Human-induced fear in wildlife: A review

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ABSTRACT

Humans, like natural predators, can induce fear in wildlife, which has the potential to alter species-level survival and fitness. Though anthropogenic impacts on wildlife have been studied in detail, how wildlife respond behaviorally to human presence has been less studied. Here, we provide a literature review on how humans interact with wildlife populations through the ecology of fear framework. Fear responses can be proactive or reactive, and can go beyond behavioral changes to alterations in physiology (such as increases in stress) or alterations in individual chromosome structure. Wildlife are more likely to flee from humans if they possess a larger body size, are female, or have fear-associated genotypes. Intelligence and individual differences lead to variations in wildlife's fear responses to humans that can make studying fear difficult. Wildlife fear responses to humans depend on environmental factors, including context-specific human presentation and whether the animal was in urban or rural habitats. Human-induced fear in wildlife may have cascading impacts on broader wildlife communities and habitat structure caused by changes in how individual species interact with other species and the environment.

Keywords: human-induced fear, ecology of fear, anthropogenic disturbance, animal behavior

INTRODUCTION

The ‘ecology of fear’ predicts that prey use anti-predation strategies such as fleeing or habitat avoidance as a psychological response to predator-induced stress (Brown et al. 1999). The concept of ‘fear’ in animals has been the subject of a considerable debate concentrating around whether ‘fear’ is experienced by wildlife, or if what humans perceive as fear in wildlife is more akin to risk perception or other behaviors that can be correlated with stimuli humans associate with fear (Gaynor et al. 2019). ‘Fear’ in wildlife can be defined as ‘changes in specific wildlife behaviors (such as spatiotemporal avoidance behavior, fleeing) or physiology (such as increased cortisol levels) in response to a stimulus (Brown et al. 1999). Some authors believe that 'fear’ induced by a predator upon prey is a product of an interspecific interaction in which predators alter prey behavior through indirect means (i.e., inducing fear) in addition to direct predation that alters population density (density-mediated interactions; Abrams 1995; Gaynor et al. 2019). Changes in prey behavior can lead to a decreased use of important resources to avoid high predation risk, which can negatively impact prey survival and reproduction (Anderson et al. 2022; Montgomery et al. 2020; Palmer et al. 2017). African herbivores, for example, avoid woodlands where ambush predators hunt frequently, which can impact herbivore foraging efficacy (Ford et al. 2014; Riginos and Grace 2008; Riginos 2015; Thaker et al. 2011; Valeix et al. 2009). Predator-induced fear may, therefore, change how prey interact with foraged plant species (Caravantes 2020; Clinchy et al. 2016; Pringle 2018; Ripple and Beschta 2004; Schmitz et al. 2004; Wang et al. 2015). This phenomenon was famously observed in Yellowstone National Park, USA, where the presence of wolves (*Canis lupus*) decreased foraging efficacy of elk (*Cervus canadensis*) on aspens (*Populus tremuloides*; Ripple and Beschta 2004). By changing prey foraging behavior, predator-induced fear may promote heterogeneity and ecosystem functioning (Ford 2015; Schmitz et al. 2010; Suraci et al. 2019), such as through alterations in nutrient deposition in various habitats (see Pringle 2018).

Humans, like natural predators, can induce fear in wildlife, and have the potential to alter species survival and broader community dynamics (Ford 2015; Gaynor et al. 2019; Schmitz et al. 2010; Suraci et al. 2019). Though human-induced fear may have similar impacts on wildlife compared to predator-induced fear (Gaynor et al. 2019), it is a far less-studied phenomenon that may differ from predator-induced fear due to the pervasive impacts of humans on nature (Ford 2015; Gaynor et al. 2019; Schmitz et al. 2010; Suraci et al. 2019). Human activity is increasingly altering fear behavior in wildlife and impacting how species respond to non-human landscapes of fear (Gaynor et al. 2019). Multiple papers have documented the consequences of human-induced fear (see Gaynor et al. 2019), but there has not yet been a systematic review of the literature on how fear of humans affects wildlife and ecosystems. Such a review is timely and warranted because human ecological disturbances are increasingly detrimental to wildlife populations and are threatening numerous species with extinction (Ford 2015; Schmitz et al. 2010; Suraci et al. 2019). Furthermore, wildlife management practitioners are increasingly using human activities to intentionally induce fear in wildlife (Gaynor et al. 2020; Wilkinson et al. 2020). It will be important to shed light onto how human presence may change wildlife behavior, which has the capacity to alter species vital rates (Ford 2015; Schmitz et al. 2010; Suraci et al. 2019) and further risk shrinking populations.

