Title: Are super-predators also super-scary? A systematic review and meta-analysis of animal responses to human interactions

Authors:

Shawn Dsouza[1*]

Email: shawn27.dsouza@pm.me

Kartik Shanker[1]

Email: kshanker@iisc.ac.in

Maria Thaker[1]

Email: mariathaker@iisc.ac.in

[1] Center for Ecological Sciences, Indian Institute of Science, Bengaluru, India.

***Corresponding Author:**

Shawn Dsouza

Mob No.: +91 9821158693

Email: shawn27.dsouza@pm.me

Address: Center for Ecological Sciences, Indian Institute of Science, CV Raman Ave, Bangalore – 560097

Abstract

Human induced rapid environmental change has been recognized as a global threat to natural systems and the organisms that inhabit them. Human hunters and fishers interact with animals in natural spaces as predators, and are more effective in capturing prey and reducing populations than natural predators overall. On the other hand, seemingly benign interactions with humans, such as tourism, may also be perceived as threatening and have negative impacts on animal populations. Here, we provide a synthesis of the current knowledge of the combined effects of lethal and non-lethal human interactions on the behavioural responses of animals in natural spaces. We conducted a systematic review and meta-analysis of literature published over the past three decades, and built a dataset to determine the relative effect of lethal and non-lethal human interactions on foraging, vigilance, and movement behaviors of wild animals. Lethal human interactions included hunting, fishing, and retaliatory killing in response to conflict, and non-lethal human interactions were distinguished as active (snorkeling, scuba diving, pedestrians, hiking, and tourists) or passive (roads, human settlements, sonar, and boat traffic). We also considered how the trophic level of the species and body size could influence the effect of human interactions on animal behavior. Our findings show that lethal human interactions had a significant effect on the behaviors of animals, causing animals that are actively hunted by humans to increase vigilance, reduce foraging, and alter movements. Both active and passive non-lethal interactions had weaker and non-significant effects on altering these behaviours of animals. Overall, our meta-analysis shows that the impact of non-lethal human activities in eliciting fear-driven behavioural changes in prey does not seem to have broad empirical support. It also suggests that the intensity of effect of the “human super-predator” may depend on the trophic level of affected species, or the history of the human-animal interactions in that landscape, In order to understand the nuances of these effects, systematic studies across more species and geographic regions are needed.

Keywords: HIREC, risk – disturbance hypothesis, non – consumptive effects, predator – prey interactions, fear

Contents

I. Introduction

Humans are a pervasive species that interact with and change their environment in a multitude of ways. Over the past two centuries, human development has led to the alteration of global ecosystems at a rate that has not been witnessed in the history of the planet. From climate change to the rampant extraction of biological resources, the effects of human-induced rapid environmental change (HIREC) are large in scale and magnitude (Estes et al. 2011; Sih 2013). Given their unique ecology, humans not only occupy every eco-region of the world, but have multiple functional roles that can shift trophic ecology in intensive and extensive ways. Animals therefore have no choice but to respond to human activities in the natural world.

Throughout most of their evolutionary history, humans have been hunter–gatherers (Treves and Naughton-Treves 1999). As predators, however, humans are extraordinarily deadly, as they out-compete most natural predators in the rate and efficacy of killing their prey (Darimont et al. 2009; 2015). Through social organisation and tool use, humans can target multiple trophic levels at high efficiency (Treves and Naughton-Treves 1999). Thus, humans have been referred to as generalist super-predators (Clinchy et al. 2016), taking a disproportionately large number of animals from ecosystems. In fact, the rate of mortality of prey species from human predators, such as hunters and fishers, are much greater in magnitude than the sum of kill by all natural predators in both terrestrial and marine ecosystems (Darimont et al. 2015). Thus, humans create truly risky conditions for both wild prey and predators in natural systems (Oriol-Cotterill et al. 2015).

