BEHAVIORAL ECOLOGY

Fear of large carnivores amplifies human-caused mortality for mesopredators

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The challenge that large carnivores face in coexisting with humans calls into question their ability to carry out critical ecosystem functions such as mesopredator suppression outside protected areas. In this study, we examined the movements and fates of mesopredators and large carnivores across rural landscapes characterized by substantial human influences. Mesopredators shifted their movements toward areas with twofold-greater human influence in regions occupied by large carnivores, indicating that they perceived humans to be less of a threat. However, rather than shielding mesopredators, human-caused mortality was more than three times higher than large carnivore–caused mortality. Mesopredator suppression by apex predators may thus be amplified, rather than dampened, outside protected areas, because fear of large carnivores drives mesopredators into areas of even greater risk from human super predators.

Apex predators can exert a strong influence on ecosystems through cascading top-down effects on lower trophic levels (*1*). Human persecution and habitat loss have reduced the ranges of large carnivores by an average of ~50% worldwide (*2*), and most large-mammal populations persist outside protected areas where they remain subject to strong human influence (*3*). Persecution outside protected areas can even reduce populations within protected areas because of source-sink dynamics (*4*). Sustaining functional populations of wide-ranging species such as carnivores thus requires understanding dynamics outside protected areas (*5*). However, the ecological roles of large carnivores have been investigated largely within protected areas (*6*), which leaves a critical gap in understanding the ecosystem functioning of human-dominated landscapes.

Even within protected areas, human presence can substantially alter wildlife behavior, with large carnivores often avoiding areas frequented by human visitors (*7*). This avoidance can lead to increased use of human-affected areas by subordinate species, a phenomenon known as the "human shield" effect (*8*–*10*). The use of human shields in areas where hunting by people is restricted can indeed yield increased survival rates (*11*, *12*). Outside protected areas, however, human shields can become lethal for ungulates and mesopredators that may preferentially use anthropogenic areas to avoid large carnivores. Human shields can impose mortality risks on wildlife through hunting and trapping, vehicular collisions, and conflict removals. The lethality of human shields may be especially intense for mesopredators, which are typically subject to harvest policies with few restrictions. Humans function as dominant "super predators" in ecosystems worldwide, resulting in human-caused mortality rates that can greatly exceed other causes of death at all trophic levels (*13*). Indeed, playback experiments indicate that the mere sound of humans induces strong avoidance by large and small carnivores alike (*14*, *15*). Mesopredators must therefore navigate competing risks from humans and large carnivores outside protected areas, which may increase the spatial heterogeneity of trophic interactions and cascading top-down effects. Whether mesopredators perceive humans as yet another compe risk to manage or as a shield protecting ag large carnivores should fundamentally influence ecosystem dynamics in human-dominated systems (*16*).

Human mediation of carnivore community dynamics

Here, we examined the movements of mesopredators in relation to large-carnivore activity and human impacts to test competing hypotheses about how interactions among carnivores are moderated by human influences. If mesopredators perceive large carnivores to be a greater threat than humans, then we expected selection for human-affected areas to increase in the presence of large carnivores (human shield hypothesis). If mesopredators instead perceive humans to be a greater threat, then we expected human-affected areas to be avoided regardless of large-carnivore presence (human super predator hypothesis). We used integrated step selection functions to quantify the responses of GPS-collared coyotes (*Canis latrans*, *n* = 35) and bobcats (*Lynx rufus n* = 37) to wolves (*Canis lupus*, *n* = 22 wolves in 9 packs) and cougars (*Puma concolor*, *n* = 60) across rural landscapes in northern Washington, USA characterized by human impacts such as agriculture, livestock production, logging, hunting, recreation, and residential development (*n* = 283,536 GPS locations) (Fig. 1 and data S1 and S2) . We then used cumulative incidence function models of competing risks to estimate cause-specific mortality rates for coyotes and bobcats, examining dynamics across our two large study areas (each ~5000 km^2). Wolves began naturally