Here, we review literature on wildlife's responses to human-induced fear, defined as fear (an increase in fear-associated behaviors in wildlife, such as avoidance or fleeing) in response to the presence of humans. We first provide an overview of the human-induced fear literature, and then evaluate common responses of wildlife to human-induced fear, including changes in activity/behavior, physiology/fitness, and habituation to humans. We then discuss situational factors that can influence wildlife responses to human-induced fear, such as species traits, type of human disturbance (s.a. recreationalists or hunters), habitat, genetic variability, and individual variability. We also discuss currently known cascading impacts of human-induced fear on communities and ecosystems. We conclude by identifying several gaps in the current understanding of human-induced fear and discuss the implications of human-induced fear for wildlife conservation. This paper provides an in-depth overview into how human-caused fear in wildlife can impact free-living animals across numerous ecological scales, and how we can improve future research endeavors to shed light on the impacts of the human predator.

METHODS

We conducted a literature search using Web of Science on February 8, 2022, using the following search terms:

> *TS=(human* OR anthropogenic) AND TS=(fear) AND WC=("Ecology" OR "Biodiversity Conservation" OR "Marine & Freshwater Biology" OR "Entomology" OR "Evolutionary Biology" OR "Fisheries" OR "Ornithology")*

We also filtered for document types of articles that were not reviews or meta-analyses (i.e., only original research articles). Studies that appeared in the search were then included in this review if they met the following criteria:

1. *Fear*. The study specifically mentions any fear-associated response (e.g., avoidance, risk-taking, vigilance, fleeing, faster movement), as well as any potential effects this had on the species physiology, interactions, or on the inlying community or ecosystem.
2. *Human-induced.* Whether or not wildlife directly responded to human presence or proxy of human presence. Studies that included fear of infrastructure (such as buildings, vehicles, urbanization, residential areas, human settlements) or land use (e.g., commercial, industrial) were not included unless the land use was specific to use of humans on foot (such as areas protected from hunting or hunting zones). This is to limit confounding factors, including but not limited to wildlife showing fear towards light, sounds, vehicles, or other stimuli that are not humans themselves, which can also cause fear but were not of interest in this study.
3. *Effects on wildlife.* Studies were included if they specifically analyzed how wildlife responded to humans and how this affected the species, community, or ecosystem.

We extracted several variables from each of the papers included in this review (Table 1). We identified whether an article was observational or experimental, and collected the year, country, and habitat in which the study was conducted (Table 1). Habitat categories were adapted from Landsat satellite imagery classification scheme (Landsat 8) and are listed in Table 1. If the majority (~80%+) of the study was conducted in a single habitat type, then that habitat type was assigned to the study, otherwise we chose ‘multiple’ habitat types. The species being studied and its associated trophic level (carnivore, omnivore, herbivore) and group (mammal, bird, reptile, amphibian, bird, fish, invertebrate) were also recorded. How humans induced fear in wildlife, such as human presence or hunting pressure, was recorded (Table 1). Whether the responses of wildlife to human-induced fear caused changes in wildlife behavior (movement patterns, foraging behavior, species occupancy, etc.) or vital rates (changes in physiology, survival, reproduction, population size, etc.) was recorded as the ‘type of response’ (Table 1). We also recorded the scale on which human-induced fear caused changes, which could be the following: species (whether species-scale responses were recorded in response to human-induced fear, such as changes in flight initiation distance or species occupancy), community (changes induced in species interactions, such as changes in predation), or ecosystem (changes seen at the ecosystem scale, such as nutrient deposition or landscape-level effects). Because human-induced fear responses in individual animals were rarely provided on an individual-animal basis - instead usually offered as an averaged response from several individuals - individual and population-wide responses to human-induced fear were pooled into a general ‘species-scale’ response category. Finally, we also recorded whether the response to human-induced fear was considered significant by the study’s authors and recorded the specific information about how wildlife responded to human-induced fear (Table 1). All data were recorded in Google Sheets and summarized in figures produced by Tableau Public (version 2020.3).

OVERVIEW OF HUMAN-INDUCED FEAR IN LITERATURE

An extensive literature search revealed 81 peer-reviewed papers that documented human-induced fear on wildlife populations. Literature on human-induced fear has drastically increased since 2010 (Fig 1a). Though human-induced fear has been studied on all non-Antarctic continents, a substantial portion (n=21 out of 81 articles, or 25.9%) of studies have been based in the United States (Fig 1b). Though most studies (n=45) were conducted in more than one habitat, the most frequently studied habitat categories were human-dominated (n=46) followed by woody plant-dominated (n=41), grass-dominated (n=30), agriculture (n=16), and finally aquatic (n=14; Fig 1c). Most studies analyzed the impacts of human approach (n=34 articles), human presence/activity (n=24), and hunting (n=20; Fig 1d) on wildlife's fearful responses to anthropogenic disturbance. Mammals (n=50) and birds (n=38) were by far the most studied groups, and only three articles in this review studied human-induced fear responses in fish. No articles on reptiles, amphibians, or invertebrates were found in this review. Large-bodied mammals - notably cougars (*Puma concolor*; 6 studies) and deer (*Cervidae sp.*; 17 studies) - were studied the most frequently.

