PERSPECTIVE

The roles of humans and apex predators in sustaining ecosystem structure and function: Contrast, complementarity and coexistence

Robert J. Lennox[1,2,3] | Jacob W. Brownscombe[2,4] | Chris Darimont[5] |
Andrij Horodysky[6] | Taal Levi[7] | Graham D. Raby[8] | Steven J. Cooke[2]

[1]Laboratory for Freshwater Ecology and Inland Fisheries at NORCE Norwegian Research Center, Bergen, Norway; [2]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario, Canada; [3]Norwegian Institute for Nature Research (NINA), Trondheim, Norway; [4]Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, Burlington, Ontario, Canada; [5]University of Victoria, Victoria, British Columbia, Canada; [6]Department of Marine and Environmental Science, Hampton University, Hampton, Virginia, USA; [7]Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA and [8]Department of Biology, Trent University, Peterborough, Ontario, Canada

Correspondence
Robert J. Lennox
Email: robertlennox9@gmail.com;
role@norceresearch.no

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Abstract

1. In nearly every ecosystem, human predators (hunters and fishers) exploit animals at extraordinarily high rates, as well as target different age classes and phenotypes, compared to other apex predators. Demographically decoupled from prey populations and technologically advanced, humans now impose widespread and significant ecological and evolutionary change.

2. In this paper, we investigate whether there is evidence that humans provide complementary services and whether ecosystem services of predators can be maintained by humans where wild predators are lost. Our objective is to contribute to two key ecological themes: the compatibility of human harvesting within ecosystems and management approaches in consideration of the intentional or unintentional loss of predators.

3. We reviewed evidence for five key effects of predators: natural selection of prey, disease dynamics, landscape effects, carbon cycling and human well-being. Without carefully designed management strategies, such changes can impose harm to ecosystems and their constituents, including humankind.

4. Ultimately, we applied this information to consider management paradigms in which humans could better support the role of, and potentially behave more like, apex predators and discuss the challenges to such coexistence.

KEYWORDS
ecosystem function, fisheries management, nutrient cycling, predator–prey dynamics, wildlife management

1 | INTRODUCTION

Apex predators occupy the highest trophic positions in food webs and serve profoundly important roles in ecological and evolutionary processes, shaping and re-shaping the traits of prey and how they interact with one another and the ecosystem. Wallach et al. (2015) presented some simple traits that define apex predators among carnivora, especially size >34kg and the capacity for self-regulation. Defining where humans fit in trophic webs is challenging and has changed with time as knowledge and technology have developed. The ecological role of humans as predators seems to have began in the Pleistocene. Efficient harvesting by trapping, hunting and fishing using tools to subvert prey defences has enabled humans to kill an unprecedented variety of species, to target high trophic level prey that most other predators cannot access (e.g. adult bluefin tuna; *Thunnus thynnus*), and focus on large reproductive-aged individuals within populations (e.g. age 2- to 6-year-old moose; *Alces alces*) that are often most costly for apex predators to hunt (Darimont et al., 2015). Additionally enabled by economic or nutritional subsidies (Sala et al., 2018) that offset the costs of otherwise unprofitable hunts that apex predators would rather avoid, humans can in some cases rapidly overexploit resources and create ratchet and Allee-Bowen effects that delay recovery of prey (Branch et al., 2006; Kleiven et al., 2019). The human predator is therefore an ecological curiosity.

The efficiency with which humans harvest wild animals has fundamentally important implications for the role of humans in ecosystems and relationships among humans, predators and prey. As agents exerting control on ecosystems, humans hold an important node in the trophic web, but one that is not necessarily unique, and we can therefore compare the actions of humans with those of apex predator species (Figure 1). In this essay, we question how the loss of other predators and replacement by humans can affect key ecosystem functions. We review evidence for five key effects that apex predators have (1) driving natural selection, (2) modulating disease, (3) controlling biogeography, (4) sinking carbon and (5) contributing to human well-being and discuss whether human predation yields similar or different effects in the presence and absence of apex predators. In doing so, we reveal two key narratives about ecology and conservation, a need to consider the ecological compatibility of human harvesting in the context of trophic networks and predator–prey systems and the implications of losing predators and the need to better consider options for coexistence with predators.

2 | COMPARING APEX AND HUMAN PREDATORS

2.1 | On prey phenotypes

All predators are agents of natural selection, shaping prey phenotypes over time (Jørgensen & Holt, 2013). Apex predators tend to impose selection against phenotypes that are slow, weak, disease prone or otherwise vulnerable to attack as dictated in part by the capabilities of the predator (Bro-Jørgensen, 2013). Humans, however, have escaped much of the constraints that have driven evolutionary trajectories among prey species because they exploit vulnerabilities in fundamentally different ways by the use of tools, such as ammunition or nearly invisible tangle nets (e.g. Lennox et al., 2017; Montgomery et al., 2022). Whereas most apex predators have a tendency to target animals in infancy or senescence, humans typically prefer reproductive age classes within populations and do so at median rates up to 14 times higher than apex predator counterparts (Darimont et al., 2015). Theoretical and modelling approaches have long suggested that predation by humans can lead to morphological (e.g. smaller size-at-age, growth rates, ornament size), life-history (e.g. reproduction at younger ages and sizes; Law, 2000) and behavioural changes (Monk et al., 2021) to prey populations in ways that are different from apex predators (Figure 1). Phenotypic change arising from harvest can also be incurred from density-dependent selection that erodes competition among offspring for size and growth (Bouffet-Halle et al., 2019). The consequences of harvest selection can be observed in changing demographics of harvested populations and trophic changes (reviewed in detail by Allendorf & Hard, 2009).

