Introduction and Definitions

Deciding how much to invest in antipredator behavior, rather than in foraging or other activities, is a fundamental problem faced by most animals. Behaviors that lower an animal's probability of death by predation – vigilance, hiding, avoidance of risky sites, and others – carry the cost of reduced access to resources for growth and reproduction. Ecologists have approached this problem, using evolutionary principles. They have developed predation risk theory, often expressed mathematically, which assumes that prey maximize fitness (e.g., lifetime reproductive success) by making behavioral decisions that optimize trade-offs between predator avoidance and resource acquisition. Predation risk theory can be used to estimate the 'risk effects' of predators on prey: the lost foraging opportunities and lower levels of growth and reproduction experienced by prey investing in antipredator behavior (also known as nonlethal or nonconsumptive effects). Importantly, risk effects can be major components of trophic cascades: the indirect effects of top predators on the population processes of plants and animal species at lower trophic levels, as mediated by the density and foraging behavior of intermediate consumers (i.e., herbivores and mesopredators, collectively termed mesoconsumers). Thus, risk effects can potentially affect community structure and ecosystem function.

This article surveys how human influences can affect antipredator behavior, potentially altering the risk effects and mortality rates experienced by prey and the indirect effects of predators on ecosystems. For example, human consumption of space and resources (e.g., fishing, forestry, agriculture, urbanization, etc.) and climate change may create resource shortages for mesoconsumers, thereby limiting their scope for antipredator behavior and indirectly increasing the rates at which they are killed by non-human predators. Nonlethal human activities, such as ecotourism, can cause animals to experience energetic and reproductive costs that resemble the costs of predator avoidance. Notoriously, humans have eliminated top predators in many systems, relaxing the need for mesoconsumers to invoke antipredator behavior, potentially disrupting trophic cascades. As illustrated in the following sections, predation risk theory can provide tools for predicting, detecting, and potentially mitigating these and other conservation problems.

State-Dependent Risk-Taking: Why Human-Caused Resource Declines Can Increase Predation Rates

During the 1980s, Marc Mangel, Colin Clark, John McNamara, and Alasdair Houston pioneered models of state-dependent behavior (also known as dynamic state variable models), which, among their many capabilities, predict the effect of residual reproductive value on behavioral decisions that maximize fitness. State-dependent risk-taking, a subset of this theory, predicts that resource declines and associated losses of body condition should increase risk-taking and predation rates for individuals attempting to avoid imminent starvation or other net fitness losses. Bradley Anholt and Earl Werner provided early empirical support for this prediction by experimentally exposing bullfrog tadpoles (Rana catesbeiana) to predation risk from larval dragonflies (Tramea lacerata) under contrasting levels of food abundance. Tadpoles experiencing low food levels moved, on average, 1.5 times more frequently and at higher speeds than tadpoles experiencing high food levels. Higher movement rates under food scarcity, which reflect greater foraging effort, also increased exposure to predators and caused a 60% rise in mean predation rates, despite predator densities remaining constant (Figure 1). This and later experiments by Anholt and Werner provided ground-breaking evidence that, consistent with the theory on state-dependent behavior, dichotomous views about resource-driven (‘bottom-up’) versus consumer-driven (‘top-down’) effects on population regulation are simplistic. Rather, these mesocosm experiments suggested that synergisms between resources and predators are fundamental to population and community processes, and adaptive variation in prey behavior is inherent to these synergisms. Subsequent field studies suggest that these synergisms scale up to large vertebrates using vast landscapes. Data on sea turtles, ungulates, and other large vertebrates suggest that individuals in poor body condition spend more time in habitats with better food quality and higher predation risk and consequently, may suffer higher predation rates than individuals in better condition.

State-dependent risk-taking potentially has profound conservation implications because humans influence the global distribution and abundance of resources used by animals. For example, models of state-dependent behavior predict that overfishing can force harbor seals
on foot or on motorized vehicles often approach wildlife to the point of altering the animals' activity and eliciting antipredator behavior like fleeing. These responses by wildlife to humans are referred to as 'disturbance' and their context includes ecotourism (e.g., wildlife viewing, photography), resource extraction (e.g., machinery use, blasting, helicopter access to remote sites), and the nonlethal component of hunting (i.e., the search for quarry). Animal responses to disturbance stimuli may carry the same cost of predator avoidance – lost opportunities for feeding, mating, parental care, or other fitness-enhancing activities – and often include the energetic costs of locomotion while fleeing.

