding of both the ecological and evolutionary effects of human disturbances.

As we have seen above, different hunting strategies can elicit different prey responses. Hunting is usually spatially and temporally predictable, with designated harvest seasons and locations [47], leading to shifts in behavior by targeted species. However, to utilize these behavioral indicators to our advantage, we must consider the repercussions of hunting for survivors and non-hunted species. In ungulate hunting, bow hunting will elicit less of a fear response and for the hunter's sake should precede firearm hunting so that animals are less skittish. Wildlife managers can use the evolutionary context of a species and its traits to their advantage by considering whether or not certain responses are of value (e.g., anti-predator behaviors and morphologies). This information can then be used to adjust management plans to better align and promote evolutionary and ecological goals [104].

It is well documented that the harvesting of fish results in changes in behaviors, morphology and life histories [129,130]. The same is true for harvesting birds and mammals. Even in the absence of hunting, rapid evolution occurs in human-dominated landscapes [131]. Globally, rodents inhabiting cities rapidly evolve and converge on urban ecotypes [132]. Rapid evolution in response to humans will involve changes in behaviors including fear responses. Some of these changes will help species to acclimate and adapt to humans. Losses and changes in fear responses may benefit the species, as in the case of swallows dodging traffic [25]. In other cases, management may aim to preserve fear response as natural behaviors or permit time for new and appropriate fear responses to emerge and evolve. Perhaps the Stephen's Island Wren (*Xenicus lyalli*) of New Zealand could have evolved appropriate fear responses to the small population of introduced domestic cats, but they had too little time and nowhere to hide on their small island [133]. The adoption of new fear responses may contribute to a species' evolutionary rescue following a catastrophic anthropogenic change to their environment [134,135].

The evolution of humans in Africa and their spread from Africa left a gradient of megafaunal diversity with the highest diversity remaining in Africa, moderate diversity remaining in Eurasia and the lowest diversity remaining in North and South America [136–138]. The opportunity for hunted species to acclimate and adapt to humans may explain this pattern. African wildlife had the most time to coevolve morphologically and behaviorally to the slowly improving capacity of humans to hunt. Many African species have an evolutionary history congruent with that of hominids—these include lions, hyenas, elephants and others [139]. Hominids were low in abundance, so total predation pressure was likely not great. Slow and steady selection permitted evolutionary rescue, even as human numbers grew and technology advanced. Time was not on the side of mammoths, mastodons, giant beavers, short-faced bears and ground sloths as humans entered North America some 20,000 years ago. These humans brought with them the best skills and tools available at the time for killing large mammals. Such humans must have been astonished (and perhaps delighted) to see how these animals had little fear of humans or exhibited stand-your-ground fear responses that may have been effective against saber tooth cats, wolves and other predators. The rapid speed with which humans spread across the Americas may have been driven by the opportunity to continually exploit new areas of naïve prey [140,141].

8. Socio-Economics: Fear Responses of Other Species as a Reflection of Ourselves

An animal's fear response to humans says much about how we treat and think about that species. The eastern grey (*Sciurus carolinensis*) and eastern fox squirrel (*Sciurus niger*) of North America provide cases in point [142]. Where they are hunted, these two species flee at the sight of humans; where they are ignored, they ignore us; and where they are fed, such as in parks and on college campuses, they approach and even harass people. The fear and anti-predator behaviors of fox squirrels change in a consistent pattern across an urban to rural gradient [143]. Oak Park, a suburb near Chicago, USA, shows these two squirrels as a reflection of changing cultural norms [144]. When homes sprung up from the 1890s to the 1920s, there were no squirrels, as they had been hunted for food and as threats to gardens and crops. In time, discharging firearms in urban settings was deemed unacceptable, and squirrels were seen more as a curiosity. They returned, particularly the fox squirrel, as they outcompeted the grey squirrel under conditions of high predation risk [145]. During the 1990s, Oak Park enacted leash laws for dogs, banned air rifles and promoted keeping cats indoors. This increased safety for squirrels, and over time, grey squirrels replaced fox squirrels throughout most of the town. Presumably, had one watched the behaviors of these squirrel species over the last 150 years, it would have been evident that we had gone from being one of their fiercest predators to becoming one of their greatest benefactors.

The absence of many species from human-dominated landscapes includes both over-hunting and persecution, and also their fear responses to simply avoid such areas. When threats subside, there can be spectacular comebacks of animal species, even to the point of them becoming pests. Such examples include rhesus macaques (*Macaca mulatta*) in India and Nepal, marabou storks (*Leptoptilos crumenifer*) in Kampala, Uganda, sandhill cranes (*Grus canadensis*) in cities of North America, and red foxes in the United Kingdom, just to name a few. In all cases, the behaviors of these animals towards us reflects our norms towards them.

Such fear responses can provide indicators of continued human persecution. Himalayan tahr in the Annapurna region of the Himalayas will keep their distance from humans, preferring to have the high ground or a valley between them and people. While protected, hunting continues. In the Everest Range further east, the Himalayan tahr reside close to people, often feeding in fallow fields and paths with heavy foot traffic. Their indifference speaks to safety from humans. The fear response of animals to the approach of humans may provide a more accurate indicator of how we hunt or treat them, than what we humans might report or admit to ourselves. Cultural norms in time and space loom large in the fear responses of animals to humans.

Western ideologies differ widely from Indigenous practices. Lessons from Indigenous people and how they manage their forestlands can inform the sustainable management of non-tribal, public forestlands. Indigenous people, the Ojibwe in particular, respect and revere wolves and do not approve of sport hunting or trapping [146]. Does this attitude of welcoming and supporting wolf populations also shape the low deer density observed on tribal lands? Cascading effects of wolves, an apex predator, on deer behavior and densities in North America have been documented [147].

Indigenous nations and non-indigenous managers may have similar management goals: to sustain resource values, yields, biodiversity, and ecosystem productivity [146]. However, outcomes are not necessarily the same. In a study on the structure, composition and diversity of Ojibwe and Menominee tribal forests compared to those of non-tribal forests on what is now northern Wisconsin, non-tribal lands lost substantial plant diversity and have failed to regenerate tree species degraded by deer herbivory [146]. Indigenous lands support higher native and rare species richness [148]. Deer density is also lower on tribal lands, which promotes the higher diversity and regeneration of understory plant species there [146]. On tribal lands, there are flexible hunting policies (no hunting season or bag limits), socially enforced rules and safety [146,149] with a focus on cultural values [150]. Maintaining natural and human-induced fear responses in deer may contribute to the successful balance seen in these tribal forests and should be an example for biodiversity managers.

9. Conclusions

Human relationships with animals have had a great influence on both the biological and cultural evolution of humans [151]. More consideration should be made in terms of the evolutionary and ecological impacts on those animals, especially as hunting pressures on those animals intensify. Despite humanity's cultural and technological development, human hunting pressures on animals remain large. A 2022 national survey by the United States Fish and Wildlife Service reported that 21% of Americans participated in hunting and fishing activities [152]. If a species can persist in the face of natural predators, climatic and environmental changes, etc., we should not be surprised at how quickly animals adapt to human predation. This review is intended to shed light on the evolutionary impacts of humans harvesting vertebrates, which can serve to inform more enlightened conservation and management strategies.

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