Table 1. Fates of radio-collared coyotes and bobcats. Numbers of individuals in each category are shown. The "other" category consisted of 1 accident (drowning; bobcat), 1 disease (nematodiasis; bobcat), 1 starvation or disease (bobcat), and 3 cases of intraspecific strife (2 coyotes and 1 bobcat). The human-caused category consisted of 8 bobcats killed by trappers (7 male and 1 female), 3 bobcats shot (all male), 13 coyotes shot (6 female and 7 male), and 1 coyote hit by a vehicle. Of the 11 predator-caused mortalities (including intraspecific), carcasses were consumed in 4 cases (all cougar kills; 1 cougar-killed coyote was not eaten). Two cases in which the predator species could not be identified were included in the large-carnivore category to allow the maximum mortality risk posed by large carnivores to be calculated.

Fate	Bobcats	Coyotes	Total
Large carnivore			
Black bear	0	1	1
Cougar	2	3	5
Unknown predator	1	1	2
Total large carnivore	3	5	8
Human	11	14	25
Other	4	2	6
Unknown cause of death	0	3	3
Survived/censored	19	11	30
Total	37	35	72

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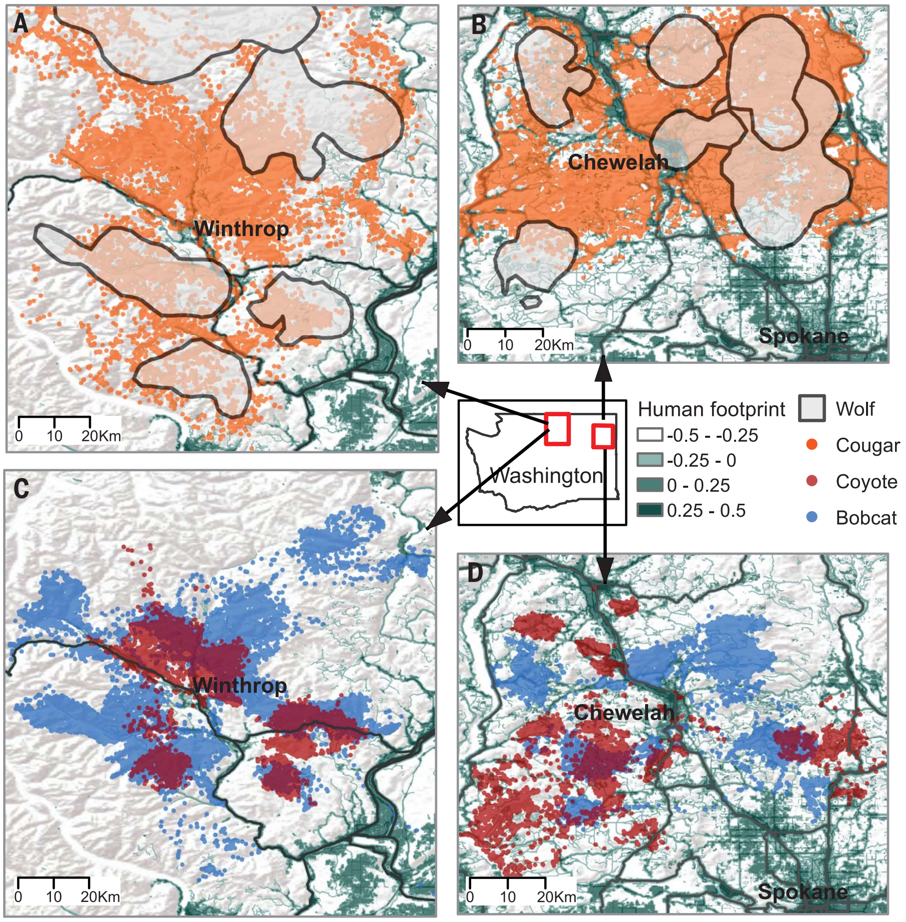

Fig. 1. Carnivore movements outside protected areas in Washington, USA. (**A** and **C**) Okanogan study area, ~5000 km^2. (**B** and **D**) Northeast study area, ~5000 km^2. The human footprint index (background) was scaled from –0.5 (corresponding to wilderness) to 0.5 (corresponding to urban areas), with a mean value of –0.33 across these landscapes. Locations of [(A) and (B)] collared large carnivores and [(C) and (D)] mesopredators are shown. All locations from 2017 to 2020 are shown for cougars (orange), bobcats (blue), and coyotes (red), and 90% kernel density polygons from summer 2020 are shown for wolf packs (gray).