Studies were conducted across all guilds, with 21, 32, 16, and 22 studies analyzing human-induced fear in carnivores, herbivores, omnivores, and multiple guilds, respectively. All the articles in the review analyzed how human-induced fear impacts individual species, with a handful of articles further analyzing how human-induced fear can broadly impact ecological communities (n=3 articles) and ecosystems (n=1). Only three (n=3) studies found a non-significant response to human-induced fear; all others (n=79) found a significant response. Finally, 74 articles studied behavioral responses of wildlife, and only seven articles analyzed how human-induced fear could alter animal fitness or survival.

RESPONSES OF WILDLIFE TO HUMAN-INDUCED FEAR

In this section, we review common observations of how wildlife change activity patterns or behaviors in response to human-induced fear in the literature.

Changes activity and behavior

The literature on human-induced fear highlights two main categories of responses of wildlife to human-induced fear: reactive responses (fleeing from an approaching human) or proactive responses (spatial or temporal avoidance). Flight initiation distance, or the distance at which an animal flees from human approach, was a common metric used to identify reactive human-induced fear responses in various species, especially in birds (see Appendix 1). Most species fled from human approach, regardless of taxa, though there were often extreme differences in flight initiation distances depending on previous interactions individuals had with humans. For example, black-headed gulls in urban areas fled an average flight distance of 0.59 ± 0.71m (Feng and Liang 2020a), while large-billed crows (*Corvus macrorhynchos*) in Japan fled at a distance of 20.5m after the population had experienced previous culling from humans (Fujioka 2020). Research by van Dongen et al. (2015) discovered that black swans (*Cygnus atratus*) at non-urban sites fled at more than seven times the distance from human approach than swans that frequently encounter humans at urban sites (mean flight distance of 96m and 13m, respectively). Most studies analyzed initial flight behavior only, though one study (Ordiz et al. 2019) also analyzed brown bear (*Ursus arctos*) movements after initial approach by humans and found that bears decreased diurnal movements for three days after an initial human approach.

Wildlife also proactively shift natural daily or seasonal activity patterns to avoid humans (see Appendix 1). Many studies in this review found that wildlife decreased diurnal and increased nocturnal activity when humans were present in a system (see Appendix 1). One author (Spitz et al. 2019) also found that elk more strongly responded to human hunting during the day than at night. These studies suggest that wildlife likely perceive humans as a more dangerous predator during diurnal compared to nocturnal hours. Seasonal changes in wildlife behavior in response to humans were also observed; notably, many game species altered their responses to humans depending on whether hunting season was open (Fujioka 2020; Gaynor et al. 2022; Paton et al. 2017; Proudman et al. 2021). In Canada, one author found that elk were more than three times as likely to be vigilant during the fall hunting season than outside of hunting season (Paton et al. 2017).

Wildlife also decreased spatial overlap with humans by avoiding areas of human activity (Mohlman et al. 2019; Ordiz et al. 2019; Santiago et al. 2020; Spitz et al. 2019), especially areas with roads (Magle et al. 2014; Spitz et al. 2019). Avoiding disturbances can negatively impact wildlife, especially when such avoidance alters feeding behavior (Benevides et al. 2019; Clinchy et al. 2016; Lodberg-Holm et al. 2019; McGrath et al. 2018; Smith et al. 2017; Sullivan et al. 2018). Human presence can lead wildlife to decrease the total amount of time (Benevides et al. 2019; Clinchy et al. 2016; Lodberg-Holm et al. 2019; Smith et al. 2017) and frequency (Clinchy et al. 2016; McGrath et al. 2018; Sullivan et al. 2018) of foraging compared to naturally-observed foraging behavior. For example, Lodberg-Holm et al. (2019) found that brown bears would avoid preferred food sources (bilberries) in areas with high human hunting mortality during previous years. African elephants (Loxodonta africana; Wittemyer et al. 2017) and elk (Spitz et al. 2019) were less likely to use human-disturbed areas, even when these areas had quality resources (water and forage, respectively). Notably, wildlife can use a combination of techniques to avoid humans, e.g., both spatial and temporal avoidance. For example, two research groups (Jones et al. 2020; Yamaguchi et al. 2020) found that the probability of elk being observed at a site after a hunting event was negatively associated with hunt duration, suggesting that deer were spatially avoiding sites for certain temporal periods.

Changes to physiology and fitness

This literature review identified two papers that analyzed how human-induced fear can alter the physiology and fitness of wildlife. Greater tits (*Parus major*) were shown to have higher corticosterone levels, fewer hatchlings, and poorer body condition when disturbed by researchers (using human approach) compared to when they were not disturbed (Tablado et al. 2022). This study also found a 94% probability that male great tits would have a shorter telomere in experimentally disturbed plots compared to non-disturbed plots, suggesting that human disturbance may impact stress-mediated alterations in individual genomes. Lopucki et al. (2019) discovered that urban striped field mice (*Apodemus agrarius*) had 30% lower fecal cortisol concentrations than that found in rural mice (Lopucki et al. 2019). Thus, urban mice, which had more anthropogenic stressors compared to their rural counterparts, also had less physiological stress than rural mice. This suggests that physiological stress reactions of wildlife to human-induced fear likely depend on prior experiences with humans.