Selective harvest by humans is well studied, particularly in fisheries (Heino et al., 2015; Kuparinen & Merilä, 2007), but not in contrast to the hunting of apex predators (Table 1). Apex predators chase or ambush prey, and prey defend by being large, fast or cryptic (Bro-Jørgensen, 2013). Humans rarely fill the role of cursorial or ambush predators although some capture modes might have similar effects, such as fish trawlers that Killen et al. (2015) suggested would capture poor swimmers more effectively than more athletic counterparts. Vehicles can outpace the fastest impalas *Aepyceros melampus* and bullets can penetrate the tightest circle of muskox *Ovibos mochatus*, so vulnerabilities to human capture tactics are very different compared to vulnerabilities to predator hunting (Lennox et al., 2017). Monk et al. (2021) studied the struggle between natural and artificial selection on size and activity of Northern pike *Esox lucius* in a lake, showing that harvest-induced selection was stronger and yielded smaller and shyer pike; simulations revealed that the artificial selection imposed against large fish outpaced the natural selection for larger size in the lake system. Managing human harvest to mitigate selection would need to enhance harvest of lower fitness classes within populations and avoid large changes to the size-frequency distributions of a population (Fenberg & Roy, 2008). To compensate, management can shift harvesting targets for certain phenotypes with licensing or closures that disincentivize or prohibit harvest of vulnerable phenotypes that would drive selection in an unwanted direction. A recognition that harvest selection is mostly implicit due to the gear that individuals are vulnerable to must be accounted for; the technology has evolved specifically to exploit the vulnerabilities of animals and more research is needed to account for this. Management options are already accounting for this by managing mesh sizes
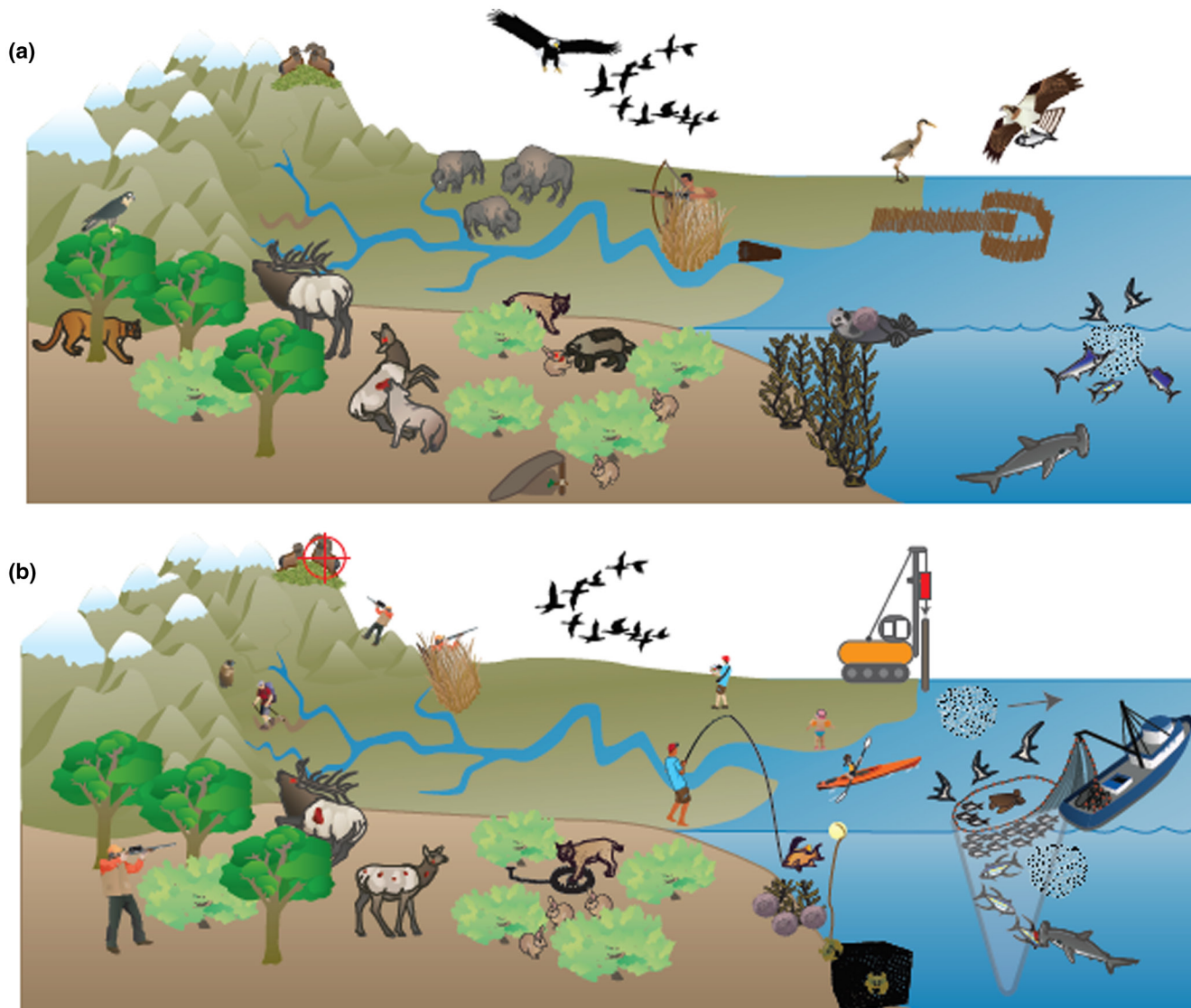
FIGURE 1 Schematic contrast of the human environment and its influence on the nature of predator–prey systems. The top panel shows predator–prey systems characterized by biodiversity of predators and prey on land and in water with no to low human exploitation. The lower panel demonstrates effects of modern human predator behaviour across present-day ecosystems. Humans are selectively hunting elk and sheep of large size and large ornament size. Commercial fishers are aggregating avian and shark predators to nets and capturing turtles as bycatch. Recreational rod and reel and spearfishers often demonstrate trophy-targeting behaviour. Noise from pile driving is driving fish away. Presence of humans elicits fear among the animals. Ubiquitous presence of humans generates changes to ecological community diversity, individual traits, and resilience of populations, communities and ecosystems to disturbances such as disease epidemics and climate change. (a) Predator-prey landscapes pre-industrialization illustrating the relationships between predator and prey. (b) Industrialization and globalization of humans has altered predator-prey relationships and human hunting has formed novel predator-prey interactions that affect the trajectory of natural selection, disease dynamics, landscape processes, carbon sinking, and even human health and wellbeing. Figure includes select images by T. Saxby, J. Thomas and J. Hawkey. IAN-UMCES. Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

of fishing nets or hook sizes for hook-and-line fisheries. Explicit selection occurs when hunters or spearfishers visually discriminate an individual animal to pursue, or when live capture permits the discard of unwanted individuals (e.g. catch-and-release fishing). When individuals can be targeted, these systems may be most readily managed to avoid undesirable evolution of prey species via selective harvest.

2.2 | On disease dynamics in ecosystems

Disease can reduce animal populations substantially when it spreads unchecked, reaching epidemic proportions that can spread to adjacent populations or related species, including domesticated animals (Mysterud & Edmunds, 2019). Disease impairs physiological functioning and can render hosts more susceptible

TABLE 1 Canonical generalizations about apex predators and human harvesting behaviour. We summarize what apex predators and humans tend to do and contrast the effect on prey. Acknowledging that there are exceptions to these tendencies, we refer to effects and paradigms that correspond to these phenomena. These examples generally fit within our framework and demonstrate how polarized human harvesting behaviour can be from apex predators. Comparisons are drawn to reveal similarities and differences we have established in our review. Effects refer to ecological and evolutionary paradigms into which each statement fits

