Large mammal behavioral defenses induced by the cues of human predation

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Abstract

Large mammals respond to human hunting via proactive and reactive responses, which can induce subsequent nonconsumptive effects (NCEs). Thus, there is evidence that large mammals exhibit considerable behavioral plasticity in response to human hunting risk. Currently, however, it is unclear which cues of human hunting large mammals may be responding to. We conducted a literature review to quantify the large mammal behavioral responses induced by the cues of human hunting. We detected 106 studies published between 1978 and 2022 of which 34 (32%) included at least one measure of cue, typically visual ($n = 26$ of 106, 25%) or auditory ($n = 11$ of 106, 10%). Space use ($n = 37$ of 106, 35%) and flight ($n = 31$ of 106, 29%) were the most common behavioral responses studied. Among the 34 studies that assessed at least one cue, six (18%) measured large mammal behavioral responses in relation to proxies of human hunting (e.g. hunting site or season). Only 14% ($n = 15$ of 106) of the studies quantified an NCE associated with an animal's response to human hunting. Moreover, the association between cues measured and antipredator behaviors is unclear due to a consistent lack of controls. Thus, while human hunting can shape animal populations via consumptive effects, the cues triggering these responses are poorly understood. There hence remains a need to link cues, responses, NCEs, and the dynamics of large mammal populations. Human activities can then be adjusted accordingly to prevent both overexploitation and unintended NCEs in animal populations.

Keywords: behavioral response, cue, human hunting, large mammals, nonconsumptive effect

Introduction

Predators control prey populations via both consumptive and predation-risk, or nonconsumptive, effects (1–6). Consumptive effects (CEs) refer to direct lethal offtake that occurs when predators kill and consume prey individuals (7–10). In contrast, predation-risk effects encompass all behavioral, morphological, and life-history responses to predators (3, 4, 11). They also include the resulting fitness consequences experienced by prey, and the impact these changes have across species and trophic levels (4, 12–14). There are four broad classes of predation-risk effects: behavioral responses to reduce likelihood of encountering a predator or depredation once encountered (risk-induced trait response), fitness costs resulting from these responses (nonconsumptive effect; hereafter "NCE"), changes in interactions between the prey and another species (interaction modification), and resultant cascading impacts on that third species or the broader community (trait-mediated indirect effect) (4, 11, 13–19). Risk-induced trait responses (hereafter "antipredator response") are the most common and evident effects of predators in large mammals (6). These responses are triggered upon detection of cues of predation risk whether they are visual, auditory, or olfactory (20–23). The antipredator responses of prey are influenced by the distribution and intensity of these cues, which in turn vary by predator hunting mode (21, 23, 24).

Throughout the animal kingdom, there are generally three predator hunting modes including active, sit-and-pursue, and sit-and-wait (23, 25, 26). Active hunting is employed by predators that are constantly moving in search of prey, sit-and-pursue predators wait for prey to pass and subsequently follow over short distances, and sit-and-wait predators capture prey only once they are within striking distance (21, 23, 26, 27). These cues are most diffused in the active hunting mode given that these predators seldom remain in one place for extended periods of time (21, 23, 27). Conversely, cues from sit-and-pursue and sit-and-wait predators are more concentrated because the predator stays in one location waiting for a target to pass (23, 27, 28). Consequently, the more sedentary hunting modes (i.e. sit-and-wait, sit-and-pursue) are most likely to elicit "reactive" responses (e.g. fleeing, freezing, and fighting) in prey given that the cues are indicative of imminent risk. In contrast, prey is expected to respond to active predators via "proactive" responses (e.g. changes in space use, movement, and group size) as cues provide less reliable indicators of immediate risk (6, 23, 26, 29, 30). According to the *control of risk framework*, the risk of an active predator would be expected to induce nutritional and energetic costs as prey forgo foraging opportunities to decrease their likelihood of encountering a predator (31–34). Sit-and-pursue and sit-and-wait predators would impose mostly stress-mediated costs in prey due to a rapid response upon detection of a cue (31, 35–37). Combined with CEs, the NCEs emerging from these antipredator decisions could shape animal populations by lowering growth rate, recruitment, and survival (16, 19, 38–40).

While much attention has been given to how nonhuman predators affect prey populations via both CEs and NCEs, less is known about how humans may impact animal populations via NCEs (6, 18).