Habituation to humans

Though the literature in this review broadly supports that wildlife are fearful of humans, a handful of studies analyzing human-induced fear found that wildlife habituated to human presence. Alldredge et al. (2019) discovered that aversive conditioning and relocation of pumas did not appear to influence future livestock depredation. Magle et al. (2014) found that coyotes were more likely to occupy a site when humans visited sites at a higher rate. The propensity to be fearful may depend on how long the human disturbance has been established (Moller 2010), as well as several situational factors, many of which are discussed in the following section.

As seen in Alldredge et al. (2019), fear can be actively manipulated by wildlife practitioners to reduce wildlife habituation to humans and reduce the likelihood of human-wildlife conflicts such as livestock predation or crop raiding (Gaynor et al. 2020; Wilkinson et al. 2020). These efforts are often utilized as non-lethal methods of wildlife control in hopes of 'keeping wildlife wild' by normalizing human-induced fear and alleviating human-wildlife conflict (Alldredge et al. 2019; Gaynor et al. 2020; Wilkinson et al. 2020).

SITUATIONAL FACTORS INFLUENCING HUMAN-INDUCED FEAR

Several species-specific and environmental factors impact how wildlife respond to human-induced fear. This section highlights several key factors influencing fear responses of wildlife, including life history traits, human presentation, habitat, genotype, and individual variation (Fig 2).

Species traits

Species functional traits, including breeding season (Carrete and Tella 2017; Cavalli et al. 2016; Hohmann and Woog 2021), diet (Morelli et al. 2019), body size (Gnanapragasam et al. 2021; Halassi et al. 2022; Morelli et al. 2019), social group size (Halassi et al. 2022; Jiang et al. 2020; Kiffner et al. 2014; Morelli et al. 2019; Vincze et al. 2016; Yamashita et al. 2018), and intelligence (Cornell et al. 2012; Goldenberg et al. 2018; Nowak et al. 2016; Reisland et al. 2021) influence species-scale responses to human-induced fear. Birds with larger body sizes are often quicker to flee from humans (Gnanapragasam et al. 2021; Halassi et al. 2022; Moller 2012; Morelli et al. 2019). Gnanapragasam et al. (2021) believe that, since larger birds are often preferred by human hunters, these species may have experienced lasting trauma from humans and are thus more likely to be fearful of humans.

Group size had variable effects on fleeing behavior; while wildebeest (*Connochaetes taurinus* - Yamashita et al. 2018), gazelle (*Eudorcas thomsoni* - Kiffner et al. 2014), zebra (*Equus quagga* - Kiffner et al. 2014), house sparrows (*Passer domesticus* - Vincze et al. 2016), various waterbirds (Halassi et al. 2022), and several European songbirds (Morelli et al. 2019) were quicker to flee from humans when in larger social groups, larger groups of Eurasian tree sparrows (*Passer montanus* - Jiang et al. 2020) and dik-diks (*Madoqua guentheri* - Kiffner et al. 2014) were slower to flee from humans than smaller groups. Many gregarious species may use sociality as an antipredator strategy (Morelli et al. 2019), which could explain why species that commonly occur in larger groups were more likely to flee from humans. However, the dilution effect of predation risk (i.e., larger groups of prey animals have a smaller chance that any individual will be a victim to predation - Delm 1990) may lead to certain species to be less likely to flee (Jiang et al. 2020; Kiffner et al. 2014). Potentially, whether larger groups are more or less likely to flee from humans may be indicative of the species' evolutionary history, and if larger groups are used to increase predator detection or diluting predation risk.

Intelligent animals like American crows (*Corvus brachyrhynchos* - Cornell et al. 2012), Samango monkeys (*Cercopithecus albogularis* - Nowak et al. 2016), African elephants (Goldenberg et al. 2018), and Javan gibbons (*Hylobates moloch* - Reisland et al. 2021) may display complex, situational-based responses to human-induced fear compared to the less diverse responses of less-intelligent species. For example, Cornell et al. (2012) found that, when researchers wore a mask after trapping individual American crows, crows would 'scold' (i.e., produce warning calls) any person wearing the mask in future encounters, and other crows would join in to 'mob' the same person, even if the mobbers themselves were never captured. In West Java, groups of Javan gibbons showed extensive variability in their responses to human disturbance, with each group studied reacting differently to human presence (Reisland et al. 2021). More intelligent species may display greater variability in their responses to human-induced fear due to their ability to quickly adapt to novel situations, making generalizations about impacts of human-induced fear on these species more difficult.