Apex predators tend to	Humans tend to	Comparison	Effect
Kill young animals or post-senescence animals	Kill reproductively prime individuals	Humans exert an unnatural selective effect on prey	Fishing (or harvest) induced evolution
Kill small or disadvantaged animals (e.g. wolves on mountain sheep)	Kill large and heavily ornamented animals (e.g. hunters on mountain sheep)	Humans drive evolution of traits	Undesirable evolution
Kill animals during or after reproduction (e.g. bears on spawning salmon)	Kill animals during the pre-reproductive period (e.g. anglers on migrating salmon)	Humans limit reproductive output of population	Compensatory mortality by predators
Detect weakness or illness in compromised prey, and exploit it	Ignore or fail to detect weakness or illness in compromised prey	Predators prefer easy targets	Compensatory mortality by predators
Capture diseased animals with compromised predator detection or escape	Avoid diseased animals or discard individuals with signs of illness/parasitism	Predators exert a sanitation effect on prey populations	Sanitation effect
Chase prey until one becomes exhausted	Chase prey with vehicles	Predators make calculated choices based on energy budgets	Anaerobic metabolism
Are ineffective at exploiting rare prey	Can sustain exploitation of rare prey via subsidization (no fear of bankruptcy; Kleiven et al., 2019) or bycatch	Predators allow rare prey to recover, whereas humans continue to exploit due to market supply/demand adjustment	Functional response
Switch to alternative prey when primary species are depleted	Adjust market prices for depleted species, maintaining demand despite poor supply	Sustained levels of exploitation on rare species drive depensation and alternative stable states	Ratchet effect
Exert non-consumptive effects on prey distribution	Exert even stronger non-consumptive effects on prey distribution	Humans may increase vulnerability of prey to predators because of their strong fear effects	Landscape of fear
Return energy and nutrients acquired from prey to the ecosystem, cycle nutrients across ecotones	Concentrate energy and nutrients acquired from prey, driving local eutrophication and oligotrophication	Predators support scavengers, decomposers, and a circle of life, whereas humans create local ecological extremes	Eutrophication
Limit release of herbivores and mesopredators	Fail to limit herbivore or mesopredator release	Predators naturally maintain order in ecosystems that is very difficult for humans to emulate	Trophic cascade
Reduce vehicle collisions by maintenance of large herbivore populations	Fail to effectively limit large herbivores	Predators provide immense economic value	Ecological economics

to predation (Genovart et al., 2010; Krumm et al., 2010). The ecological role of predators can therefore be viewed as important, if not central, to regulating the spread of disease within a prey population and selecting against genotypes encoding poor pathogen immunity (unless the predator facilitates disease spread; see Cáceres et al., 2009). Literature on the role of predators in disease dynamics of prey is interesting but the topic is full of context dependence and uncertainty that should be interesting to address with further research (Table 2). The nature of disease transmission and the role of predators, including humans, in facilitating or reducing the spread is therefore of substantial importance to eco-evolutionary dynamics of populations as well as to management of populations and ecosystems (Darimont & Bryan, 2020).

Cases of predators removing diseased individuals from populations (i.e. 'healthy herds' hypothesis, sanitation effect) have been documented across taxa (Genovart et al., 2010; Krumm et al., 2010; Tanner et al., 2019); however, it is not known whether humans are able to emulate this ecosystem service (Table 1). In some cases, mechanisms that render hosts vulnerable to other predators may also make them prone to harvest by humans. Hunters in Newfoundland, Canada, for example, removed infected moose (an introduced species) where there are no wild predators left that are capable of doing so (Rau & Caron, 1979). Ben-Horin et al. (2016) simulated selective removal of diseased red abalone *Haliotis rufescens* by fishers and showed that harvest of sick individuals could offset natural mortality from disease. Disease spread among ungulates has been a challenge to management and Mysterud and Rolandsen (2018)

TABLE 2 Can predation by humans and apex predators be complementary? Research questions emanating from our perspective, organized by the five sections presented

Section	Research Question
1	Is harvest-induced evolution density dependent or density independent?
	What are the selection coefficients (on heritable traits) of different hunting and fishing gear types?
	What are the selection coefficients (on heritable traits) of different hunting modes by predators?
	Is tool use by non-human predators reversing selective gradients on wild prey phenotypes?
	Are selective patterns stronger for apex predators than mesopredators?
	Can harvest decisions (explicit selection) be modified by changing perceptions of harvesters?
2	Do predators target diseased prey at epidemiologically meaningful scales?
	How do pathogens drive vulnerability to hunting and fishing gears?
	In areas where predators are lost does human harvest compensate to remove sick individuals?
	How does overt illness of an animal drive harvest decisions via explicit selection?
	How do predation and harvest modulate the reproductive rate (R0) of pathogens among prey?
	At what level of selection and harvest intensity on diseased individuals are predation and harvest equivalent for disease regulation among prey?
3	How does the absence of predators drive grazing patterns of herbivores with and without harvest?
	Do prey evolve or learn to avoid humans in hunted landscapes?
	How effective are different spatial management strategies for managing naivety in prey populations?
	Where predators have been lost, can hunting impose strong fear effects to avoid trophic cascades and regime shifts?
4	How strongly do different predator species contribute to cycling carbon and nutrients across landscapes?
	What is the carbon balance with and without predators in odd and even numbered food chains with and without harvesting?
	Are artificial compensations strong enough to maintain carbon and nutrient cycles in the absence of apex predators?
	Does restoration of predators in modified landscapes (loss of native species, addition of non-native species) restore carbon flux?
	Are there differences among marine, terrestrial and freshwater ecosystems in the role of predators cycling carbon?
5	Do subsistence systems become less productive in the absence of predators in the long term?
	Are there hidden values to predators maintaining prey populations that should be accounted for?
	Can harvesting be maintained at a level that emulates the control of prey populations by apex predators?
	How acceptable are bioeconomic simulations to explain the value of predator conservation and restoration to stakeholders?

studied how mass killing could quell disease spread. However, Wild et al. (2011) concluded that predation by wolves would be a much more effective and economical method of managing epidemics such as chronic wasting disease in a deer population than would be culling by human hunters, which is less selective for infected animals than predator killing seems to be. Krumm et al. (2010) also suggested that humans were less effective at harvesting deer afflicted by chronic

wasting disease than were mountain lions *Puma concolor*, positing that restoration and protection of mountain lions would be efficient for disease management. Diseases that decrease activity may make prey more vulnerable to capture by active nets or trawls, by spearfishing or by hunting, but less vulnerable to passive traps that rely on individual mobility to increase encounter probability (Lennox et al., 2017). Explicit selection by people may result in hunters

ignoring sick looking animals or fishers discarding fungus-covered fish that pred. The capacity for humans to regulate disease will probably depend on the selection decision of harvesters and food safety recommendations made to sportspeople (Kaemingk et al., 2020) and effects of the disease on vulnerability to capture by different gears; both represent important areas for research.

2.3 | On landscape processes

Animal distributions and abundances are constrained by physical and non-physical aspects of the landscape (Figure 1). Humans are major ecosystem engineers that have modified the world with infrastructure, interventions such as burning, and other physical changes to habitat that have dramatically shifted the biodiversity on Earth (Smith, 2007). Few predators are equivalent ecosystem engineers, except perhaps some invertebrates that fill space with traps to catch prey. A recently common focal point of how humans affect landscapes is the fear effects imposed by predators that can delimit the habitat used by prey species (Lima, 1998). Fear of predators, including humans, can influence prey physiology and behaviour, which, in turn, can impact prey fitness, population dynamics and their roles in ecosystems (Crawford et al., 2022). In addition, top predators alter the distribution of their competitors, including mesopredators, which has a cascading impact on the ecosystems structure and function such that loss of these predators can greatly alter the exposure of prey to predation pressure (Gordon et al., 2015). Although the relative influences of consumptive and non-consumptive effects are challenging to untangle, there is growing evidence that non-consumptive effects of predators can have a major influence on prey population and ecosystem dynamics in diverse systems. Human predators also impose strong non-consumptive effects (Cromsigt et al., 2013; Suraci et al., 2019), which may be more powerful than the effects apex predators have on prey (Ciuti et al., 2012; Crawford et al., 2022; Gehr et al., 2018; Kays et al., 2017) or manifest on the behaviour of apex predators themselves (Støen et al., 2015).