Human cues come in different forms and vary in the degree to which they might induce antipredator responses within an animal population. Traits evolve in populations when they vary across individuals, are heritable, and result in fitness differences (41). The evolution of inducible defenses, in turn, requires four additional conditions (42): (i) The threat must vary in strength across space and time, (ii) The sensory cue must accurately reflect the threat, hence triggering a response, (iii) The prey response must reduce likelihood of predation, and (iv) That response must carry a cost that would otherwise have been avoided. There is evidence that certain animals have stronger behavioral responses to human hunting than natural predators (43, 44). Certain forms of human hunting are also usually predictable in time and space where laws are enforced based on hunting proxies, causing animals to quickly learn to associate cues with predation risk (45). Animals likely escalate their antipredator strategies in the face of human expansion into natural areas because anthropogenic cues signaling risk become more prevalent (46–49). This increase in antipredator strategies could manifest in heightened costs and subsequent consequences at the ecosystem-scale (6, 20, 23, 40, 47, 50).

Large mammals, specifically *Ungulata*, *Carnivora*, and *Proboscidea*, respond to nonhuman predators based on visual, auditory, and olfactory cues (28, 51–56). Scent however is likely the most important sensory modality for these taxa as predators often conceal themselves before approaching prey (57–59). Ungulates, carnivores, and proboscides are also heavily hunted by humans, comparatively intelligent, and long-lived (60–62). Therefore, there is reason to expect that they should demonstrate behavioral plasticity in response to hunting (18, 63). Yet with regard to human predators, a species with the highest exploitation rates on the planet (64), it is unknown which cues induce proactive and reactive responses and associated nutritional, energetic, reproductive, or survival costs. Prey frequently uses multiple senses to detect predators, further complicating linking antipredator behaviors to a given visual, auditory, or olfactory cue (65, 66). If the nature, strength, and cause of an NCE are unknown, reductions in reproduction and survival will be attributed to other causes, such as food supply (16). There is good reason to believe that animal responses to humans may also carry costs given the rates at which humans predate and disturb nonhuman species (*sensu* Frid and Dill (63)). Human hunting modes parallel those used by natural predators, albeit with more sophisticated tools (64, 67, 68). Hunting dogs are a characteristic example of the active hunting mode, whereas the two sedentary modes are characterized by traps or waiting in ambush for a prey item to pass (67). Guns can be employed across all three modes. Although human hunting is associated with novel cues to which animals were not exposed throughout their evolutionary history (e.g. traps, spears, and guns), antipredator responses and associated costs are likely similar as those used in response to natural predators based on the degree to which cues are diffused and represent imminent risk (20, 47, 63). Yet these questions cannot be adequately addressed because the cues that induce large mammal behavioral plasticity to human hunting are unclear.

Awareness of what cues trigger an antipredator response is vital to quantifying the degree to which humans shape animal populations nonconsumptively as well as consumptively (46, 47, 64, 69, 70). Thus, we conducted a literature review to document cues of human hunting, associated proactive and reactive responses of large mammals, and affiliated costs of these responses.

Based on our findings, we emphasize the need to link animal behavioral responses with sensory cues, as this knowledge will help clarify how nonhuman species perceive anthropogenic disturbances. Human activities can then be adjusted accordingly to prevent both overexploitation and unintended NCEs in animal populations where desired.

Results

Taxa and geographic distribution

Ungulata species were the most common research subjects among this literature occurring in 72% ($n = 76$ of 106) of the studies. The next most common were *Carnivora* species ($n = 26$ of 106, 25%) followed by *Proboscidea* ($n = 9$ of 106, ~8%). Cervids, notably various deer species, moose (*Alces alces*), and elk (*Cervus elaphus*), were assessed in 44% ($n = 47$ of 106) of studies, whereas bovids were included in 25 (24%). Bears were the most common carnivorans, occurring in nine studies (~8%). Most research was positioned in Europe ($n = 36$ of 106, 34%), Africa ($n = 24$ of 106, 23%), and North America ($n = 31$ of 106, 29%), composing 86% of the literature (Fig. 1). Asia ($n = 10$ of 106, 9%) and South America ($n = 5$ of 106, ~5%) were less represented, and no studies among this literature originated from Australia.