Theoretically, decisions by animals encountering humans should follow the same principles as antipredator behavior: optimization of trade-offs between access to resources (or net energy gain) and avoidance of perceived danger. Consistent with this hypothesis, factors that influence perceived risk of predation also affect animal responses to disturbance stimuli. For instance, when approached directly by a helicopter, Dall's sheep (Ovis dalli dalli) farther from steep rocky slopes (a refuge from predation), flee sooner than sheep closer to these slopes (Figure 3).

Antipredator behavior and responses to disturbance are analogous even when disturbance stimuli derive from modern technologies that prey had not encountered previously (e.g., motorized vehicles). This occurs because prey have evolved antipredator responses to generalized threatening stimuli, such as rapidly approaching objects that cross a threshold of perceived safety. Early support for this hypothesis was provided by Larry Dill's experiments in which zebra danios (Brachydanio rerio, a small fish) were exposed to real predators, a predator-shaped model, and a 'cinematographic' predator (a film of a black dot increasing in size, simulating an approaching object). In all cases, zebra danios fled when the angle subtended by the predator at the prey's eye reached a threshold rate of change (loom rate). The threshold loom rates depended on the size and speed of the approaching 'predator.' Thus, danios appeared to decide when to flee by relating the loom rate to a margin of safety, regardless of whether the predator was real, a model, or a film. Such generalized responses, however, are not mutually exclusive with predator-specific responses.

Importantly, lack of overt response to disturbance stimuli does not necessarily imply a lack of impact. According to models of state-dependent behavior, an individual's scope for antipredator behavior is influenced by the availability of its resources, its current body condition, and other factors affecting residual reproductive value. Thus, animals lacking alternative sites with adequate resources or struggling to maintain adequate body condition may be unable to afford to abandon their resource patch and flee from disturbance stimuli. (The same principle applies to the decision to abandon or care for dependent offspring.) People encountering wildlife often misinterpret lack of

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**Nonlethal Interactions Between Wildlife and Humans**

Humans interact with animals in many ways that are nonlethal yet potentially damaging. For instance, people...
fleeing as a neutral or even benign interaction. Yet beneath this superficial appearance, animals may experience decreased foraging efficiency due to increased vigilance, disrupted cycles of rest and digestion (which are particularly important for ruminants), and physiological responses to stress.

Similar to chronic risk effects from non-human predators, it is theoretically plausible for chronic disturbance stimuli to indirectly influence plant community structure by causing herbivores to underutilize plant resources in areas perceived to be dangerous while increasing use of plants in areas that are perceived as safer.

Should animals not recognize that nonlethal stimuli do not warrant the costs of antipredator behavior? Animals rarely have perfect information and, theoretically, should maximize fitness by overestimating rather than underestimating risk. Overestimation costs, such as lost feeding opportunities, are lower than underestimation costs, which are death and loss of all future fitness. Thus, habituation to disturbance stimuli is only partial for chronic disturbance stimuli to indirectly influence plant community structure by causing herbivores to underutilize plant resources in areas perceived to be dangerous while increasing use of plants in areas that are perceived as safer.