Human presentation

How humans are presented in the environment often influence fearful behaviors displayed by wildlife. Both the context of human presence (e.g., proximity to roads) and presentation of humans (e.g., clothing outfit, face mask) can influence fear responses. Kiffner et al. (2014) found that the likelihood of several African ungulates responding to human approach declined with increased distance from roads. One author found that urban birds were less fearful of pedestrians when humans were in larger groups (Mikula 2014), and Lethlean et al. (2017) found that Australian birds were quicker to flee from joggers compared to walking humans. Sbragaglia et al. (2018) found that several reef fish species were faster to flee from humans wearing spearfishing outfits than those wearing snorkeling outfits. Other authors found that some coastal bird species were more likely to flee from humans in casual outfits compared to fisherman outfits (Feng and Liang 2020a), and Eurasian tree sparrows were less likely to flee from humans wearing a face mask (Jiang et al. 2020). Zhou and Liang (2020) suggest that wildlife may be more likely to detect humans in certain situations, such as wearing brighter colors, and thus might cause them to flee at a quicker rate. It appears that wildlife may be more likely to respond fearfully if humans are out of the general context of an ‘average’ situation, such as wearing clothes that are not ordinarily observed (e.g., wearing a face mask when previously very few humans wore a face mask) or seeing humans away from where they are usually observed (such as near roads). If so, this may be an indication of fear of novelty rather than the fear of the humans themselves.

Habitat

In general, most studies found that wildlife in urban areas were less quick to flee than animals in rural areas (see Appendix 1). For example, Uchida et al. (2020) found that Eurasian red squirrels (*Sciurus vulgaris*) in Japan displayed reduced stress responses and vertical escape distances (i.e., distance fled up a tree after an approach by a human) when in urban areas compared to squirrels in rural areas. This is potentially due to animals in urban areas having habituated to the more frequent presence of humans, leading to less extreme reactions to human-induced fear by urban species. Other habitat characteristics may also be important for human-induced fear responses; one study by Lee et al. (2015) discovered that parrotbills from closed habitats (reedbeds, forests) were more likely to vocalize than birds from open habitats. Potentially, the use of habitats with lower visibility may indicate a more risk-averse individual and could correlate with the strength of fear response.

Genetic influences

Certain genotypes have been associated with a species' propensity to act fearfully towards humans (Reimers et al. 2012; van Dongen 2015). van Dongen (2015) found that 40% of rural black swans (*Cygnus atratus*) possess a rare genotype associated with longer flight initiation distances compared to only 11.2% of urban black swans possessing this genotype. Similarly, Reimers et al. (2012) found that wild reindeer (*Rangifer tarandus*) descending from domestic reindeer lineages decreased vigilance, alert, and flight responses compared to herds from wild lineages. Schell et al. (2018) found that captive coyote pups from a breeding pair's second litter had higher, heritable cortisol concentrations and were more likely to display risk-taking behaviors compared to siblings in the first litter, suggesting that the parent's experience with humans impacted the cub's behavioral and physiological responses towards humans. Jiang and Moller (2017) studied 96 bird species in Europe and found that threatened species were more likely to have longer flight initiation distance than closely related, non-threatened species, again suggesting the importance of heredity on human-induced fear responses. These genome-specific associations of wildlife responses to human-induced fear may indicate that previous fear experiences in wildlife populations can have 'legacy effects' on how future generations respond to humans, potentially *via* changes in allele frequency of fear-associated genomes (van Dongen 2015; Reimers et al. 2012). Populations with genotypes associated with higher fear of humans may especially be vulnerable to extinction if human-dominated areas are all that remains of their occupied habitat.

Individual variability

In some cases, different species populations or individual animals may display different responses to human-induced fear. Carrete and Tella (2010) discovered that burrowing owls' flight distance in response to human approach varied greatly among individuals, but was repeatable within individuals. Ciuti et al. (2012) discovered that elk harvested during the hunting season had previously displayed bolder behavior, including increased movement and use of open areas, compared to their non-harvested counterparts.

An individual's biological sex was often found to lead to differentiation in reactions to human-induced fear (Ciuti et al. 2012; Lee et al. 2015). Two research groups found that females were more fearful of humans than males of the same species: Lee et al. (2015) found that female vinous-throated parrotbills (*Paradoxornis webbianus*) were more likely to produce fear screams when being handled compared to males, and Ciuti et al. (2012) found that female elk were more cautious during hunting season. Female animals are often more risk-averse (likely due to their need to raise or care for offspring – see Berger 2007) and may show greater behavioral or physiological responses to trait-mediated interactions - including human-induced fear - which can have drastic effects on population recruitment (see Berger 2007).

Cascading effects on communities and ecosystems

Studies on community- and ecosystem-scale alterations caused by wildlife responding fearfully to humans were rare in this review (Fig 3). Suraci et al. (2019) found that three predators (bobcat *Lynx rufus*, striped skunks, and Virginia opossums) decreased overall or diurnal activity at human voice treatments. In response, these predators' prey (deer mice *Peromyscus maniculatus* and wood rats *Neotoma fuscipes*) increased habitat use and foraging at sites with the human voice treatment. Haswell et al. (2020) discovered that humans altered predator activity, and specifically noted that human trail use dampens the top-down effects of large carnivores (gray wolves) on mid-level predator (red foxes *Vulpes vulpes*) activity. Mols et al. (2022) found that increased space use by fallow (*Dama dama*) and red (*Cervus elaphus*) deer in areas without recreation or hunting also increased browsing intensity in the area, causing lower sapling growth and survival in heathlands.