Cues measured and antipredator responses

Via our literature review, we retained 106 studies that met our search criteria (Dataset S1), of which 32% ($n = 34$ of 106) measured at least one cue of human predation on large mammals (Fig. 2). The most common cues measured among this literature were visual occurring among 25% ($n = 26$ of the 106 studies). These cues were most notably represented by an observer approaching the focal animal or herd ($n = 22$ of 106, 21%). The next most common cues were acoustic ($n = 11$ of 106, 10%) and measured via playbacks of humans speaking ($n = 10$ of 106, 9%) and dogs barking ($n = 10$ of 106, 9%). There were two studies (~2%) that considered olfactory cues via scent from a motionless human. Nine studies (~8%) used vehicle presence as a cue test (visual), and two of these (~2%) included another measure of cue in assessing reactions to a vehicle engine (auditory). However, of the 34 studies that measured a cue, only six ($n = 6$ of 106, ~6%) also drew comparisons between proxies representing different degrees of hunting presence or intensity (Table 1). The remaining studies that included a measure of cue only provided descriptive statistics of behaviors in the region overall, or modeled behavioral differences based on variables that were unaffiliated with hunting (e.g. sex, age, and group size). Space use, flight, movement, and diel patterns were the behaviors that were most often quantified in relation to human hunting risk (Fig. 2). Fifteen studies (14%) measured some form of cost associated with the response, most notably nutritional ($n = 13$ of 106, 12%), followed by survival ($n = 2$ of 106, ~2%) and reproductive ($n = 1$ of 106, ~1%) and energetic ($n = 1$ of 106, ~1%). No study measured costs resulting from responses to a cue between hunting proxies.

Hunting proxies and study methodologies

There were 76 studies (72%) that compared responses between hunting proxies, of which hunting season and hunting intensity were the most common (Fig. 3). Tracking large mammals via GPS or radio telemetry was most implemented ($n = 43$ of 106, 41%), followed by observation ($n = 34$ of 106, 32%), camera traps ($n = 23$ of 106, 22%), and large mammal signs ($n = 7$ of 106, ~7%).
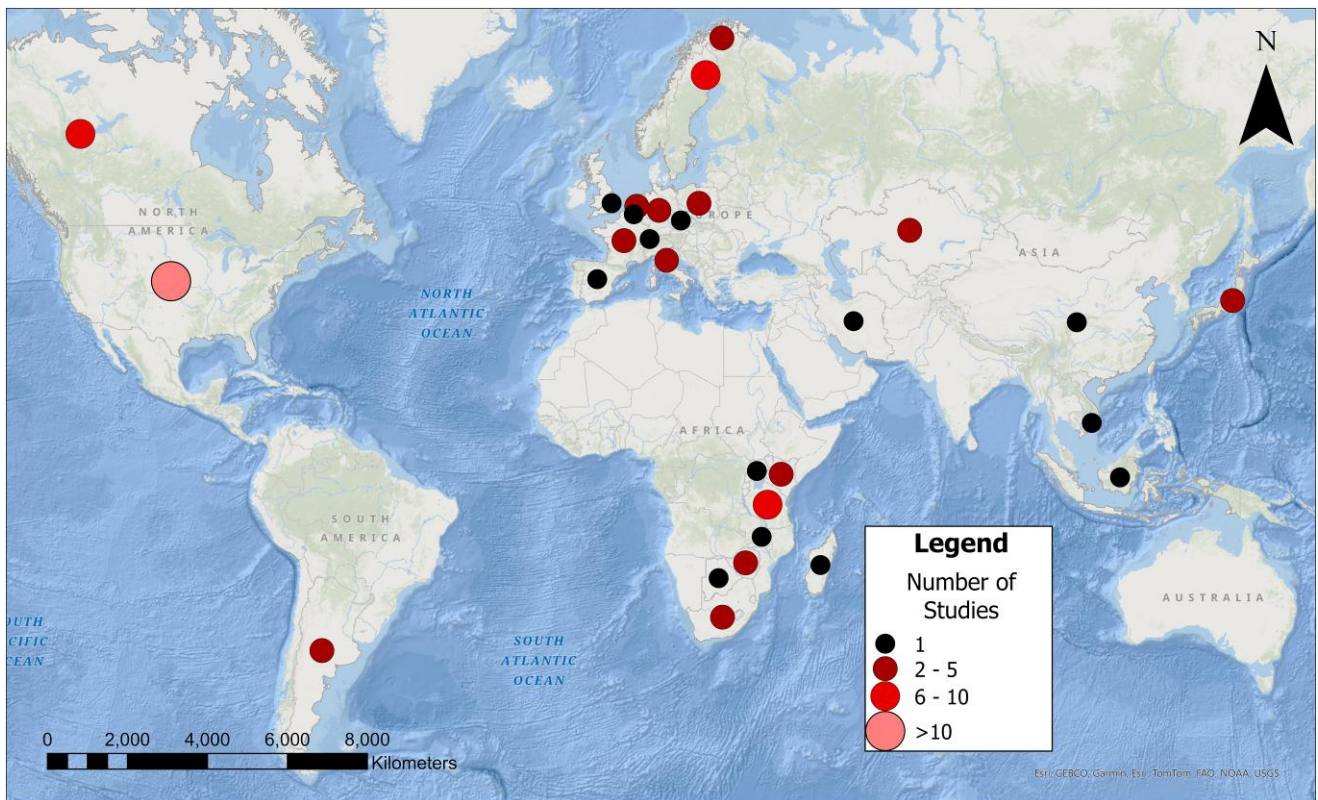
Fig. 1. The geographic distribution of studies extracted from a literature review of 106 peer-reviewed studies measuring proactive and reactive responses of large mammals to cues of human hunting from 1978 to 2022. Basemap: Esri, GEBCO, Garmin, TomTom, FAO, NOAA, USGS (71).