In addition to hunting and fishing, humans also interact with wild animals through non–lethal activities (Boyle and Samson 1985). Non-lethal interactions of humans with animals can be further distinguished as active or passive. Active non-lethal interactions include tourism, walking in parks, hiking in nature reserves, mountaineering and off-road bicycling, and have been shown to negatively influence animals even-though the humans in their habitats are not actively killing them (e.g. Loehr et al. 2005; Newey 2007; Brown et al. 2012; Montero-Quintana et al. 2020). Passive non-lethal interactions are even more pervasive, as they include alterations to environments. Roads and settlements, in particular, have the greatest potential to influence the behaviour of animals (e.g. Mehlhoop et al. 2002; Cappa et al. 2017, etc). Given the number of bird collisions on glass (Loss, Will, and Marra 2015) and high occurrence of roadkill globally (Benson, Mahoney, and Patterson 2015), animals are facing mortality from human interactions that they may not perceive as risky.

Other non-lethal activities such as air and sea travel may also affect animal behavior (e.g. Van der Kolk et al. 2024; see Harris et al. 2019 for review). Although compelling evidence suggests that non-lethal human activities can be extremely strong in changing animal behaviours (Boyle and Samson 1985; selected examples: (Davis et al. 1997; Christopher M. Papouchis et al. 2001; Nevin and Gilbert 2005; Westekemper et al. 2018; Ladle et al. 2019), many other studies show that animals habituate quickly to human encounters (see Smith et al. 2024). Thus, it remains unclear whether the non-lethal interactions of humans on animals are as strong as the lethal interactions in eliciting fear and changing behaviours.

Given that humans have both lethal and non-lethal interactions with animals in the wild, the individual and combined effects of these on animal behaviors can potentially be very high. In a recent narrative review, Smith et al. (2024) outlined a framework describing the pathways by which lethal and non-lethal human interactions can change phenotypic (behavioral and physiological) responses of animals, with consequence for population growth and abundance. They find that the perceived risk of humans can induce phenotypic changes in wild animals, but as expected, the evidence is mixed (Smith et al 2024). What is still missing is a quantitative assessment of the relative magnitude of effect for different types of human activities, which would illustrate when and why animals respond to human-induced risk.

In this paper, we use a meta-analysis to synthesize the current evidence for human-induced behavioural changes in wild animals. We separated studies based on whether the interactions were lethal (hunting, fishing), active and nonlethal (ecotourism, hiking) and passive and nonlethal (roads and human settlements). One of the clearest and fastest responses that prey use to minimize risk is by shifting behaviour. Decades of research has shown that natural predators change their foraging and vigilance patterns, as well as the movement and habitat use patterns of prey (Brown and Kotler 2004; Sih 1984). Thus, we focused on changes in foraging behaviours (bite rates and foraging time), vigilance (vigilance time and proportion) and movement (displacement, home range size and rate) of animals due to human interactions. We predict that in areas where humans hunt, animals would strongly invest in anti-predator behavioural strategies, spending more time being vigilant, less time in foraging, and increasing their movement rate or displacement (Figure 1). We also expect animals to perceive non-lethal activities of humans as threatening but to a lesser degree; thus, we expect a lower intensity of anti predator responses to active and passive non-lethal interactions of humans (Figure 1). We also tested the potential influence of body size on the magnitude of behavioural effects based on the hypothesis that larger animals would react to a greater extent to human disturbance as they are disproportionately targeted by the lethal actions of humans.

From a systematic review of published studies, we derived effect sizes that describe the magnitude of behavioural change across these categories of human interactions. We synthesise our meta-analysis to determine whether non-lethal effects of humans that are active or passive influence wild animal behaviours to the same extent as lethal human effects. Finally, we highlight where gaps in the literature have yielded skewed conclusions about human impacts on the behaviour of animals in natural spaces and suggestavenues for future research in this field.

II. Methods

To determine the strength of behavioural change (i.e. effect sizes) caused by human activities, we conducted a systematic literature survey that included studies where foraging, vigilance or movement behaviours were measured in animals in response to lethal human interactions (hunting, including poaching and trapping, and fishing), nonlethal but active interactions (walking in parks, hiking in nature reserves, off-road bicycling and animal watching), and nonlethal but passive interactions (roads and human settlements).