From these studies, it appears that human-induced fear in wildlife may cause changes in species interactions. However, there is still little research into community and ecosystem effects of human-induced fear, likely due to challenges associated with analyzing impacts of fear across broad spatial and temporal scales. Such broad-scale research would improve our understanding of how human-induced fear can affect ecosystems.

Study Limitations

The purpose of this review is to provide an in-depth overview of current literature on human-induced fear in wildlife and should not be considered an exhaustive review of all literature on this topic. Notably, any relevant literature that did not use the word "fear" to describe human-induced fear in wildlife was likely excluded from our search criteria, such as literature that used the key words ‘risk perception’, ‘avoidance’, or ‘behaviorally-mediated interactions’ to describe fear-associated behaviors in wildlife. Furthermore, how human-induced fear can be applied for wildlife management purposes was only discussed briefly in this paper, but significant literature exists on this topic. For these reasons, these findings should be used to become familiar with current human-induced fear literature, but should not be used as an exhaustive list of all literature analyzing fear-like behaviors in wildlife towards humans.

Future Directions

Based on currently available literature, there are several aspects of human-induced fear effects on wildlife that are still unknown or understudied. Here, we present several noteworthy areas for future research on how human-induced fear impacts wildlife:

1. This review did not uncover any literature on the effects of human-induced fear on several taxa, notably reptiles, amphibians, fish, and invertebrates. Herptiles and fish are known to portray anti-predator behaviors like those displayed by mammals and birds, including fleeing and predator avoidance behaviors (Petranka et al. 1987). Thus, these taxa likely display fearful behavior towards humans as well. Herptiles, fish, and invertebrates are historically understudied yet possess a large portion of endangered species (IUCN 2022). Several herptiles are hunted for skins or the exotic pet trade (Cox et al. 2022) and many fishes are targeted for sport or harvest, making understanding of these taxa's fear responses to humans especially important to improve current understanding of anthropogenic threats to these populations.
2. We found few studies analyzing human-induced fear in the Middle East, Central Africa, and Southeast Asia. The Global South has historically been neglected for ecological research (Pettorelli et al. 2021), despite holding a large portion of the global biodiversity (Borthakur and Singh 2018). Improving knowledge of human impacts on wildlife in these regions should be of principal importance to safeguard the Global South's abundance of biodiversity against global climate change and human overconsumption.
3. Two studies mentioned that female animals show more fear of humans than males (Ciuti et al. 2012; Lee et al. 2015), but there may be many factors that influence sex-dependent responses to human-induced fear. Notably, sex may impact an individual's response to human-induced fear similarly to how sexual dimorphism can impact an individual's ecology (Shaffer et al. 2001). For example, male albatrosses may be more likely to persist in the windier regions of the Antarctic due to male's wing's higher wind loading capacity (Shaffer et al. 2001). Both the mechanism driving sex-specific differences in response to

human-induced fear and how these differences might impact each sex's fitness will be an important consideration in future human-induced fear studies.

4. Though a broad literature exists on human-induced fear impacts on wildlife behavior, how human-induced fear can impact physiology or genetics of individuals is less understood. Physiological and genetic changes in species populations have the capacity to impact species fitness (Lopucki et al. 2019; Tablado et al. 2022) and population persistence (Reimers et al. 2012; van Dongen 2015), albeit in different capacities. Though a few studies in this review highlighted such potential impacts (Lopucki et al. 2019; Tablado et al. 2022; Reimers et al. 2012; van Dongen 2015), there is still much to uncover to understand how fear of humans may impact wildlife fitness or survival. We suggest that future research focuses on determining a) if there is a genetic component to fear that persists in various species, b) if this genetic component that impacts responses to human-induced fear is shared across numerous species populations,, and c) if human-induced fear causes high levels of stress that could impact an individual's reproductive capacity.
5. Several studies in this review highlighted how the context of human presence (such as the clothing that the human subject was wearing - Zhou and Liang 2020) can impact the strength of fearful responses of animals to humans. However, many animals react more fearfully to novel situations and contexts than to those they experience frequently (Biondi et al. 2020). Therefore, separating the fear of context of human presentation from a general fear of novelty will be important to understand the driver of human-induced fear, as well as to improve management techniques that utilize fear behaviors in wildlife.