Figure 2 Predictions from a model of state-dependent behavior on the relationship between fisheries and antipredator behavior (arrows show causal links). (a) Pacific sleeper shark caught as bycatch in a trawl net targeting walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. On the one hand, the removal of top predators like sharks may relax predation risk and alter the behavior of mesoconsumers, such as (b) harbor seals, thereby disrupting indirect effects of top predators on species at lower trophic levels. The model predicts that shark removals will (c) greatly increase the proportion of dives to deep strata by seals, where both walleye pollock – the seals’ most predictable resource – and sharks are most abundant. Consequently, shark removals should (d) greatly decrease and increase, respectively, rates of seal-inflicted mortality on (e) Pacific herring (*Clupea palasi*) in shallow and mid-depth strata and (f) pollock in deep strata. (Note that Panels c and d represent only seals in good body conditions, which have greater scope for antipredator behavior than seals in poor body condition.) On the other hand, fisheries depleting resources while top predators are still present may increase state-dependent risk-taking and predation rates for mesoconsumers. When herring are not sufficiently abundant to compensate for pollock declines and sharks are present at a constant density, overfishing of pollock should increase for seals the rates of (g) deep diving and, consequently, of (h) shark-inflicted mortality. Risk-taking and predation rates are exacerbated if seals are in poor body condition (*g, h*). This modeling approach can explore net effects of (a) concurrent removals of resources and top predators. Data are the outcome of computer experiments (*N* = 1000 forward iterations per treatment) simulating a 3-week winter period with the model and protocols described in Frid A, Baker G G, and Dill L M (2008) Do shark declines create fear-released systems? *Oikos* 117: 191–201. Photo credits: (a) Elliott Lee Hazen; (b) Alejandro Frid, (e, f) R.E. Thorne. In (b), the seal was captured for research purposes and is about to be released carrying recording devices that measure diving behavior.
nondomesticated animals. Even corvids and squirrels in urban parks – archetypal examples of habituation – maintain levels of response to disturbance stimuli that are consistent with principles of antipredator behavior.

Importantly, when habituation levels for prey surpass those for predators, human infrastructure and its associated disturbance stimuli effectively provide prey with antipredator shields. For instance, Joel Berger found that moose (*Alces alces*) in the Yellowstone Ecosystem, USA, generally avoid the vicinity of roads except during parturition. This choice of parturition sites may reduce calf losses to predation by grizzly bears (*Ursus arctos*), which avoid roads more than moose do.

### Relationships Between Risk Effects and the Structure and Function of Ecosystems

Increasing evidence suggests that top predators can influence the structure and function of ecosystems via a combination of direct predation and risk effects on their prey. For example, the 1926 extirpation of wolves (*Canis lupus*) from Yellowstone National Park led to population increases and unrestrained browsing by elk (*Cervus elaphus*) released from the lethal and risk effects of wolves. The combined population and behavioral changes by elk lowered recruitment of woody riparian vegetation and upland deciduous trees. Since the 1995 reintroduction of wolves, plant recruitment has improved partly because direct predation by wolves has reduced elk numbers and consequently, the overall browsing pressure. Antipredator responses by elk, however, have influenced spatial variation in the strength of the indirect effects of wolves on vegetation. This trophic cascade was strongest in riskier areas where elk foraged least: sites with abundant logs, particularly in riparian zones, where poor visibility and obstacles hindering escape may increase the probability of death by predation, given an encounter with wolves (Figure 5).

Trophic cascades mediated by antipredator behavior can modify physical habitat structures. For example, in Zion National Park, unrestrained foraging by mule deer (*Odocoileus hemionus*) experiencing reduced predation risk from cougars (*Puma concolor*) appears to have eroded stream banks and reduced abundances of flora and fauna associated with riparian zones. Similarly, in Yellowstone National Park, the overgrazing of riparian trees and shrubs by elk released from wolf predation risk may have influenced the density and dam-building activities of beavers (*Castor canadensis*), which require woody plants to construct dams. These correlational studies suggest that, as mediated by ungulate herbivory and damming by beavers, the loss of large carnivores has the potential to indirectly alter hydrological processes that in turn influence the structure and composition of aquatic and terrestrial communities. More generally, there is evidence that herbivores across a wide range of body sizes and ecosystems (e.g., from grasshoppers to marine turtles) can influence recruitment and community structure of primary producers, but risk and lethal effects of predators limit this influence.

It is plausible for risk effects also to influence the dynamics of nutrient flow across ecosystems. For example,
a recent study by Joseph Bump and colleagues indicates
that moose on Isle Royale, Lake Superior, spend much of
their time foraging on aquatic macrophytes and transfer
considerable amounts of aquatic nitrogen to terrestrial
communities. Moose habitat use and, consequently, the
spatial pattern and magnitude of their nitrogen deposition
on land are influenced by wolf predation risk. The loss of
wolves could, therefore, alter the nutrient dynamics
of communities surrounding wetlands. Similarly, marine
fishes that forage in seagrass ecosystems often shelter from
predators among mangrove prop roots or in reefs, thereby
transporting seagrass-derived nutrients and energy into
reef and mangrove habitats. Declines of predators in sea
glass system, therefore, can potentially alter the nutrient
subsides into these habitats.