The ecological consequences of landscapes alterations include changes to biodiversity, nutrient fluxes, energy distribution and more (Laundré et al., 2001). However, the differences implied by landscapes effects imposed by humans and apex predators are not well studied (Table 1). A key question is how to separate the direct effects of exploitation from the effects of other activities that constrain animal movements such as barriers, light, noise, incidental mortality from vehicular collisions and other ways that humans can scare animals without exploiting them (Ciuti et al., 2012). Conditioned responses may evolve, for example, fear of roads or engine noise because it is associated with vehicles or hunters. Humans instil fear in prey but they may find refuge from predators that are even more afraid, driving complex ecosystem effects that alter the structure and function in unpredictable ways (Muhly et al., 2011). Ciuti et al. (2012) concluded that the fear effects of humans are stronger in hunted areas than recreational areas, but experimental studies in replicated areas would be useful to study the nature of

innate and learned fear responses to different human activity levels in the presence and absence of other predators. Predators are lost or excluded in many areas due to intentional removal programmes or habitat loss, releasing competitors and prey species from the strong lethal and non-lethal effects. Overgrazing, trophic cascades and regime shifts can occur when herbivores move into areas they were too afraid to frequent in the presence of predation risk (Baum & Worm, 2009). Maintenance of ecosystem structure therefore requires conservation of predator populations to sustain these fear effects and distributional impacts on prey or equally strong fear effects imposed by humans to avoid trophic cascades.

2.4 | On carbon and nutrient cycles

Predators influence the cycling of elements by killing prey, moving carcasses and redistributing the constituent nutrients in faeces or in their own bodies consumed by parasites, other predators or scavengers. For example, predators alter carbon cycling and biosequestration rates through changes they impose on the abundance, morphology, physiology, behaviour or life history of animal populations at intermediate trophic levels (e.g. herbivores; Atwood et al., 2013, 2015). Fear of predation, for instance, accelerates metabolic rates in herbivores and can shift their diet from proteins towards carbohydrates to manage the energetic costs (Hawlena et al., 2012). Healthy predator populations are thought to increase carbon flux to the atmosphere in even-numbered food chains but increase carbon storage in odd-numbered food chains (Atwood et al., 2015). Extirpation of sea otter *Enhydra lutris* from kelp forests, for example, yielded an explosion of sea urchin prey (*Strongylocentrotus* spp.) and a concomitant decline in carbon-sequestering kelp. Should they reoccupy habitat across their former range, sea otters' role in facilitating kelp growth could yield a 4.4–8.7 teragram increase in C storage, valued at ~$205–408 million (USD) on the European Carbon Exchange (Wilmers et al., 2012). Given that humans generally do not consume their prey (or excrete the remains) within the ecosystem of provenance, wild capture fisheries and hunting do not return nutrients to the ecosystem the way that wild predators do. Whereas bears (*Ursus arctos*, *U. americanus*) and wolves (*Canis lupus*) scatter nutrients and carbon from carcasses across the landscape, humans will discard them far away from the rivers and forests these carcasses would otherwise fertilize (Mysterud et al., 2020). Instead, landfills and sewage treatment facilities concentrate much of the nutrients that humans extract from oceans, rivers, forests and plains into rivers, ponds or coastal zones that end up facing the risk of eutrophication (Wang et al., 2019). Local oligotrophication may ensue in ecosystems from which nutrients are extracted and not returned to scavengers or decomposers (Stockner et al., 2000).

Can humans emulate some, or any, of the functional effects that other predators can have on carbon and nutrient cycling (Table 1)? If restoring predators is not an option, there could conceivably be an artificial alternative to most ecosystem functions lost when wild predators disappear (Turner et al., 2003). Fishery managers in British

Columbia (Canada) have used artificial fertilizer to enhance the productivity of salmon-rearing lakes and generate a bottom-up effect on juvenile salmon growth and survival (Hyatt et al., 2004). Iron fertilization to promote carbon sequestration by phytoplankton in the Southern Ocean has received limited support (Chisholm et al., 2001), an action that would compensate for the historical overexploitation of sperm whales that defecate iron-rich faeces at the surface that stimulates phytoplankton blooms (Lavery et al. 2010). Carbon sequestration technology instead could be used to offset the changes to the cycle stimulated by predator declines. These solutions are relatively challenging, bordering on farfetched; ultimately, the best way to restore natural elemental cycling would be to rebuild and maintain healthy populations of natural predators in cases where carbon sequestration benefits from their presence.

2.5 | On human well-being

Discussing how predators influence safety, welfare and economy of humans may seem to invite discussion of direct conflict between humans and predators. Despite large apex predators being a direct threat to people and dependents such as livestock, that safety cost may be offset by some broader benefits provided by their functional role of top-down control. Over-abundant populations of prey species in the absence of apex predators can negatively affect human well-being. For example, in the United States, vehicle collisions with ungulates cost millions of dollars in property damage and are a cause of many injuries and some deaths. In Norway, Storaas et al. (2001) estimated that the costs associated with moose traffic collisions (up to $80 million USD per year) may exceed the market value to the moose hunting tourism sector (up to $70 million USD per year). Economic analyses similarly suggest equilibria for wolf *Canis lupus* populations in Scandinavia that contribute to reducing vehicular collisions with moose (Skonhoft, 2006). Gilbert et al. (2017) established a correlation between deer abundance and collisions and showed that the presence of mountain lion reduces deer populations and the associated costs of collisions, suggesting that recolonization of the eastern United States by mountain lions would save $50 million USD and 150 lives within 30 years. In Wisconsin, wolves reduced deer-vehicle collisions by 24%, offsetting the costs of livestock losses by 63 times (Raynor et al., 2021). Leopards *Panthera pardus* may be responsible for saving even more lives in India, where direct predation of stray dogs *Canis lupus familiaris* is estimated to save up to 90 lives per year that would otherwise be lost to rabies or other bite-related fatalities (Braczkowski et al., 2018). Regulation of mammalian reservoirs of human zoonoses, especially rodents that carry Lyme disease, bubonic plague, monkeypox, hanta and lanta viruses, and others may be carried out indirectly by many predators that consume the host species of these zoonoses, reducing the reservoir size and potential for spillover to humans and their domestic animals (Ostfeld & Holt, 2004).