Three studies (~3%) used fecal samples to measure physiological responses, and one (~1%) used a biologger.

Discussion

Large mammals respond to human hunting in a diversity of ways. Proactive and reactive responses reduce the likelihood of either encountering a predator or avoiding capture once detected (3, 11). These behaviors come at a cost, although not all are substantial enough to reduce an individual's health or alter a population's long-term dynamics (78–80). The intensity of these behaviors and resultant NCEs likely depend on the nature and concentration of predatory cues, including those of human predators (23, 67). We reviewed 106 studies that assessed large mammal behavioral plasticity in relation to human hunting and found that very few measured the cue that triggered responses. Although 76 studies (72%) compared responses between hunting proxies, few measured the sensory cue to which animals actually responded. Of the six studies that did include a measure of cue between proxies, each one detected a significant effect of hunting on the behavioral plasticity of at least one species. Hunting, therefore, likely varied spatiotemporally in presence or degree (i.e. the proxies used indeed represented different levels of threat), and the visual cues approximated that threat (20, 42). The behaviors measured in these six studies were all reactive, meaning that they occurred in response to encountering a human rather than beforehand. Thus, there is a need to link cues with changes in proactive responses. None of the six studies determined whether these reactive responses resulted in nutritional or energetic consequences substantial enough to impact individual health or broader population dynamics (6, 40).