1. Search and literature database

We conducted a scoping search using the web of science database and their advanced search function. Our initial search term was “(risk OR fear) AND (human OR anthropogenic) AND (behavio*) AND ALL=(predate*)”. The search terms were applied across all fields. The initial search returned 2319 results on 12th January 2023. We downloaded the data and conducted a literature mapping analysis to identify additional search terms and updated our search string to “(human OR anthropo*) AND (risk OR fear OR NCE OR trait mediated effect OR nonconsumptive* effect) AND (behavio*) AND (predat*)". Using our updated search string, we conducted searches on the SCOPUS and WOS database as well as grey literature databases such as OpenThesis on 14th February 2023. We then used Rayyan, a literature management and screening software to deduplicate our database (Ouzzani et al. 2016; Foo et al. 2021). After deduplication we were left with 7562 abstracts. This review was not registered.

2. Initial screening

We piloted our initial screening protocol on 100 randomly selected papers using Rayyan (Ouzzani et al., 2016). We decided inclusion and exclusion criteria by evaluating titles, abstracts, and key words to determine the population studied, the exposure or intervention to the population, the control if any and the outcome (see Appendix A.1 for detailed inclusion criteria). The initial screening was conducted by three independent researchers. The three researchers discussed conflicting decisions on inclusion or exclusion of abstracts until a consensus was reached. We applied the finalised screening protocol to all abstracts in our database and were left with 436 papers to further evaluate.

3. Full text screening and data collection

After conducting initial screening, the screened database was downloaded from Rayyan (Ouzzani et al., 2016). We then cleaned the database and extracted PICO data in a workable format using R. Papers chosen for inclusion during our initial screening were full-text screened. We determined our protocol based on variables in our initial screening, the methods used, study design and reporting (Appendix A.2) (Foo et al., 2021). We collected data on the study species identity and trophic level, location of the study, treatment, controls, responses, mean effects, variance measures and sample size. We piloted the protocol on 39 papers. Where results were not clearly reported we either used published data to calculate mean effects and variance measures or used a plot digitiser to extract data from figures. Studies in which data extraction was not possible were excluded from our meta-analysis. We included 71 studies at this stage.

4. Backward and forward search

We identified key studies and reviews during our screening for backward and forward search. Backward search identified papers cited by these studies and reviews, and forward search identified papers that cite these key papers. We added the results to our existing database and deduplicated it to create the final paper database for the review (Foo et al., 2021). After screening the additional abstracts, we added an additional 40 studies to our final selection. Of these, 14 were added after full-text screening. We have included a PRISMA (EcoEvo) checklist and flowchart in Appendix A and E (Page et al. 2021; O’Dea et al. 2021).

5. Types of studies

There were several types of study approaches that measured animal responses to human activities. The majority of studies were observational or natural experiments. This included spatial or temporal contrast. Spatial contrasts included designs in which behaviors were compared across protected and unprotected areas for lethal interactions (n = 8), areas with and without tourist for active interactions (n = 6) and areas close and far away from roads or settlements for passive interactions (n = 4). Studies also employed auditory stimuli (n = 5) for example road noise or human speech in areas with hunting pressure or high traffic to test for the effect of lethal interactions and passive interactions respectively. Other experimental studies employed direct pedestrian disturbance to simulate active interactions (n = 3) and lethal interactions in areas with hunting (n = 3). Four studies used temporal contrast in human activities such as hunting closures and tourist seasons to determine the effects of active (n = 1) and lethal (n = 3) interactions. Finally, ten studies did not implement or utilize a contrast for their comparison and instead determined correlations between human activities for active interactions and distance from road for passive interaction to study their effects on behavior.

We have focused on studies that deal with foraging, vigilance and movement behaviors. Studies dealing with foraging and vigilance behaviors used focal individual sampling and scan sampling. The measured behaviors were time spent vigilant, time spent foraging, frequency of vigilance behavior in a group, rate of individual vigilance behavior, and foraging (bite) rates. We included movement studies that measured movement rates (speed), displacement (distance traveled), and home range size using GPS tags, collars and transmitters. Home range size was included as it is function of displacement and speed in a given sampling period.