Mescosm experiments by Oswald Schmitz provide
evidence that, for invertebrate predator–prey interactions
in grasslands, the hunting mode of different predator
species (spiders) indirectly influences ecosystem function,
as mediated by predator-specific antipredator responses
of herbivores (grasshoppers). Sit-and-wait ambush spiders
leave persistent, point-source cues of predation risk.
Consequently, grasshoppers can respond with chronic habitat
shifts and their foraging pressure shifts from preferred
plants associated with greater risk to less preferred plants
that can be accessed more safely. As mediated by these
risk effects on grasshoppers, the indirect effect of roaming spiders on ecosystem function is opposite to
that of sit-and-wait spiders: lower plant diversity but
greater productivity and nitrogen mineralization. The
similar nature of risk effects across diverse taxa and eco-
systems suggests that these processes scale up and that
conserving species diversity within guilds of large preda-
tors might be important to the maintenance of many
ecosystem functions.

While the plight of top predators in terrestrial sysems
has long been recognized, only recently has it become
apparent that marine ecosystems are experiencing cata-
strophic losses of large predators through target and
bycatch fisheries. These losses may create risk-released
systems mirroring those on land, where unrestricted
grazing by herbivores or increased predation by mesocon-
sumers affects the foundations of food webs. For example,
studies in Shark Bay, Western Australia, reveal that taxa
ranging from herbivorous turtles and dugongs to piscivo-
rorous dolphins and seabirds modify their foraging locations
and behaviors to minimize risk from tiger sharks (*Galeo-
cerdo cuvier*) and suggest that these antipredator behaviors
may influence the structure of seagrass communities.
Changes in seagrass communities in regions where tiger
sharks have been overfished further suggest that releasing
marine herbivores from predation risk may alter benthic

**Figure 4** Conceptual model outlining the behavioral mechanisms by which increased rates of human-caused disturbance or
predator encounters by prey could cause population size to decline. Downward-facing arrows inside boxes indicate a negative
response and upward-facing arrows indicate a positive response. Modified and reprinted with permission from Frid A and Dill LM (2002)
communities. Losses of other large marine predators may also disrupt trophic cascades that are mediated by the antipredator behavior of mesopredators. Theoretical predictions suggest that the removal of Pacific sleeper sharks from northeastern Pacific ecosystems could shift pinniped predation from fishes in safer shallow waters to profitable fish species in deeper waters that pinnipeds might otherwise avoid to reduce predation risk (Figure 2). Just as in terrestrial systems, maintaining or restoring viable populations of large marine predators is likely important to marine conservation.

### Anthropogenic Climate Change and Risk Effects

Global climate change caused by human activities is altering the resources, geographic distributions, phenology, and physiological and behavioral performance of many species at rates that exceed the range of natural historical variability. Therefore, it can potentially create novel ecological circumstances that attenuate or amplify risk effects or that indirectly increase predation rates through state-dependent risk-taking (Figure 6).

### Climate-Related Mechanisms That Can Attenuate Risk Effects

It is plausible that climate change indirectly attenuates risk effects in some systems by altering environmental conditions that facilitate hunting success by predators. During winter on Isle Royale, the pack size and hunting success of wolves on moose increases with snow depth. Historically, the North Atlantic Oscillation has driven snow depth variation in the area. Under anthropogenic climate change, however, the frequency of winters with shallow snow packs could increase and moose could potentially experience more frequent winters of relaxed predation risk. Under this scenario, climate change would weaken the indirect effects of wolves on woody vegetation, as mediated by moose density and browsing behavior.

Climate change might also diminish the hunting effectiveness of some predators through physiological mechanisms. Pursuit-diving seabirds and pinnipeds are endothermic (warm-blooded) and consequently, their burst speed while hunting is unaffected by water temperature. In contrast, fish, their primary prey, are ectothermic (cold-blooded), and rising ocean temperatures are predicted to increase their burst speeds and escape ability, potentially reducing the risk effects of seabirds and pinnipeds on fish.