A visual, auditory, or olfactory hunting cue may evoke an antipredator response and associated NCE in a prey individual (24, 38, 52, 81). However, it is difficult to quantify the strength of these behaviors without drawing comparisons across times or places that differ in hunting pressure. Variations in proactive and reactive responses can only be linked to measured cues when those cues represent different levels of risk depending on the context (47). There were six studies that included both a measure of cue and compared animal responses to that cue between hunting proxies. We refer to a "proxy" as a measure of hunting presence or intensity (e.g. hunting vs. no-hunting season or site; Montgomery et al. (18)), across which cues might differ in the degree to which they represent risk. Of these, three detected no reactions to human hunting. For instance, some mammals demonstrated no difference in vigilance, flight, or deterrence signals in relation to conservation status or distance to protected area (75, 77). This result could be due to illegal poaching occurring within protected areas as well as outside (82). Thus, in these cases the threat might not vary sufficiently in time and space (40, 83), failing to meet one of the conditions required for inducible defenses to evolve (40, 42, 83). Alternatively, animals might not detect a difference in threat because their perception does not match reality (20, 47, 84). This mismatch can occur when anthropogenic cues of risk are unreliable, representing both benign and lethal activities (47, 70, 85, 86). Hence, animals might perceive protected and unprotected areas as equally risky even though lethal offtake differs between them, resulting in no detectable differences in response. Future work should quantify variation in antipredator strategies based on perceived versus actual risk (*sensu* Goumas et al. (20)). These experimental designs could assess animal responses to various cues (e.g. one human acting as a poacher and another as a tourist)
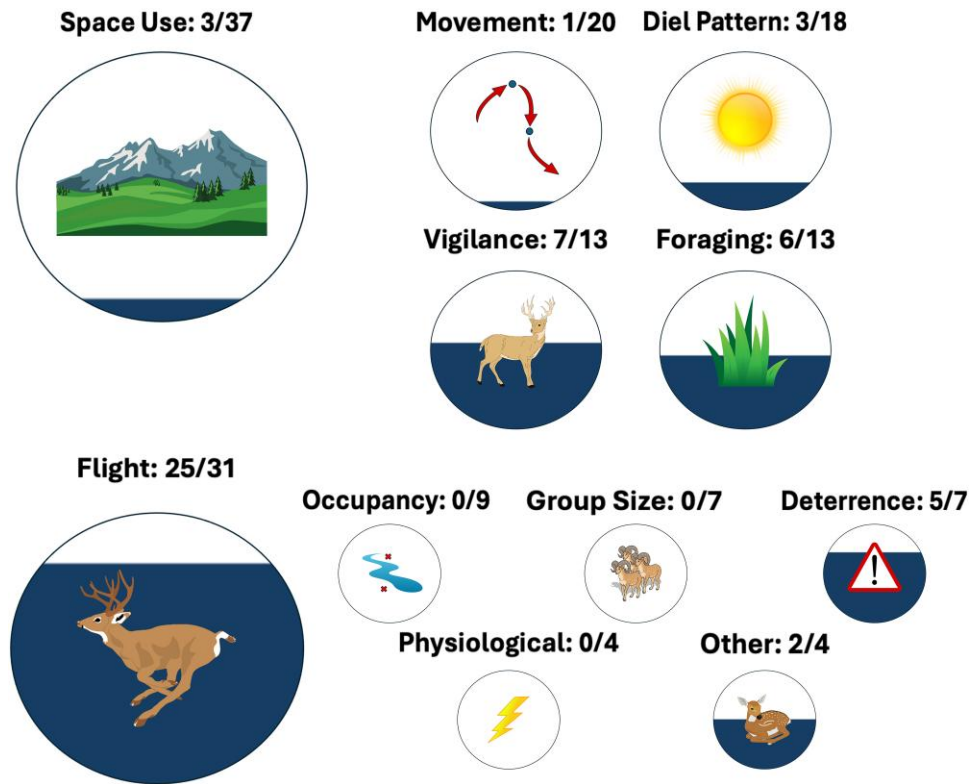
Fig. 2. The count of studies measuring a given behavioral response from a literature review of 106 peer-reviewed studies assessing proactive and reactive responses of large mammals to cues of human hunting from 1978 to 2022. The sizes of the circles are based on numbers of studies: 1–10 (small), 11–20 (medium), and greater than 20 (large). The fraction above each icon represents the proportion of studies that included at least one measure of cue, also indicated as shading in the circle. All icons obtained from Pixabay.com.

Table 1. Summary of six studies that assessed differences in large mammal responses to a cue between hunting proxies.

Hunting proxy	Cue	Response measured	Response significant?	Description	Reference
Time spent in protected area, time since entering protected area	Visual	Flight	Mixed	Elephants were less likely to react to a vehicle with increased poaching pressure. Time spent in the protected area was negatively associated with reaction index, and time since entering the protected area had no effect.	Goldenberg et al. (72)
Hunting area, hunting season	Visual	Flight	Yes	Three species of African ungulates fled more quickly upon encountering a human on foot in hunting vs. a no-hunting area. Flight initiation distance was longer in the hunting season.	Muposhi et al. (73)
Hunting area	Visual	Flight	Yes	Two species of African ungulates were more likely to exhibit extreme flight responses upon encountering a vehicle in a hunting vs. a no-hunting area.	Ndiweni et al. (74)
Distance to protected area, areas differing in protection/ conservation status	Visual	Flight, vigilance	Mixed	For guanacos, distance to protected area had no effect on likelihood of vigilance or flight upon sighting a vehicle. Flight and vigilance behaviors were amplified in less-protected areas.	Puig et al. (75)
Areas differing in protection/ conservation status	Visual	Flight, vigilance	Yes	Impala displayed longer flight initiation distances and heightened vigilance in a partially protected vs. a protected area. This occurred in the presence of both a vehicle and an approaching human.	Setsaas et al. (76)
Areas differing in protection/ conservation status	Visual	Flight, deterrence signals	Mixed	Four species of African mammals displayed heightened flight and deterrence signal reactions to humans sitting in a vehicle within nonprotected compared to fully protected areas. Three other species demonstrated no effect.	Kiffner et al. (77)

Results are from a literature review of 106 peer-reviewed studies measuring proactive and reactive responses of large mammals to cues of human hunting from 1978 to 2022.

between hunting proxies (see Papworth et al. (87)). Animals might also accurately judge the level of threat but choose not to respond to mitigate potential costs or obtain certain benefits (47, 88, 89).