6. Meta-analysis

We used studies that reported all necessary metrics for comparison including treatment means, measures of uncertainty, and sample sizes for further analysis (Mikolajewicz and Komarova 2019, Appendix A.2). We did not include papers that only reported test statistics in our meta-analysis. We gathered secondary data including trophic level, dietary guild and body mass, on the species from each study from mammalbase (Lintulaakso 2021), animaltraits database

(Herberstein et al. 2022), handbook of the birds of the world (Del Hoyo et al. 1992) and fishbase (Froese and Pauly 2010).

We divided the studies into categories based on their study designs as experimental or observational. We converted proportional and percentage data (means and measures of uncertainty) to absolute values (number of individuals or time in seconds), and we converted all measures of uncertainty to variance before analysis. We calculated standardised mean difference for studies that reported an explicit treatment and control (negative or positive), as $d=\frac{x_{control}-x_{treatment}}{s_{pooled}}$, where x_i is the mean of treatment and control outcomes respectively and $s_{pooled}=\sqrt{\frac{s_{control}^2(n_{control}-1)+s_{treatmen}^2(n_{treatment}-1)}{n_{treatment}+n_{control}-2}}$, here s_i^2 is the sample variance and n_i is the sample size. All the correlational studies we included reported unstandarized regression coefficients (*b*), we thus calculated the standardised mean differences from *b* as $d=\frac{b}{s_{pooled}}$, where $s_{pooled}=\sqrt{\frac{s_y^2(N-1)-b^2\left(\frac{n_{treatment}n_{control}}{n_{treatmen}+n_{control}}\right)}{N-2}}$ here N is the total sample size (Lipsey and Wilson 2001). The model coefficients of studies which used a treatment:control contrast were multiplied by -1 to maintain consistency across studies. We assigned each study a unique identifier (study ID); when we extracted multiple data points from studies, we assigned a unique identifier to each datapoint (data ID).

We first fit an intercept only multilevel meta-analytic (MLMA) model with species, study and data id as random effects to determine the degree of heterogeneity across studies after accounting for known sources of variation as follows:

$$y_{ijk} = \mu + u_{ijk} + s_i + d_j + \eta_{ij}$$

where, y_{ij} is the effect from j^{th} data point of the i^{th} study, μ is the overall mean across studies, u_{ij} of the i^{th} estimate withing the j^{th} study, s_i is the random effect due to the i^{th} study, d_j is the random effect due to the j^{th} data point and η_{ij} is the error of the j^{th} estimate from the i^{th} study. The random effect framework assumes that each study has its own true effect size which is derived from a population of true effect sizes. Since this meta-analysis involves a comparison across taxa in different habitats and geographies, the random effect framework is appropriate (Nakagawa et al. 2022; Noble et al. 2022). We also fit a phylogenetic model with relatedness as random effect.

$$y_{ijk} = \mu + u_{ij} + s_i + d_j + p_k + \eta_{ij}$$

where, p_k is random effect due to the k^{th} species. Phylogeny did not capture significant variation across all outcomes (Chamberlain et al. 2012; Cinar, et al. 2022). We thus used a model with only study identity, and data identity as random effects. We used the Q statistic to determine left over variation. We used both I^2 and H^2 to determine heterogeneity across studies (Harrer et al. 2021). We used the final MLMA to determine whether there was an overall significant effect across studies. Finally, we used the MLMA to perform a multiple regression to determine the effect of type of human interactions and animal size on the observed effects.