Because apex predators regulate prey species, the presence of strong predator populations likely provides ecosystem services that directly benefit human health and safety (Table 1; O'Bryan et al., 2018). Prominent examples include those in which prey populations are primarily regulated by top-down control (although some are regulated by bottom-up processes; Frederiksen et al., 2006). Managing human harvests to better emulate the positive influence that predators have on human well-being, however, is challenging. Predator removal may be championed as a mode of releasing more prey for humans to harvest, despite the reality that the approach rarely works (Lennox et al., 2018). Increasing hunting effort or modifying hunting to reduce vehicular collisions or disease spreading from animals to humans is unlikely to compensate for predators that are lost, at least not efficiently. Costly prey management schemes can be instituted to regulate populations at healthy levels (Mysterud et al., 2020). Hunting can suppress deer and moose populations, but economic analyses confirm that predation is needed to attain sufficiently small ungulate population sizes at which herbivore conflict costs are minimized (Skonhoft, 2006). In India, feral dogs are sterilized to reduce the population at a cost of $11.90 USD per dog (numbers current to Braczkowski et al., 2018), but conflicts with feral dogs still occur. Our thesis here is an exception to the rest of the essay in that it focuses on ecosystem services, but it is nevertheless a crucial argument to make in any discussion about restoring populations of predators that can be a threat to people (e.g. large terrestrial carnivores). Emulating the sustainability of services provided by some predators directly to humans seems to be one that is not easily replaced by humans where predators are lost and should be a major consideration when making decisions about restoration.

3 | SYNTHESIS AND APPLICATION

We have endeavoured to provide a perspective of the myriad ways in which the behaviour and influence of humans differs from other apex predators (Box 1). Despite a large and growing literature on vulnerability to harvest (Lennox et al., 2017), landscape effects (Ciuti et al., 2012), harvest-induced evolution (Allendorf & Hard, 2009), disease ecology (Ostfeld & Holt, 2004), predator removal (Lennox et al., 2018) and ecosystem services of predators (O'Bryan et al., 2018), no research has yet provided this comprehensive comparison between predators and humans (Table 1; Figure 1). Accordingly, we have developed a perspective that invites new fundamental research into the dynamics among humans, apex predators and ecosystems, identifying applied research on the value of predators, as well as management approaches informed by apex predator ecology (Table 2).

Our perspective necessarily returns to the question of predator terminology and where humans fit. Wallach et al. (2015) described humans as a special case of mesopredator release, not an apex predator. Humans have been described as 'hyperkeystone predators' (Worm & Paine, 2016) and 'superpredators' (although the origins of the term are problematic; Darimont et al., 2015). Vulnerability of prey to the tools used by humans seems to be a strong driving force behind differences between humans and apex predators (Lennox et al., 2017). However,

BOX 1   Illustrative examples of the ecosystem service dynamic among wild predators, prey and humans focused on cervids and chronic wasting disease, salmon anglers and nutrient cycling, and conflicts between fishers and predators

Can management alleviate the so-called undesirable evolution exerted by human harvesting? The arms race between predators and prey is a major driver of prey phenotypes. Physiological capabilities of prey are indeed shaped by the hunting modes of their predators (Bro-Jørgensen, 2013). Selection by predators is somewhat implicit as predators capture the slower, weaker individuals and drive 'natural selection' for phenotypes that are perceptive and capable of identifying and escaping predators, pushing the species' phenotypes to optimize fitness-providing traits. Human hunters have been demonstrated to drive an undesirable evolution by selecting large, fit and dominant prey phenotypes out of the population. Fisheries-induced evolution has been observed as a consequence of fishing, which is generally agreed to be an undesirable evolutionary trajectory for a species that yields smaller individuals. Monk et al. (2021) conducted an explicit experiment using northern pike *Esox lucius* to show that fishing generated a stronger selective force than sexual selection did, resulting in a fitness landscape biased by human intervention.

Strategies for managing selective effects of human harvesting have been implemented in many fisheries by instituting restrictions on the phenotypes available to harvest. However, these regulations depend on selective harvest where non-target individuals can be released in good condition. Bycatch and collateral damage remains a major challenge to limiting the selective forces of human harvest that must be considered to maintain the genetic and ecological integrity of prey populations.

Can management prescriptions that increase hunter harvest control the spread of Chronic Wasting Disease (CWD) in cervids? The distribution and abundance of cervids have responded to urbanization and loss of native predators. Now, many cervid populations are imminently threatened by CWD, which is a highly transmissible and lethal prion disease. Spread of CWD throughout North America and into Europe has been met by management measures including mass culls of wild animals (e.g. Mysterud & Rolandsen, 2018) as well as relaxed hunting legislation to enhance harvest rates.

Strategies for managing CWD spread are under evaluation but in general the early, selective removal of infected individuals is the objective. Infected animals are thought to be less perceptive, less evasive and more vulnerable to predation. However, comparative studies suggest predators are better than humans at removing infected animals, and by eating the carcass they limit the potential for it to act as a reservoir (Wild et al., 2011). In contrast, the high mobility of human hunters, their transportation of meat, knives and hunting dogs might facilitate disease transmission. Research is needed to evaluate the role of wild predators in controlling the spread of CWD and maintaining an effective balance among prey, wild predators and human predators.

humans are not the only users of tools in the animal kingdom and more research into how non-human tool users affect prey populations is needed (Shumaker et al., 2011). What are the selective properties of innovative animal hunting systems such as bubble nets used by humpback whales to corral krill (Goldbogen et al., 2013), and are they comparable to nets used by commercial fishers? There are many dynamics to predator–prey systems and more work is needed to understand where human modes of predation fit in this context. Like most of ecology, it is probably context specific how human predation compares with that of apex predators and not quite as binary as presented here. A major

reason is regional differences in ecology, human relationships with nature and animals, and affluence. Indeed, management of coastal ecosystems has often failed to act at the fine scale of resolution needed to address major challenges to how humans interact with their prey (Aswani, 2019). Nevertheless, contrasts between humans and apex predators seem to suggest consistently different patterns of selection with implications for evolutionary trajectories, disease dynamics, prey distributions, carbon and nutrient cycles, and human societies.

A key application of our synthesis is in the innovation and validation of management strategies used to support sustainable

Do salmon fishers divert marine nutrients otherwise bound to coastal forests? The annual spawning migrations of salmon from the Pacific and Atlantic Ocean into spawning rivers transfers marine nutrients up to thousands of kilometres and into relatively oligotrophic areas. These nutrients create a significant subsidy to the recipient ecosystems and killer whales, salmon sharks, bears and wolves all make substantial movements to exploit this seasonal influx. Indigenous, recreational and commercial fisheries are substantial exploiters of these migratory runs, with gear selectively targeting certain size classes, run timings, sexes and more with implications for stock evolution.

Bears and otters preferentially eat certain parts of the salmon and leave much of the carcass (inset image—an Atlantic salmon (*Salmo salar*) carcass partially eaten by an otter *Lutra lutra* in western Norway). Predators therefore play an important role in the cycling of nutrients in this ecosystem. Although humans also preferentially eat only parts of the carcass, the remains are not returned to the environment. The consequences include a loss of biomass available to predators (with potential implications for subsequent human-bear conflict) as well as a reduction in the potential nutrient availability to the salmon-consuming predators and ecosystem. The ecosystem then benefits from salmon in terms of tree growth, avian abundance and juvenile salmon production.