Another mechanism potentially attenuating risk effects is interspecific variation in climate-driven phenological responses. Christiaan Both and colleagues have analyzed responses to earlier spring warming by organisms at four trophic levels: deciduous oak trees (*Quercus robur*), caterpillars of the winter moth (*Operophtera brumata*) that feed on oak buds, several species of passerine songbirds that prey on caterpillars, and sparrowhawks (*Accipiter nisus*)...
that prey on songbirds. Their findings indicate that over the last two decades, oak budburst has been occurring progressively earlier and moths are reproducing earlier, apparently tracking shifts in plant phenology. Similarly, songbird reproduction is occurring earlier, apparently tracking moth reproduction. Sparrowhawks reproduction, however, has not shifted to match the earlier peak abundance of songbird nestlings, which would enhance the ability of sparrowhawk parents to provision their nests. As underscored by this study, climate change may indirectly decouple some predator–prey relationships, with mesoconsumers (e.g., songbirds) experiencing a seasonal lowering of risk effects from their predators (e.g., sparrowhawks).

Climate-Related Mechanisms That Can Amplify Risk Effects

Range shifts and expansions in response to climate change will result in mesoconsumers encountering novel predators, and animals that were top predators previously may become mesopredators. For example, warming ocean temperatures are predicted to facilitate the expansion to higher latitudes of ectothermic sharks that are currently restricted to lower latitudes. These range expansions could amplify risk effects for endothermic marine mammals and other prey that currently live under lower predation risk from sharks at higher latitudes.

Climate Change May Indirectly Alter Mortality Rate Through State-Dependent Behavior

A general prediction derived from predation risk theory is that climate change, which affects resource availability, can indirectly alter rates of mortality inflicted by predators (or analogous agents; see below) through behavioral mechanisms of state-dependent risk-taking. Data for diverse taxa – including amphibians, polar bears (*Ursus maritimus*), and humans – are consistent with this prediction.

Efts (terrestrial juveniles) of the eastern red-spotted newt (*Notophthalmus viridescens*) compromise predator avoidance when dry conditions force them to invest more on behaviors that relieve desiccation stress. Live efts emit chemical cues signaling conspecific attraction, which facilitates huddling to reduce water losses. Recently killed efts, however, appear to emit a mixture of these attractive chemical cues and of repulsive chemical cues signaling predation risk. Experimental data indicate that efts experiencing moist conditions avoid chemical cues emitted by recently killed individuals, while these same cues attract efts stressed by desiccation. Drying trends associated with global climate change, therefore, can potentially exacerbate predator-inflicted mortality rates for amphibians via these behavioral mechanisms.

Notably, climate-induced resource losses may force top predators to invoke foraging modes that increase the risk of human-caused mortality, creating a situation resembling that of reduced antipredator behavior by

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**Figure 6** Simplified pathways illustrating hypothetical indirect effects of anthropogenic resource consumption and climate change on community structure and ecosystem function, as mediated by mesoconsumer antipredator behavior. Solid and dotted lines represent, respectively, direct and indirect links. Double pointed arrows indicate two-way relationships. To emphasize potentially dominant mechanisms and maintain visual clarity, some plausible relationships are not shown (e.g., climate change may influence the local density of top predators and predation risk may alter the timing of reproduction). Whether human influences are predicted to attenuate or amplify risk effects depends on ecological context (see text).
energetically stressed mesoconsumers. Under normal conditions of sea ice, polar bears can meet energetic needs by hunting for seals at breathing holes on the ice pack and therefore, can avoid human settlements. In western Hudson Bay, however, earlier break-up of sea ice during spring has increased the period in which polar bears fast on land unable to access seals. Consequently, nutritionally stressed polar bears increasingly search for human-related food sources at settlements or camps, where humans kill them in self-protection. Sea ice break up is predicted to keep shifting to progressively earlier dates, raising concern for polar bear conservation and the management of human–bear interactions.