6. Only two studies in this review investigated the cascading impacts of human-induced fear on wildlife communities or ecosystems. Though predators have been found to impact prey resource selection (Caravantes 2020; Clinchy et al. 2016; Pringle 2018; Ripple and Beschta 2004; Schmitz et al. 2004; Wang et al. 2015), human-induced fear may have differing effects on prey resource selection due to the pervasiveness of humans in natural habitats. For example, habituation to human presence, a phenomenon not observed from prey towards natural predator-induced fear, may allow a species to lose fear behavior towards humans (Alldredge et al. 2019; Magle et al. 2014; Moller 2010). What allows wildlife to transition from fearful responses of humans to habituating to human presence, and how fear or habituation of one species towards humans impacts its interspecific relationships, will be important for understanding indirect human impacts on broader ecological systems.

Concluding Remarks

This review supplies an overview of current knowledge of how humans incite fear in free-living animals and corresponding changes to their indwelling communities and ecosystems. Many findings from this literature review suggest that wildlife respond to humans similarly to how they respond to their natural predators, such as fleeing from both human and predator approaches. However, there were also numerous instances in which specific responses to human-induced fear differed from responses of wildlife to predator-induced fear (such as responding in opposite ways to humans compared to predators across different habitat types - see Pringle 2018; Valeix et al. 2009), indicating that wildlife may associate humans with different risks than natural predators. In fact, several studies (including Crawford et al. 2022; Proudman et al. 2021; Suraci et al. 2019) found that humans may elicit an even greater fear response from wildlife compared to natural predators, making them a separate, notable, novel disturbance in ecosystems.

Fortunately, other studies highlight how animals alter their behavior to mitigate the effects of human-induced fear (such as using covered habitats in human-disturbed areas; Bonnot et al. 2013; Mols et al. 2022; Nickel et al. 2020). Management techniques can be modified to minimize the effects of human-induced fear, such as providing resources used to mitigate or lessen human disturbance. Specifically, increasing cover availability may mitigate the effects of human-induced fear on human-sensitive species.

As outdoor recreation increases in popularity and humans continue to expand their use of undeveloped areas, human-induced changes in wildlife will become more prevalent. Furthermore, the use of fear in wildlife management practices for decreasing human-wildlife conflicts likely has significant current and future applications (Alldredge et al. 2019; Anderson et al. 2022; Gaynor et al. 2020; Wilkinson et al. 2020). Specifically, inducing fear in individual animals that conflict with humans via livestock depredation, crop raiding, or threat to life or property will likely be a necessary non-lethal wildlife control method as human development continues. Human-induced fear is only one aspect of the ecology of fear in natural systems, in which numerous species interactions can lead to complex relationships between humans and ecosystems (Anderson et al. 2022). Anthropogenic impacts on wildlife exist in every ecosystem on earth, and most species are likely to encounter humans across some part of their range. Thus, efforts to address the knowledge gaps highlighted in this review and further research on the cascading effects of the fear of humans on free-living animals will advance knowledge relevant to conservation. By knowing how different species react to humans, we can take steps to minimize negative impacts of behavior and well-being of at-risk species (e.g., avoiding areas where at-risk species are feeding or nesting, or limiting human activity in certain areas or times of day/seasons to reduce disturbance). Furthermore, human-induced fear likely has applications for wildlife managers aiming to manipulate fear dynamics to control wildlife behavioral responses to human presence. Fear of human activities can impact wildlife interactions and ecological relationships, and studying this phenomenon will provide a deeper understanding of the role species play in the overall health and functioning of an ecosystem.

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TABLES

Table 1. Variables collected for each paper in this review.

Variable Name	**Description**	**Possible Values**
Study Type	Whether the study was experimental (i.e., had a treatment) or observational (no manipulation).	Observational, experimental
Study Date(s)	Year(s) during which the study took place.	Year (2001, 1987, etc.)
Country	The governmental entity that presides over the territory in which the study was conducted.	Any of the 195 countries currently (or previously) in existence. Example: Canada
Species	Common and scientific name of each species studied. If multiple species were studied, they were separated by a semicolon.	Example: red fox (*Vulpes vulpes)*
Trophic Level	The trophic level of the species of interest for the study.	Carnivore, omnivore, herbivore, multiple
Animal Group	The general group of animals in which the species of interest belongs.	Mammal, reptile, amphibian, bird, fish, invertebrate, multiple
Habitat (Landsat)	Land cover classification of the study area based on Landsat satellite imagery classification scheme (Landsat 8) and categorized into one of five categories: human-dominated (urban, suburban, semiurban, or developed open space habitats), woody plant-dominated (temperate, boreal, and tropical forests, as well as woodlands), grass-dominated (savanna, grassland, and montane habitats), agriculture (pastures for livestock or croplands), or aquatic (wetland, marine, coastal, and freshwater habitats)	freshwater, marine, PerennialIce/Snow, coastal, wetland, urban, suburban/semiurban, OpenSpace(developed), barren/arid, montane, rocky, Temperate Forest, Tropical Forest, Boreal Forest, shrub/woodland, savanna/grassland, pasture/crops, other/multiple(notes) Overall categories (see left): human-dominated, woody plant-dominated, grass-dominated, agriculture, or aquatic