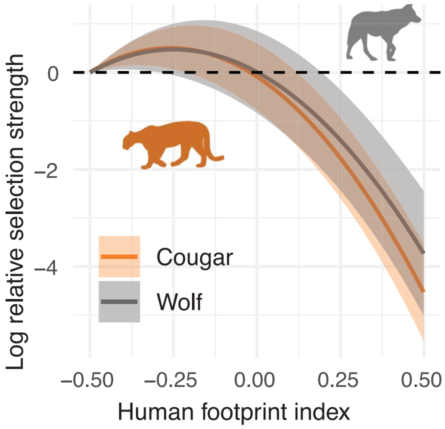

Fig. 2. Large carnivores avoid humans. Resource-selection functions show that wolves and cougars strongly avoid areas with high human footprint, thereby creating a human shield that can be used by mesopredators. Selection strength was quantified relative to areas with the lowest observed human footprint index values (human = –0.5, corresponding to wilderness), with positive values indicating selection, and negative values indicating avoidance.

recolonizing Washington in 2008 (*17*), whereas cougars were never extirpated, providing a distinct opportunity to assess the roles of recovering and established large-carnivore populations outside protected areas.

Mesopredators use a lethal human shield

Wolves and cougars strongly avoided areas with a high human footprint, thereby creating a human shield (Fig. 2 and table S1). Coyotes strongly avoided areas of high wolf use, and their selection tended to decline with increasing use by cougars (Fig. 3A and table S2). Bobcats had weaker direct responses to large carnivores, with no detectable response to wolves and a modest positive response to cougars that was likely driven by strong selection for forested habitats by both felids (Fig. 3B and table S2). However, relative use of human-affected areas by both coyotes and bobcats was higher in the presence of both wolves and cougars (Fig. 3, C to F), which supports the human shield hypothesis. Peak use by coyotes shifted from a human footprint index value of –0.03 when wolves were absent to 0.27 when wolves were present (Fig. 3C). Use of human-affected areas by coyotes was less influenced by the presence of cougars; peak use shifted from a value of -0.01 when cougars were absent to 0.10 when cougars were present (Fig. 3E). Bobcats selected far more strongly for human-affected areas when both wolves and cougars were present (table S2). In the absence of wolves and cougars, landscape use by bobcats peaked at human footprint values of -0.33 and -0.38, respectively, and then declined sharply (Fig. 3, D and F). In the presence of wolves and cougars, bobcat use remained high and did not decline until values of 0.02 and 0.08, respectively (Fig. 3, D and F). Taken together, mesopredators preferred areas with human footprint index values that were, on average, 31 percentage points higher where large carnivores were present, which corresponds to a twofold increase in human influence.

These findings indicate that mesopredators perceived large carnivores to be a greater threat than humans. Contrary to this perception, humans functioned as super predators in this system, as they were responsible for the overwhelming majority of mortality for all four species (Table 1, Fig. 4, and supplementary text). The annual risk of mortality from humans was three times higher than the risk from large carnivores for coyotes ($-x$ = 0.30 versus 0.10) (Fig. 4) and 3.8 times higher for bobcats ($-x$ = 0.25 versus 0.07) (Fig. 4).