There is evidence that animals can distinguish among threats, an ability which is often learned over time (20, 47). Variations in responses to cues representing different levels of risk support
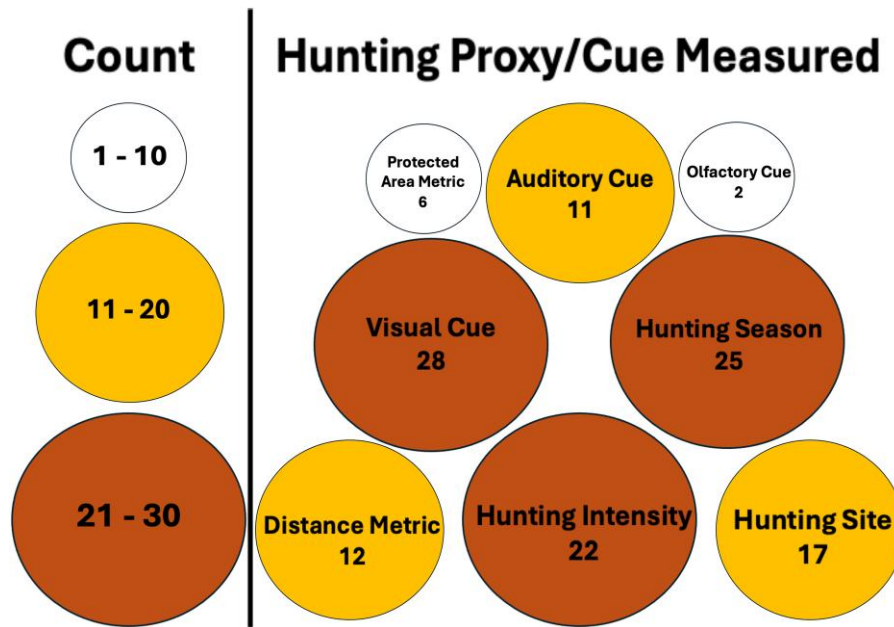
Fig. 3. The count of studies using a given cue or proxy of human hunting from a literature review of 106 peer-reviewed studies measuring proactive and reactive responses of large mammals to cues of human hunting from 1978 to 2022. Hunting intensity is typically measured in number of hunter detections or harvest rates. The distance metric indicates distances to either safety (e.g. prohibited hunting areas) or danger (e.g. hunter access points). Protected area metrics largely refer to degree of protection. Some studies included multiple measures of cue or hunting proxy, hence the total count listed here is >106.

this conclusion. Auditory playbacks provide an ideal setup to test this assumption, as animals frequently responded to hearing a human voice but were less responsive upon hearing a dog barking or a natural sound (13, 90–92). Future work could consider other auditory playbacks more representative of human lethality (e.g. gunshots) to further assess which factors trigger a reaction. Of those studies included in our review, species were also generally more reactive to a human approaching than the presence of a vehicle, suggesting that animals perceived the presence of the former as a greater threat (93–95). A person on foot could resemble an approaching predator (95, 96), although humans in these studies did not employ behaviors specific to hunters (e.g. carrying a weapon and approaching stealthily, see Papworth et al. (87)). Vehicles might not be as threatening given that humans don't often hunt from within a truck or car, obscuring the association between threat and cue (95, 97, 98). Hence the ability of an animal to associate a cue with danger, and respond accordingly, will depend on whether a perceived threat followed detection of the cue in previous encounters (47). However, in many studies it is unclear to which degree wildlife responded to a visual stimulus as opposed to scent. Olfaction is one of the most common senses used by vertebrate prey to initially detect and avoid a threat (57, 99), and thus responses to humans or vehicles could very well be attributed to scent rather than sight or sound. Nevertheless, the influence of olfaction could also be minimal given that humans were already within sighting distance of the animals when beginning their approach. Future experimental designs should thus link cues and behaviors, as well as assess additive effects, by comparing responses to single (e.g. only visual or auditory) vs. paired cues (visual and auditory together). These responses should be captured by remote video to minimize the influence of confounding factors, most notably scent (91, 92).