Human Impact (independent var)	The human-related variable or condition that induced fear in wildlife (must be based on human presence, not infrastructure).	The types of human impacts found in the studies included in this review were: Human presence/activity (not approaching animal but humans doing other activities nearby, such as walking on a path, can also be experimental presence such as walking around study area) Human approach (direct approach by a human) Hunting (lethal contact with a human) Trapping/handling (often for research purposes) Simulated presence (such as human voice playbacks to simulate human presence) Aversive conditioning (purposefully causing fear in wildlife, such as 'hazing')
Type of Response 1	The type of response exhibited by the species of interest in this study in response to human-induced fear.	Behavioral (movement, activity, foraging, occupancy), vital rates (physiological, reproductive, survival, population size)
Scale of Response 1	The ecological scale (species, community, or ecosystem) at which the effects of human-induced fear were observed.	Individual/population (telemetry, vocals, stress, mating, survival, foraging, occupancy, abundance, density), community (interactions, predation), ecosystem (nutrients, vegetation)
Type of Response 2	A secondary type of response, if multiple types of responses were observed in the study.	Behavioral (movement, Direct Response, activity), vital rates (physiological, reproductive, survival)
Scale of Response 2	A secondary scale of response, if multiple scale of responses were observed in the study.	Individual/population (telemetry, vocals, stress, mating, survival, foraging, occupancy, abundance, density), community (interactions, predation), ecosystem (nutrients, vegetation)

Sig Response?	Binary indicator of whether or not there was a significant response of species to human-induced fear.	1,0
Response Specifics	Specific results about the species response to human-induced fear.	N/A
Notes	Any notes recorded by the data collector.	N/A

FIGURE CAPTIONS

Figure 1. Summary statistics of published articles in this review. (**a**) Number of articles about human-induced fear published by year. (**b**) Number of articles on human-induced fear by country, with countries shaded a darker color having produced more articles. (**c**) Number of studies conducted for each habitat category. See Materials and Methods for the habitat category descriptions. (**d**) Stacked bar chart in which the number of articles by type of human impact (human approach, presence/activity, hunting, simulated, other) are stacked for each taxonomic group (birds, fish, mammals). In other words, the number of articles per animal group across human disturbance types.

Figure 2. There are several factors that can influence how wildlife respond to human-induced fear, including (starting at the top and moving clockwise) life history traits of the species, how humans were presented in the interaction (human presentation), the habitat in which the behavior is observed, variation among individual responses to humans, and genotypic variation within the species.

Figure 3. Observed disruptions of trophic interactions by human-induced fear in the literature. Human-induced fear has caused disruptions in relationships between predators and prey (Suraci et al. 2019), between apex and mid-level predators (Haswell et al. 2020), and between consumers and primary producers (Mols et al. 2022). Interactions between species that are intensified by human presence are indicated by a solid green line, and dampened interactions between species due to human presence are indicated by a dotted orange line.

APPENDICES

Appendix 1. Literature summary table for findings of the reviewed sources. *

Major Theme	**Authors**
Wildlife proactively shift natural daily or seasonal activity patterns to avoid humans.	Bonnot et al. 2013; Bonnot et al. 2020; Gaynor et al. 2022; Gaynor et al. 2018b; Mohlman et al. 2019; Moll et al. 2018; Nickel et al. 2020; Ordiz et al. 2019; Santiago et al. 2020; Spitz et al. 2019; Sullivan et al. 2018; Wheat and Wilmers 2016
Used flight initiation distance to identify human-induced fear responses in various species.	Halassi et al. 2022; Charutha et al. 2021; Gnanapragasam et al. 2021; Feng and Liang 2020a,b; Fujioka 2020; Hall et al. 2020; Jiang et al. 2020; Tryjanowski et al. 2020; Uchida et al. 2020; Zhou and Liang 2020; Linley et al. 2019; Morelli et al. 2019; Ordiz et al. 2019; Sbragaglia et al. 2018; Van Donselaar et al. 2018; Yamashita et al. 2018; Carrete et al. 2017; Jiang et al. 2017; Lethlean et al. 2017; Samia et al. 2017; Cavalli et al. 2016; Vincze et al. 2016; Bjorvik et al. 2015; Nunes et al. 2015; Sreekar et al. 2015; van Dongen et al. 2015; Kiffner et al. 2014; Mikula 2014; Guay et al. 2013; Moller 2012; Reimers et al. 2012; Carrete et al. 2010; Moller 2010
Wildlife in urban areas are less quick to flee than animals in rural areas.	Bjorvik et al. 2015; Carrete and Tella 2017; Cavalli et al. 2016; Charutha et al. 2021; Feng and Liang 2020b; Hall et al. 2020; Moller 2012; Morelli et al. 2019; Samia et al. 2017; Stillfried et al. 2017; Tryjanowski et al. 2020; Uchida et al. 2020; Vincze et al. 2016; Yamashita et al. 2018; Zhou and Liang 2020

* Note: this table is *not* an exhaustive summary of the literature in this review.