Humans are not exempt from their own form of state-dependent risk-taking. Historically, climate-driven resource shortages have influenced the decision by hungry societies to initiate wars that might never have occurred had human populations been well fed (Figure 7). Resource shortages induced by climate change can, consequently, exacerbate the potential for war or other human conflicts. Arguably, this is the biggest conservation issue of all, and – while not ignoring the complexities of human cultures and modern social institutions – principles of state-dependent risk-taking could contribute theoretical tools for anticipating and perhaps reducing conflicts between humans over scarce resources.

The converse of these examples is plausible when climate change is predicted to increase resource availability. For instance, Nicolas Lecomte and colleagues have shown that snow geese (Chen caerulescens atlantica) in the Arctic must leave their nests to drink. Drier conditions increase the dispersion of water sources and the duration of water acquisition trips, thereby amplifying nest losses to predation. Climate models, however, predict increased precipitation for the Arctic over the next two decades, which can potentially enhance nest guarding and reproductive success by Arctic-nesting snow geese.

Managing Irreversible Changes to the Biosphere

The conservation challenges ahead are daunting. Most pressingly, climate change has already begun and will continue to reshape the biosphere. Encouragingly, a wide range of studies suggest that the basic mechanisms of risk effects and state-dependent risk-taking have great generality. Thus, predation risk theory might have important applications to ecosystem conservation and the management of irreversible changes to the biosphere. Some examples are as follows.

Conservation Implications of State-Dependent Risk-Taking

The conservation message of studies on state-dependent risk-taking is that human-caused resource declines should not be viewed solely as bottom-up impacts (e.g., nutritional stress), as is often the case. Instead, predictions and mitigation efforts should consider how the combined effects on resource availability of human consumption, nonlethal disturbance, and global climate change might limit the scope for antipredator behavior and potentially increase rates of predation for many species. Conversely, human-caused resource subsidies may indirectly decrease predation rates for some mesoconsumers, potentially altering some predator–prey interactions.

The framework of state-dependent risk-taking can also predict the indirect influence of human-caused disturbance stimuli on mortality rates inflicted by predators. Disturbance can functionally lower resource availability through increased vigilance or distributional shifts. Thus, wildlife managers might be able to predict scenarios in which chronic disturbance can increase energetic stress, thereby raising risk-taking while foraging and increasing predation rates indirectly (Figure 4).

Managing Risk Effects of Disturbance Stimuli on Wildlife

Predation risk theory can provide a rationale for managing disturbance stimuli without over-regulating humans. For instance, routes for motorized vehicles in remote areas (e.g., helicopters used for resource extraction) may be restricted to distances from known wildlife concentrations (e.g., raptor nests, ungulate birthing sites) that optimize the conflicting objectives of reducing disturbance to wildlife while avoiding excessive detours. Similarly, predation risk theory can be used to design wildlife viewing areas such that setback distances between people and animals optimize viewing opportunities and prevention of disturbance, rather than merely stressing animals that lack alternative habitats. Another concern is that hunting regulations generally consider only the lethal component of hunting, yet hunters disturb many more animals than they kill. Thus, predation risk theory could help develop hunting regulations that account for disturbance impacts on targeted game. Further, when top predators are endangered but game species are not (e.g., Florida panther (Felis concolor coryi) and white-tailed deer (Odocoileus virginianus), respectively), regulations might also account for the reduced hunting success that natural predators might experience because prey pursued by human hunters become more alert and difficult to capture.

Significantly, the use by prey of disturbance stimuli as safe zones that top predators avoid could diminish the effectiveness of national parks for protecting biodiversity. Although national parks usually have the dual mandate of facilitating recreation and conservation, access for recreation (e.g., roads, permanent campsites) might promote safe zones for prey that disrupt predator–prey behavioral interactions inherent to many aspects of biodiversity.
State-dependent risk-taking by humans? Time series data on paleo-temperature variation, war frequency, and population growth rate, AD 1400–1900, suggesting that climatic stress indirectly influences the willingness by humans to initiate conflicts and, consequently, the rates of war-inflicted mortality (a prediction stemming from theory on state-dependent risk-taking). The mediating factors between climatic stress and war (not shown here) are drops in agricultural production and rising food prices (see Figure 2 of the original source). (a) Temperature anomaly (°C) in the Northern Hemisphere that is smoothed by 40-year Butterworth low pass filter. (b) Number of wars in the Northern Hemisphere (bright green), Asia (pink), Europe (turquoise), and the arid areas in the Northern Hemisphere (orange). (c) Number of wars worldwide (colors represent estimates by different authors; see original source). (d) Twenty-year population growth rate in Europe (turquoise), Asia (pink), and the Northern Hemisphere (blue) and the Northern Hemisphere 50-year fatality index (bright green). Cold phases are shaded as gray stripes. All war time series are in 10-year units. The bright green curves correspond to the right y axis. Caption adapted and figure reprinted (with permission) from Zhang DD, Brecke P, Lee HF, He YQ, and Zhang J (2007) Global climate change, war, and population decline in recent human history. Proceedings of the National Academy of Science 104: 19214–19219.
Predation risk theory could be applied to the design of parks so that these safe zones for prey are predicted and mitigated.