Antipredator responses may be accompanied by nutritional, energetic, reproductive, or survival costs (6, 31). However these are challenging to quantify, especially over long periods of time

(78, 100). Thus the impact of NCEs at the population level is still largely unknown (78). Of the 106 studies in our review, 91 (86%) did not measure the cost of large mammal behavioral responses to human hunting, although those that did primarily focused on nutritional costs. Developing methods for quantifying NCEs is an important area of future research, and depends on disentangling the impact of NCEs from those of CEs in systems with natural feedbacks (18, 67, 78, 101). Consequently, it is unclear whether these prospective costs are substantial enough to influence recruitment and survival, which age groups are most affected, how the implications compare to those resulting from lethal offtake, and subsequently whether these NCEs must be considered in management schemes (6, 16, 46, 78). Data on energetic, reproductive, and survival costs are too sparse to draw conclusions at this point, and the findings on nutritional costs are inconclusive. For instance, 13 studies in our review assessed foraging costs in response to auditory cues. Badgers (*Meles meles*), white-tailed deer (*Odocoileus virginianus*), and pumas (*Puma concolor*) demonstrated lower feeding time, heightened latency, and fewer visits within controlled plots in response to playbacks of a human voice (13, 91, 102, 103), although human scent in the vicinity and on the equipment might also have influenced the responses. These cues also solely depicted a human speaking, which could be a source of disturbance alone (i.e. indicative of nonlethal human activity). An individual might also simply choose an alternative location to forage, with no subsequent health consequences. One study did quantify variation in elk body fat resulting from differential space use across phases of the hunting season, finding that individuals who avoided high-risk roads had lower fat reserves at the onset of winter (104). Other times a cost is evident although indirectly tied to human activity, e.g. moose (*Alces alces*) did not alter their space use between the hunting and no-hunting seasons, although calf growth was higher in grasslands where there was also heightened vulnerability of being killed by hunters (105). Moreover, costs might only be detected at one

spatiotemporal scale (106). Elk adjusted their migration patterns in response to the hunting season, resulting in decreased access to ideal forage (107), and white-tailed deer compensated for decreased selection of anthropogenic food sources during the day, when hunting intensity was strongest, by increasing selection at night (108). Moreover, the degree to which an NCE influences an individual's health depends on the strength of the antipredator response, and by extension the concentration of cues evoking the response (23). Olfactory cues might elicit a stronger reaction than visual or auditory cues based on their ability to disperse over wide distances and remain in one place for extended periods of time (109–111). However no study assessed whether olfactory cues induced an NCE, a feat that could be accomplished via long-term monitoring of prey exposed to predator scent in predator-free enclosures (54, 57). These results all demonstrate the complexity of linking cues, responses, costs, and population dynamics, with implications for sustainable management (46, 78).

Frid and Dill (63) postulated that animal responses to human hunting and disturbance should be analogous to those of natural predators. Future research should assess behavioral responses of large mammals in relation to specific human hunting modes, which parallel those used by nonhuman species (67). While it is evident that human hunting induces fear in animals, sometimes to a greater degree than natural predators, there is still an open question regarding whether responses of animals to anthropogenic pressures are adaptive changes that have evolved over time, or mere behavioral plasticity (18, 112, 113). Of the four conditions required for inducible defenses to evolve, perhaps the most uncertain factors relate to whether the sensory cue accurately depict the threat and if the animal responses to that risk are costly (42). The threats of human hunting are expected to vary across space and time when restrictions surrounding lethal human activities are enforced (e.g. hunting vs. no-hunting site or season) (45, 114–116). However, it is difficult to assess whether and how animals perceive these cues (20, 47, 115). The challenge of linking cues to responses will become more substantive in a changing environment, where novel cues are continuously introduced into animal habitats and not always clearly tied to the activity from an animal's perspective (47). Moreover, while responses to a threat might be effective via broad- or fine-scale spatiotemporal avoidance of lethal activity, the magnitude of prospective costs is unclear (43, 68, 78, 104, 117). Although every change in behavior comes with a tradeoff, the question is rather whether such costs are substantive enough to impact long-term growth, recruitment, and survival (6, 78). We recommend that future research seek to quantify the specific cues that animals respond to, and implement experimental studies that integrate long-term monitoring of individual health, population demography, and environmental factors so as to quantify the NCEs that might emerge from these responses.

Attributing observed behaviors to measured cues is challenging due to a consistent lack of controls in experimental designs. Most studies in our review assessed responses to either a human approaching or auditory playbacks. Human approaches typically occurred after spotting the target species from a vehicle or walking transects, whereas auditory playbacks were paired with video recording devices (13, 90, 92, 118, 119). Reactions to auditory playbacks can therefore reasonably be linked to the cue measured because the influence of other cues, namely visual or olfactory, caused by direct human presence is minimal assuming measures are taken to reduce anthropogenic scent on the recording devices. Moreover, natural sounds are commonly used as a standard of comparison (90, 103). The use of approaching or motionless

humans as visual cues, however, does not rule out the influence of scent, one of the most important sensory modalities for vertebrates (99). Therefore, within our review there is a wide range of confidence regarding whether mammals were indeed responding to the cue measured. Future experimental trials could use motionless human dummies lacking scent (visual), or alternatively assess wildlife responses to various odors (olfactory). Implementing controls such as dummy prey or natural scents would solidify the link between any observed behaviors and the cue measured.