Synergistic effects of large carnivores and humans

Despite global increases in the extent of protected area networks, anthropogenic impacts on natural systems are pervasive and continuing to expand (*3*, *18*). Wildlife that persist in human-altered areas must therefore navigate a complex suite of threats and resources, which can be particularly challenging for carnivores because humans have an especially low tolerance for this guild (*19*). Here, we show that mesopredators use a human shield response to risks posed by large carnivores outside protected areas, increasing their selection for human-altered areas where large carnivores are present. Unlike in protected areas, however, these shields are lethal in most of the land area where carnivore populations persist (*3*, *4*). In our system, humans

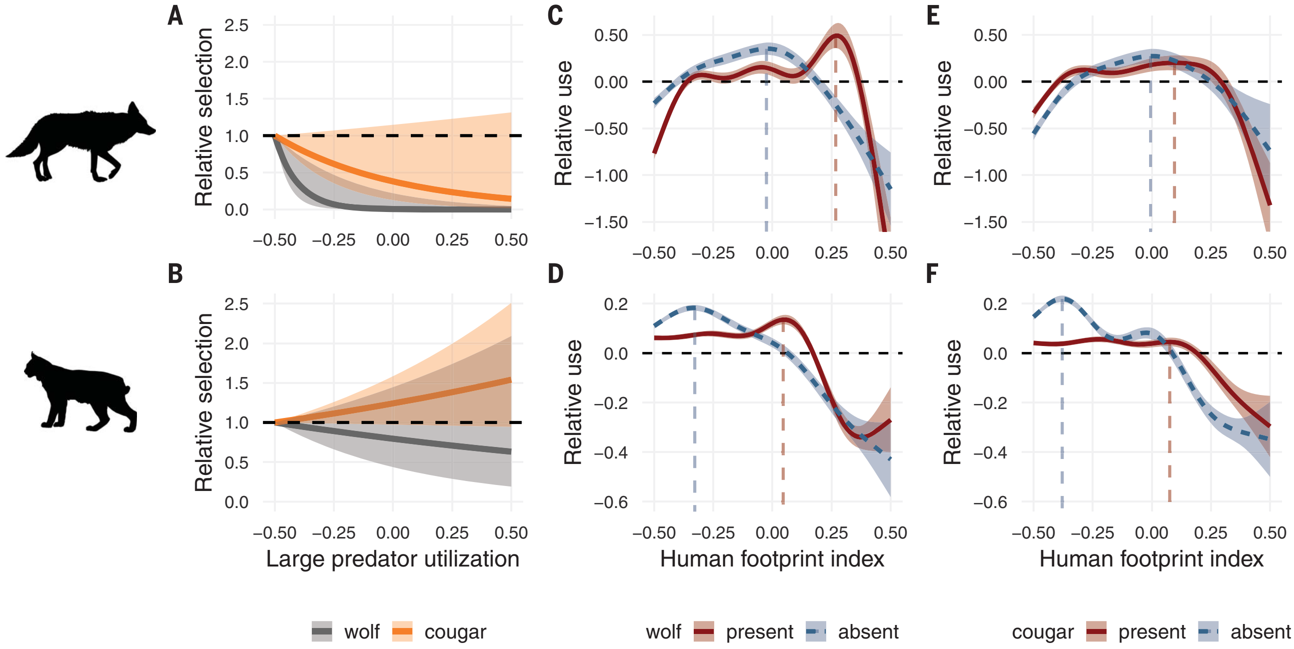

Fig. 3. Responses of mesopredators to humans and large carnivores. Relative selection strength [± 95% confidence interval (CI)] by (**A**) coyotes and (**B**) bobcats in response to large carnivores shows stronger avoidance by coyotes. Selection was quantified relative to the minimum observed value of large-carnivore utilization, corresponding to the absence of large carnivores. Values above 1 indicate selection and values below 1 indicate avoidance. (**C** to **F**) Average-effect plots show the responses of [(C) and (E)] coyotes and [(D) and (F)] bobcats to the human footprint index in the presence (red solid lines) and absence (blue dashed lines) of [(C) and (D)] wolves and [(E) and (F)] cougars (± 95% CI). Average-effect plots account for covariation among predictors by quantifying the relative change in expected use across the range of the focal variable while averaging over the observed values of other variables. Positive values indicate above-average use (on the logarithmic scale) and negative values indicate below-average use. Vertical dashed lines indicate peak use with respect to the human footprint index in the presence and absence of large carnivores. Wolf and cougar presence was determined based on home-range boundaries delineated by utilization distribution models.