Do human harvesters compete against wild predators for common fisheries resources? Large-scale commercial fishing and whaling operations, as well as smaller scale recreational and subsistence harvests, are key to securing food globally. Fishing for marine species varies from active cursorial hunting (e.g. spearfishing, hand-and-glean) to sit-and-wait tactics such as harpooning and trapping. Large-scale operations remove fish in massive quantities. There is substantial selection by marine fisheries that depend on fishing methods (e.g. hook or net mesh size; Law, 2000). Marine animals harvested by humans range from primary consumers to apex predators. Therefore, there is potentially significant niche overlap of humans and many wild predators.

Yet, efforts to find support for culling seals or whales to enhance fisheries yields have failed to find appreciable effects (Gerber et al., 2009). Bioenergetic requirements of predator populations demand relatively small numbers of prey compared to the massive quantities removed by commercial fisheries (Nilssen et al., 2019). Moreover, subsidies for commercial fishers and self-subsidizing by recreational fishers (Kleiven et al., 2019) contribute to a ratchet effect by human hunters whereby fishing persists through periods of low prey abundance, denying the normal functional and numerical responses of wild predators that facilitate prey recovery and contributing to stock depensation. Marine fisheries resources can have relatively limited overlap with the prey of wild predators on the basis of differential selection, possibly driven by technology allowing humans to target larger, healthier individuals in a population than wild predators tend to be able or willing to pursue.

activities such as fishing and hunting. Management prescriptions can alter the functional responses of humans to prey so that they become more aligned with how wild predators operate (i.e. shifting to alternatives when preferred prey are scarce). Hunting or fishing moratoriums can be effective if implemented before a stock collapse (Neubauer et al., 2013). Handling time can be simulated to compensate for the efficiency human predators achieve with the use of technology. Using bag limits or quotas can 'bend the curve' for wildlife such that human predators have lower exploitation rates. This management strategy, which often has social licence among

hunters and anglers, can reduce the selective effects of exploitation (Woodward & Griffin, 2003). In some instances, harvest of juveniles or selectively targeting animals after senescence may serve to reduce evolutionary impacts of harvest (Milner et al., 2011). Managing the timing of harvest pressure may also be important to consider, given how fear can alter diel behaviour of prey species, with consequences for ecosystem functioning (Bonnot et al., 2020). Ultimately, managing exploitative systems using quotas or limits is challenged by pressures that extend into the political and socio-economic spheres but is needed to account for selective effects of harvest

How important are predators to human well-being? Multiple lines of evidence suggest that predators are not just helpful to humans in controlling large herbivore populations, but economically valuable in their capacity to limit the number of collisions between vehicles and large herbivores. Gilbert et al. (2017) modelled the predicted benefits of cougar *Puma concolor* recolonization of the eastern United States on the number of wildlife-related collisions and fatalities. Empirical data from Wisconsin presented by Raynor et al. (2021) have confirmed that recolonization by wolves *Canis lupus* has had a positive societal impact based on reductions in vehicular collisions. Despite widespread hunting in Wisconsin, it seems human predators were unable to control the distribution or abundance of deer in a way that reduced collisions, suggesting a high value of the predators to the ecosystem.

that does not align with mortality incurred by most populations due to apex predators.

These ideas above are not novel to managers (Worm & Paine, 2016), but our review highlights how these strategies fit within the overarching lens of predation. We aim to inspire more research to understand how phenotypic targets in hunting and fishing depart from those of other predators, identifying whether management intervention could mitigate any potential changes to genotypic and phenotypic frequencies over time (Table 2). Experimental approaches may be particularly relevant, perhaps using replicated fields or ponds with different predator communities and human harvesting manipulated to track prey phenotypic change (e.g. Monk et al., 2021). Interventions including disease outbreaks and measurements of population dynamics, individual fitness-related metrics (e.g. offspring assignment), carbon flux and pathogen reproductive rate (R_0) would help fill knowledge gaps and stitch together our conceptual framework of the human niche as harvesters in ecosystems (Table 1). Such fundamental research could be used to inform management to exploit new information about disease and landscape processes for effective regulation of prey populations. A design principle that might yield new insight is one that adopts a comparative approach, which estimates how different the behaviour and impacts of predation by humans is compared to those of other predators (Darimont & Bryan, 2020).

Predators are more prone to be persecuted for the problems they are perceived to present than praised for the ecosystem processes that they are purported to provide. Indeed, predators yield valuable ecosystem services by influencing prey traits, regulating disease, modulating prey distributions through consumptive and non-consumptive effects, affecting geochemical cycles including sinking carbon in the environment, and contributing to human well-being. These roles all seem to similarly emphasize the importance of predator conservation. Conflict arises, however, from belief that the resources required by predators to carry out these effects are in excess of the value they provide; yet, the bulk of empirical evidence is mounting in opposition of that perspective. Very limited evidence, for example, supports the idea that removing predators will likely improve prey yields in the long term (Lennox et al., 2018). Indeed, simulations have shown that removal of marine mammals would most likely decrease fishing yields (Gerber et al., 2009). Return of predators to degraded ecosystems that have lost predators shows the promise of this approach to conservation and management, and more research focused on how hunting and fishing respond to restoration of healthy predator communities is needed to examine the link between productivity and complete communities (Lennox et al., 2018). There are two actionable resolutions that we foresee (1) to ensure that apex predators are able to occur at relevant densities to carry out ecosystem effects and (2) manage hunting and fishing in a way that more closely aligns with the behaviour (phenotypic targets, exploitation rates) of apex predators.

Our essay synthesizes literature from many ecological subdisciplines focused on the role of predators and emphasizes that maintaining healthy ecosystems with predators must be given more consideration as a viable management practice that aligns with the goals of managers and stakeholders. There are paths to coexistence with predators that value their contributions and do not unnecessarily persecute them as competitors or nuisances (Linnell et al., 2001). This means using management platforms to shift animal exploitation practices to emulate those observed in wild animals in predator–prey systems where predators maintain natural variation in the distribution of prey phenotypes, modulate disease against epidemics, regulate ecosystem through landscapes of fear, promote nutrient and carbon cycling and provide often underappreciated value to human well-being. By protecting predators and modelling human exploitation to emulate the role of natural predators, we propose that the long-term outlook for some conflicts between humans and wildlife can be mitigated with benefits to prey species and their predators, including humans.

AUTHORS' CONTRIBUTIONS

All authors contributed to the conception, writing, revising and intellectual development of the manuscript in a meaningful and essentially equivalent way with initiation and leadership of the lead author.

CONFLICT OF INTEREST

The authors wish to bring to light no interests in conflict with the manuscript content.

DATA AVAILABILITY STATEMENT

No data were used in the production of this manuscript and therefore no data are available to the readership.