Evaluating how animals respond to lethal human cues carries important implications for conservation (46, 55). Visual and auditory cues may be used to deter animal within contexts leading to conflict, although any tactics should be used sparingly, or in conjunction with a painful physical cue, to avoid habituation (96, 120–122). Olfactory cues could also be used for effective management given the variety of information they convey, as well as the range at which vertebrates detect them and respond accordingly (99, 123, 124). Fear that results from spatial and temporal variation in risk can condition animals to avoid areas where their presence is undesired (45, 83, 125–127). Moreover, for threatened species, NCEs could be prevented by reducing the prevalence or concentration of human cues that trigger an antipredator response. Future work will then need to consider whether the intended results show at the population level (40, 45, 67). Behaviors and associated fitness costs can also be insignificant, with trivial impacts on an individual, emphasizing the need to determine which cues and conditions evoke a response substantial enough to reduce an animal's long-term health (3, 128, 129). Predators, specifically humans, can have more substantial impacts on prey behavior and abundance than abiotic features, with ecosystem-scale consequences (13, 30, 68, 128, 130). Hence exploring how antipredator responses and NCEs vary by type and strength of cue will provide a more complete picture of how human hunting shapes animal populations (23, 67, 131, 132).

Materials and methods
Literature review
We conducted a literature review (completed in November 2023) to assess the extent to which cues are measured in studies quantifying proactive and reactive responses of large mammals to human hunting. To execute this search, we interrogated the Web of Science Core Collection using the following terms: (large carnivore* OR carnivor* OR ungulat* OR large herbivore* OR elephant*) AND (human* OR anthropogenic) AND (predat* OR hunt* OR poach* OR kill* OR cull* OR harvest* OR super predat*) AND (risk effect* OR predation risk OR risk of predation OR nonlethal OR nonlethal OR nonconsumptive OR trait-mediated OR behaviorally-mediated OR landscape of fear OR ecology of fear OR antipredator OR antipredator OR inducible defense*). Our initial search returned 929 peer-reviewed results, including those classified as "article" and "early access." We read all papers and excluded those that assessed: (i) species other than large mammals (i.e. those outside of the orders *Ungulata*, *Carnivora*, or *Proboscidea*), (ii) responses to livestock depredation or crop-raiding deterrents, (iii) human disturbance (e.g. roads, human settlements, nonlethal wildlife recreation) without any clear indication of hunting, and (iv) cue tests (e.g. observer approaching a herd) in study areas without any evidence of legal or illegal hunting or where observers intentionally imitated tourists. We then read each remaining study and quantified the: (i) cue used to represent

Table 2. Data extracted from a literature review of 106 peer-reviewed studies, published between 1978 and 2022, measuring proactive and reactive responses of large mammals to cues of human hunting.

Data	Definition	Examples (not exhaustive)
Explanatory variable	Proxy of hunting	Hunting site, hunting season, hunting intensity, distance to protected area
Measure of cue (1/0)	Was the factor that elicited the response measured?	1,0
Cue	Nature of the cue	Dog barking, human speaking, vehicle moving
Cue type	Classification of the cue	Auditory, visual, olfactory
Response variable	Behavioral or physiological response of prey	Occupancy, space use, vigilance, foraging
Technique	Method to measure response	Camera traps, GPS collars, observation, wildlife signs
Cost	Cost of response	Diet quality, feeding time, energy expenditure
Cost type	Classification of the cost	Nutritional, energetic

human hunting risk, (ii) whether a proxy of human hunting was measured, and (iii) ways in which animals responded to that risk (Table 2). We identified cues measured based on descriptions provided by the authors. Cues were recorded as visual when wildlife behaviors were observed in response to stationary or moving humans or vehicles. Auditory cues were measured using playbacks caught on remote video, and twice by assessing responses to vehicle engines. We recorded olfaction as a cue measured on two occasions based on notes by the author that wildlife responded to scent from stationary humans.

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Supplementary Material

Supplementary material is available at *PNAS Nexus* online.

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Author Contributions

S.A.S. and R.A.M. conceived and designed the study. S.A.S. conducted the literature review and drafted the initial manuscript. S.A.S. and R.A.M. edited the manuscript. Both authors read and approved the final manuscript.

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