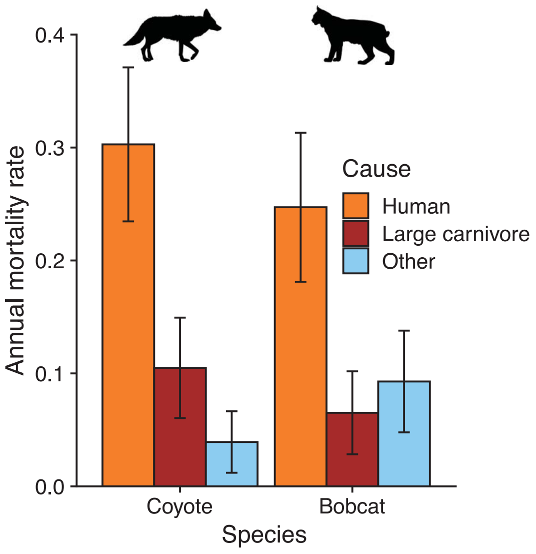

Fig. 4. Patterns of mesopredator mortality. Rates of mortality caused by humans (orange), large carnivores (brown), and other sources (blue) estimated from radio-collared bobcats (n = 37 individuals, 59 animal years) and coyotes (n = 32 individuals, 52 animal years). Mean annual mortality rates and standard error bars are shown. See Table 1 and data S1 for detailed information about causes of mortality.

were approximately three times more lethal for mesopredators than were large carnivores, indicating that fear of large carnivores may drive mesopredators into areas of even greater risk from humans. These results indicate that large carnivores can directly and indirectly perform ecosystem functions such as mesopredator suppression outside protected areas, and their impacts in human-dominated systems may paradoxically be amplified because of reduced enemy-free space and synergies with human super predators.

Multiple predator species in a system can lead to emergent effects on prey, whereby mutual interference can reduce hunting efficiency, or conversely, lead to superadditive predation rates by reducing available refuges (*6*, *20*, *21*). Our study was conducted across two large regions characterized by a diverse large carnivore guild despite strong human influences. Mesopredators faced risks from wolves, cougars, and black bears (*Ursus americanus*) in addition to humans. Although bobcats and coyotes responded similarly to both wolves and cougars by increasing their use of human-affected areas, bobcats avoided human-affected areas far more strongly in the absence of large carnivores, thus leaving a greater capacity for increased use of these areas in the presence of large carnivores. The synergistic effects of humans and large carnivores may therefore vary substantially in strength across species, highlighting the importance of multispecies studies in understanding carnivore community dynamics (*22*).

Although use of a lethal human shield may seem maladaptive, there are two likely explanations for this behavior that are not mutually exclusive. First, wildlife may be less equipped to accurately evaluate risk from contemporary humans compared with other coevolved predators (*23*), leading to behaviors that increase their risk of anthropogenic mortality. For example, modern firearms facilitate hunting by humans from distances where visual, olfactory, and auditory cues of risk may be absent. Likewise, the use of equipment such as traps and snares minimizes direct cues of risk because humans are not present at the time of capture. Wildlife may thus respond more strongly to direct cues of human presence, such as the sounds of humans talking that are used in playback experiments (*14*, *15*, *24*), than to the diffuse and heterogeneous cues that are present in human-affected areas. Second, subordinate species may benefit from increased access to anthropogenic resources such as refuse, livestock, and crops (*25*, *26*), and these benefits could offset some or all of the fitness costs associated with increased mortality risk. Whereas our analyses focused on understanding the risk landscape, the distribution of resources such as anthropogenic subsidies and scavenging opportunities should strongly affect carnivore community dynamics outside protected areas as well.