ORCID

Robert J. Lennox https://orcid.org/0000-0003-1010-0577

Jacob W. Brownscombe https://orcid.org/0000-0003-2496-8764

Chris Darimont https://orcid.org/0000-0002-2799-6894

Graham D. Raby https://orcid.org/0000-0002-0549-4017

Steven J. Cooke https://orcid.org/0000-0002-5407-0659

REFERENCES

Allendorf, F. W., & Hard, J. J. (2009). Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(supplement 1), 9987–9994.

Aswani, S. (2019). Perspectives in coastal human ecology (CHE) for marine conservation. *Biological Conservation*, *236*, 223–235.

Atwood, T. B., Connolly, R. M., Ritchie, E. G., Lovelock, C. E., Heithaus, M. R., Hays, G. C., Fourqurean, J. W., & Macreadie, P. I. (2015). Predators help protect carbon stocks in blue carbon ecosystems. *Nature Climate Change*, *5*, 1038–1045.

Atwood, T. B., Hammill, E., Greig, H. S., Kratina, P., Shurin, J. B., Srivastava, G. S., & Richardson, J. S. (2013). Predator-induced reduction of freshwater carbon dioxide emissions. *Nature Geoscience*, *6*, 191–194.

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *The Journal of Animal Ecology*, *78*, 699–714.

Ben-Horin, T., Lafferty, K. D., Bidegain, G., & Lenihan, H. (2016). Fishing diseased abalone to promote yield and conservation. *Philosophical Transactions of the Royal Society B*, *371*, 20150211.

Bonnot, N. C., Couriot, O., Berger, A., Cagnacci, F., Ciuti, S., De Groeve, J. E., Gehr, B., Heurich, M., Kjellander, P., Kröschel, M., Morellet, N., Sönnichsen, L., & Hewison, A. M. (2020). Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. *Journal of Animal Ecology*, *89*(1), 132–145.

Bouffet-Halle, A., Mériguet, J., Carmignac, D., Agostini, S., Millot, A., Perret, S., Motard, E., Decenciere, B., & Edeline, E. (2019). Density-dependent selection mediates harvest-induced evolution. *bioRxiv*, 561522.

Braczkowski, A. R., O'Bryan, C. J., Stringer, M. J., Watson, J. E., Possingham, H. P., & Beyer, H. L. (2018). Leopards provide public health benefits in Mumbai, India. *Frontiers in Ecology and the Environment*, *16*, 176–182.

Branch, T. A., Hilborn, R., Haynie, A. C., Fay, G., Flynn, L., Griffits, J., Marshall, K. N., Randall, J. K., Scheuerell, J. M., Ward, E. J., & Young, M. (2006). Fleet dynamics and fishermen behavior: Lessons for fisheries managers. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 1647–1668.

Bro-Jørgensen, J. (2013). Evolution of sprint speed in African savannah herbivores in relation to predation. *Evolution*, *67*(11), 3371–3376.

Cáceres, C. E., Knight, C. J., & Hall, S. R. (2009). Predator–spreaders: Predation can enhance parasite success in a planktonic host–parasite system. *Ecology*, *90*, 2850–2858.

Chisholm, S. W., Falkowski, P. G., & Cullen, J. J. (2001). Dis-crediting ocean fertilization. *Science*, *294*, 309–310.

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS ONE*, *7*, e50611.

Crawford, D. A., Conner, L. M., Clinchy, M., Zanette, L. Y., & Cherry, M. J. (2022). Prey tells, large herbivores fear the human 'super predator'. *Oecologia*, *198*(1), 91–98.

Cromsigt, J. P., Kuijper, D. P., Adam, M., Beschta, R. L., Churski, M., Eycott, A., Kerley, G. I. H., Mysterud, A., Schmidt, K., & West, K. (2013). Hunting for fear: Innovating management of human–wildlife conflicts. *Journal of Applied Ecology*, *50*, 544–549.

Darimont, C. T., & Bryan, H. M. (2020). Hypermobile human predators. *Nature Human Behaviour*, Open Access.

Darimont, C. T., Fox, C. H., Bryan, H. M., & Reimchen, T. E. (2015). The unique ecology of human predators. *Science*, *349*, 858–860.

Fenberg, P. B., & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Molecular Ecology*, *17*, 209–220.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., & Wanless, S. (2006). From plankton to top predators: Bottom-up control of a marine food web across four trophic levels. *The Journal of Animal Ecology*, *75*, 1259–1268.

Gehr, B., Hofer, E. J., Pewsner, M., Ryser, A., Vimercati, E., Vogt, K., & Keller, L. F. (2018). Hunting-mediated predator facilitation and superadditive mortality in a European ungulate. *Ecology and Evolution*, *8*, 109–119.

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parapl, L., & Oro, D. (2010). The young, the weak and the sick: Evidence of natural selection by predation. *PLoS ONE*, *5*, e9774.

Gerber, L. R., Morisette, L., Kaschner, K., & Pauly, D. (2009). Should whales be culled to increase fishery yields? *Science*, *323*, 880–881.

Gilbert, S. L., Sivy, K. J., Pozzanghera, C. B., DuBour, A., Overdujin, K., Smith, M. M., Zhou, J., Little, J. M., & Prugh, L. R. (2017). Socioeconomic benefits of large carnivore recolonization through reduced wildlife-vehicle collisions. *Conservation Letters*, *10*, 431–439.

Goldbogen, J. A., Friedlander, A. S., Calambokidis, J., Mckenna, M. F., Simon, M., & Nowacek, D. P. (2013). Integrative approaches to the study of baleen whale diving behavior, feeding performance, and foraging ecology. *Bioscience*, *63*, 90–100.

Gordon, C. E., Feit, A., Grüber, J., & Letnic, M. (2015). Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142870.

Hawlena, D., Strickland, M., Bradford, M., & Schmitz, O. (2012). Fear of predation slows plant-litter decomposition. *Science*, *336*, 1434–1438.

Heino, M., Diaz Pauli, B., & Dieckmann, U. (2015). Fisheries-induced evolution. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 461–480.

Hyatt, K. D., McQueen, D. J., Shortreed, K. S., & Rankin, D. P. (2004). Sockeye salmon (*Oncorhynchus nerka*) nursery lake fertilization: Review and summary of results. *Environmental Reviews*, *12*, 133–162.

Jørgensen, C., & Holt, R. E. (2013). Natural mortality: Its ecology, how it shapes fish life histories, and why it may be increased by fishing. *Journal of Sea Research*, *75*, 8–18.

Kaemingk, M. A., Hurley, K. L., Chizinski, C. J., & Pope, K. L. (2020). Harvest–release decisions in recreational fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*, 194–201.

Kays, R., Parsons, A. W., Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., Rota, C. T., Millspaugh, J. J., & McShea, W. J. (2017). Does hunting or hiking affect wildlife communities in protected areas? *Journal of Applied Ecology*, *54*, 242–252.

Killen, S. S., Nati, J. J., & Suski, C. D. (2015). Vulnerability of individual fish to capture by trawling is influenced by capacity for anaerobic metabolism. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20150603.