**Restoring and Conserving Risk Effects**

A growing body of evidence suggests that the risk and direct predation effects of predators on mesoconsumers across a wide range of body sizes and ecosystems can affect ecosystem function indirectly. If the influence of risk effects on trophic cascades and related processes is as widespread as these studies suggest, then conserving ecologically meaningful densities of top predators might be essential to many aspects of community dynamics. As experiments by Oswald Schmitz suggest, conserving predator diversity and its range of hunting modes, rather than merely conserving predator abundance, may be required to maintain some ecosystem functions (e.g., plant diversity, primary productivity, and nitrogen mineralization in grasslands).

Where extinct already, restoring populations of upper-level native predators may potentially reverse many aspects of ecosystem degradation via the reestablishment of risk and lethal effects; wolves reintroduced to Yellowstone provide a compelling case. In terrestrial systems where predator reintroductions are impossible or where human-dominated landscapes no longer support the habitat requirements of large carnivores, hunting can potentially become a management tool for reducing some ecological consequences of the loss of direct predation and risk effects on mesoconsumer populations. This potential, however, has yet to be met because hunting regulations and access logistics (e.g., the distribution of roads or navigable waterways) typically limit human hunting behavior to spatiotemporal distributions and patterns of prey selectivity that differ from those of non-human carnivores. Predation risk theory, combined with demographic analyses, could be used to optimize hunting regulations so that human hunters mimic some risk and lethal effects of non-human carnivores more closely without threatening human safety and prey populations themselves. Carnivore restoration and hunting as management tools, however, are difficult to reconcile with some values of human society, which could preclude some applications of predation risk theory.

A related concern is that predator reintroductions could cause high predation rates on prey that may have lost their antipredator skills after living under relaxed predation pressure for several generations. Data for some vertebrate taxa (e.g., moose, passerine birds, marsupials), however, suggest that predator-naïve prey can learn to recognize and avoid novel predators within one generation. Reintroduced predators, therefore, may have their highest predation rates on naïve prey early in their geographic expansion, but their kill rates may diminish as prey become savvier. Although the ability to learn antipredator skills does not negate concern that novel predators could drive extinct small populations of naïve prey, this issue generally applies to exotic predators invading small islands rather than to planned reintroductions of native carnivores. A related problem is that efforts to restore native mesoconsumers (e.g., endangered marsupials in Australia) through translocations may fail unless captive-raised mesoconsumers are trained to recognize and avoid predators before being released.

Marine top predators and their risk effects have been largely overlooked until recently. There is growing recognition that marine top predators like sharks, classic villains in popular culture, may have important indirect effects on marine communities, as mediated by the antipredator behavior of their prey. Sharks and other marine top predators have been declining almost worldwide because of target and bycatch fisheries. Their conservation and restoration may be essential to many aspects of marine ecosystem function, and predation risk theory can be used to support arguments for modifying fishery quotas and establishing marine reserves accordingly.

Although major losses of ecological integrity related to human resource consumption, climate change, and related processes will be inevitable, there is cautious optimism that predation risk theory can help predict and potentially reduce some of the damage. The maintenance of antipredator behavior over large ecological scales could well be a litmus test for our ability to conserve many levels of biodiversity.

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**See also:** Anthropogenic Noise: Implications for Conservation; Conservation and Behavior: Introduction; Ecology of Fear.

**Further Reading**