Indirect risk effects from antithetical threats

The fitness costs of antipredator behavior (i.e., risk effects) are often measured in terms of reduced foraging opportunities, physiological stress, or altered movement patterns (*27*). Our findings show that antipredator behavior can also increase risk of mortality from an opposing threat. Mortality risks posed by large carnivores and humans are not simply competing (i.e., an individual can die from one or the other, but not both); these risks are antithetical, because antipredator behavior to avoid one threat puts the individual at increased risk from the other. These indirect risk effects may be especially important in human-dominated areas where risk cues from humans can be difficult for wildlife to accurately gauge (*23*). Our findings highlight the importance of spatial dynamics in landscapes of fear, but temporal shifts in activity patterns of subordinate species could also lead to indirect risk effects (*28*). For example, Shores *et al.* (*29*) found that recolonizing wolves caused a diurnal shift in coyote activity that increased their temporal overlap with humans, which may further increase their risk. Conversely, many wildlife species shift toward increased nocturnality in response to human activity, which could increase risk from large carnivores (*30*). The spatial and temporal responses to antithetical threats should thus combine to determine the net strength of indirect risk effects (*31*).

The patterns of mortality we documented were inversely proportional to the strength of avoidance behaviors. For example, coyotes had the strongest avoidance response to wolves, followed by cougars and lastly, humans (table S2). Yet, no collared coyotes were known to have been killed by wolves in our study, whereas 3 were killed by cougars and 14 were killed by humans (13 were shot and 1 was hit by a vehicle) (Table 1). This discrepancy highlights the importance of considering the nonlethal effects of predators along with the lethal effects, because patterns of behavior or mortality alone may not accurately reflect the relative importance of competing threats in limiting population growth (*24*).

Carnivore conservation in anthropogenic landscapes

The release of mesopredator populations in the wake of large-carnivore extirpations has led to negative societal and ecological outcomes throughout the world (*1*, *32*). Amplified suppression by means of large carnivores and lethal human shields may help to limit problems caused by mesopredator overabundance, but whether this intense top-down control is ultimately beneficial remains a question. A far greater proportion of small-carnivore species are ranked as "least concern" by the International Union for Conservation of Nature (IUCN) compared with large carnivore species (64 versus 22%), but populations of both large and small carnivores are declining at alarming rates worldwide (*33*, *34*). Thus, recovery of large carnivores in anthropogenic landscapes could lead to unsustainably high levels of persecution and threaten some mesopredator populations with local extirpation. Although mesopredators such as coyotes and jackals (*Canis* spp.) have proven to be notably resilient when faced with intense persecution, this resilience is driven by a high capacity for compensatory reproduction and immigration that might not be possible for some other species (*35*–*37*). Urban-wildland gradients, where the paradox of the lethal human shield should be most influential, should thus be priority regions for monitoring trends of species that are subject to mortality from both humans and large carnivores.

Large-carnivore populations are recovering in areas throughout North America and Europe (*38*), yet the landscapes to which they are returning are vastly different than those in which they once thrived. Carnivores are often intensively managed and held to levels far below their carrying capacities outside protected areas, which calls into question whether they can perform the ecosystem functions of prey and mesopredator regulation that have been documented within protected areas (*16*). This question is critical to answer, because the importance of large carnivores for healthy ecosystems is often used as a justification to promote their recovery despite the societal costs incurred (*39*). Wolves began returning to Washington less than two decades ago, and our findings indicate that they are already affecting coyote and bobcat populations, but through behavioral effects more than direct mortality. Cougars were never extirpated from Washington, and our findings indicate that they affect coyotes and bobcats through both behavioral effects and direct mortality, despite being intensively managed themselves. As landscapes of coexistence between large carnivores and humans expand with recovery and restoration efforts (*40*, *41*), the paradox of the lethal human shield may become an increasingly dominant driver of carnivore community dynamics.

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SUPPLEMENTARY MATERIALS

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Supplementary Text
Fig. S1
Tables S1 to S4
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MDAR Reproducibility Checklist
Data S1 and S2
Code S1 to S3

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Editor's summary

In intact ecosystems, large carnivores have a regulating influence on smaller predators (mesopredators), limiting both their populations and distribution. In areas where humans are present, these smaller carnivores use developed areas to avoid larger predators. However, Prugh *et al*. found that their impression of the safety of these areas is a mistake, because the mortality rates of these species were more than three times higher than in the presence of large carnivores (see the Perspective by Darimont and Shukla). Such errors could both threaten these smaller species and influence the trophic structure of ecosystems. —Sacha Vignieri

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