Kleiven, A. R., Moland, E., & Sumaila, U. R. (2019). No fear of bankruptcy: The innate self-subsidizing forces in recreational fishing. *ICES Journal of Marine Science*, *77*, 2304–2307.

Krumm, C. E., Conner, M. M., Hobbs, N. T., Hunter, D. O., & Miller, M. W. (2010). Mountain lions prey selectively on prion-infected mule deer. *Biology Letters*, 6(2), 209–211.

Kuparinen, A., & Merilä, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in Ecology & Evolution*, 22, 652–659.

Laundré, J. W., Hernández, L., & Allendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Canadian Journal of Zoology*, 79, 1401–1409.

Lavery, T. J., Roudnew, B., Gill, P., Seymour, J., Seuront, L., Johnson, G., Mitchell, J. G., & Smetacek, V. (2010). Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proceedings of the Royal Society B: Biological Sciences*, 277(1699), 3527–3531.

Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, 57, 659–668.

Lennox, R. J., Alós, J., Arlinghaus, R., Horodysky, A., Klefoth, T., Monk, C. T., & Cooke, S. J. (2017). What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. *Fish and Fisheries*, 18, 986–1010.

Lennox, R. J., Gallagher, A. J., Ritchie, E. G., & Cooke, S. J. (2018). Evaluating the efficacy of predator removal in a conflict-prone world. *Biological Conservation*, 224, 277–289.

Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, 48, 25–34.

Linnell, J. D. C., Swenson, J. E., & Andersen, R. (2001). Predators and people: Conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, 4, 345–349.

Milner, J. M., Bonefant, C., & Mysterud, A. (2011). Hunting Bambi—Evaluating the basis for selective harvesting of juveniles. *European Journal of Wildlife Research*, 57, 565–574.

Monk, C. T., Bekkevold, D., Klefoth, T., Pagel, T., Palmer, M., & Arlinghaus, R. (2021). The battle between harvest and natural selection creates small and shy fish. *Proceedings of the National Academy of Sciences of the United States of America*, 118(9), e2009451118.

Montgomery, R. A., Raupp, J., Miller, S. A., Wijers, M., Lisowsky, R., Comar, A., Bugir, C. K., & Hayward, M. W. (2022). The hunting modes of human predation and potential nonconsumptive effects on animal populations. *Biological Conservation*, 265, 109398.

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., & Musiani, M. (2011). Human activity helps prey win the predator-prey space race. *PLoS ONE*, 6, e17050.

Mysterud, A., & Edmunds, D. R. (2019). A review of chronic wasting disease in North America with implications for Europe. *European Journal of Wildlife Research*, 65, 26.

Mysterud, A., Rivrud, I. M., Gundersen, V., Rolandsen, C. M., & Viljugrein, H. (2020). The unique spatial ecology human of hunters. *Nature Human Behaviour*, 4, 694–701.

Mysterud, A., & Rolandsen, C. M. (2018). A reindeer cull to prevent chronic wasting disease in Europe. *Nature ecology & Evolution*, 2(9), 1343–1345.

Neubauer, P., Jensen, O. P., Hutchings, J. A., & Baum, J. K. (2013). Resilience and recovery of overexploited marine populations. *Science*, 340, 347–349.

Nilssen, K. T., Lindstrøm, U., Westgaard, J. I., Lindblom, L., Bleckne, T. R., & Haug, T. (2019). Diet and prey consumption of grey seals (*Halichoerus grypus*) in Norway. *Marine Biology Research*, 15, 137–149.

O'Bryan, C. J., Braczkowski, A. R., Beyer, H. L., Carter, N. H., Watson, J. E., & McDonald-Madden, E. (2018). The contribution of predators and scavengers to human well-being. *Nature Ecology & Evolution*, 2, 229–236.

Ostfeld, R. S., & Holt, R. D. (2004). Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. *Frontiers in Ecology and the Environment*, 2(1), 13–20.

Rau, M. E., & Caron, F. R. (1979). Parasite-induced susceptibility of moose to hunting. *Canadian Journal of Zoology*, 57, 2466–2468.

Raynor, J. L., Grainger, C. A., & Parker, D. P. (2021). Wolves make roadways safer, generating large economic returns to predator conservation. *Proceedings of the National Academy of Sciences*, 118(22), e2023251118.

Sala, E., Mayorga, J., Costello, C., Kroodsma, D., Palomares, M. L., Pauly, D., Rashid Sumaila, U., & Zeller, D. (2018). The economics of fishing the high seas. *Science Advances*, 4, eaat2504.

Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: The use and manufacture of tools by animals*. JHU Press.

Skonhoft, A. (2006). The costs and benefits of animal predation: An analysis of Scandinavian wolf re-colonization. *Ecological Economics*, 58, 830–841.

Smith, B. D. (2007). The ultimate ecosystem engineers. *Science*, 315, 1797–1798.

Stockner, J. G., Rydin, E., & Hyenstrand, P. (2000). Cultural oligotrophication: Causes and consequences for fisheries resources. *Fisheries*, 25, 7–14.

Støen, O. G., Ordiz, A., Evans, A. L., Laske, T. G., Kindberg, J., Fröbert, O., Swenson, J. E., & Arnemo, J. M. (2015). Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiology & Behavior*, 152, 244–248.

Storaas, T., Gundersen, H., Hendriksen, H., & Andreassen, H. P. (2001). The economic value of moose in Norway-a review. *Alces*, 37, 97–107.

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, 22, 1578–1586.

Tanner, E., White, A., Acevedo, P., Balseiro, A., Marcos, J., & Gortázar, C. (2019). Wolves contribute to disease control in a multi-host system. *Scientific Reports*, 9, 7940.

Turner, R. K., Paavola, J., Cooper, P., Farber, S., Jessamy, V., & Georgiou, S. (2003). Valuing nature: Lessons learned and future research directions. *Ecological Economics*, 46, 493–510.

Wallach, A. D., Izhaki, I., Toms, J. D., Ripple, W. J., & Shanas, U. (2015). What is an apex predator? *Oikos*, 124, 1453–1461.

Wang, X., Daigger, G., de Vries, W., Kroeze, C., Yange, M., Ren, N. Q., Liu, J., & Butler, D. (2019). Impact hotspots of reduced nutrient discharge shift across the globe with population and dietary changes. *Nature Communications*, 10, 1–12.

Wild, M. A., Hobbs, N. T., Graham, M. S., & Miller, M. W. (2011). The role of predation in disease control: A comparison of selective and nonselective removal on prion disease dynamics in deer. *Journal of Wildlife Diseases*, 47, 78–93.

Wilmers, C. C., Estes, J. A., Edwards, M., Laidre, K. L., & Konar, B. (2012). Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and the Environment*, 10, 409–415.

Woodward, R. T., & Griffin, W. L. (2003). Size and bag limits in recreational fisheries: Theoretical and empirical analysis. *Marine Resource Economics*, 18, 239–262.

Worm, B., & Paine, R. T. (2016). Humans as a hyperkeystone species. *Trends in Ecology & Evolution*, 31, 600–607.