7. Sensitivity analysis

Our analysis draws from a global cross taxonomic dataset and, thus, there are multiple possible sources of non-independence. Bias in terms of the taxa studies and geographic location of study meant that certain populations were represented multiple times in our data set. Phylogenetic relatedness may also lead to non-independence across studies (Noble et al. 2017). We account for potential non-independence by implementing the MLMA with a random effect. We evaluated publication bias visually in our dataset using a funnel plot and used regression test for funnel plot asymmetry (Nakagawa et al. 2022, Appendix C). We also used a multilevel meta-regression on sample variance with study identity and data identity as random effect to determine publication bias. As significant results have a tendency to be published first, we plotted the effect size against the year of publication to determine any time-lag effects. To determine the robustness of our analysis, we used a leave-one-out method where we dropped each study from our data set in sequence and ran the MLMA to determine if any single study had a disproportionate effect on the summary effect size (Nakagawa et al. 2022; Noble et al. 2017) (Appendix D). All data preparation and analysis were conducted in R – 4.0.1 (R Core Team 2024). Data and code are available at https://www.github.com/cheesesnakes/superpredator-or-superscary.

III. Results

After screening, we included 85 studies in our systematic review, the majority of which were published in the past two decades (Appendix A5). Of these, 44 studies reported enough information to be included in the meta-analysis, covering 38 species and families. These studies were widely distributed across geographies and habitats ranging from 78ºN to 43ºS and 169ºE to 123ºW (Figure 2). Across outcomes, 24 studies reported measures of foraging behaviours, which included bite rate and time spent foraging, 29 studies focused on vigilance behaviours, which included time spent vigilant and vigilance rate, and 9 studies dealt with movement behaviour, which involved home range size, displacement and rate of movement (Figure 3). The majority of these papers (n = 36) studied primary consumers, such as *Cervus elaphus* and *Capreolus capreolus* (Figure 4, Appendix A.6). Only 7 studies included secondary and tertiary consumers (Figure 4), thus statistical comparisons across trophic levels and functional guilds were omitted.

The body size of the animal did not significantly influence the effect of human activities on foraging ($\beta = - 4.139 \times 10^{-6} \pm 4.352 \times 10^{-5}$, $t_{34} = -0.09$, $p = 0.924$), movement ($\beta = 0.006 \pm 0.006$, $T_5 = 0.948$, $p = 0.288$), or vigilance behaviour ($\beta = -4.139 \times 10^{-6} \pm 4.347 \times 10^{-5}$, $t_{46} = -0.0517$, $p = 0.961$). Overall, animals responded similarly to human disturbance regardless of their size.

1. Changes in behaviours across types of human interactions

The overall effect of human interactions across studies on foraging behaviours was significantly negative (SMD = -0.411, 95% CI = -0.893 – 0.071, $T_{22} = -1.73$, $p = 0.092$) and on vigilance was significantly positive (SMD = 1.31, 95% CI = 0.376 – 2.237, $T_{27} = 2.83$ $p = 0.007$). However, across studies, the effect of human interactions on movement behaviour across studies was not significant (SMD = 0.012, 95% CI = -0.694– 0.718, $T_6 = -0.04$, $p = 0.971$, Appendix C.2 – C.4, Figure 4). Upon fitting the MLMA model, there was still significant heterogeneity among studies that was not accounted for by random effects (Appendix C).

Foraging behaviour of animals was negatively affected by lethal human interactions (SMD = -1.65, 95% CI = -3.56 - 0.27), but not active non-lethal interactions (SMD = 0.071, 95% CI = -

0.38 – 0.53) or passive non-lethal interactions (SMD = -0.688, 95% CI = -1.83 – 0.46). Five data points showed a significant negative effect of active interactions on foraging behaviour and 6 data points showed a significant positive effect. Similarly, 5 data points showed a significant negative effect of passive non-lethal interactions on foraging and 2 data points showed a significant positive effect of passive interactions on foraging.

Across studies, lethal interactions had a significant positive effect on vigilance behaviours of study animals (SMD = 3.192, 95% CI = 0.85 – 5.53) but active non-lethal interactions did not have a significant effect (SMD = 0.57, 95% CI = -0.46 – 1.61) and nor did passive non-lethal interactions (SMD = 0.44, 95% CI= -1.45 – 2.34, Figure 4). There was a significant positive effect of active interactions on vigilance in 13 data points and significant positive effect of passive interactions in 5 data points (Figure 4). There was no significant effect of human interactions on movement.

Overall, when we consider all studies in this analysis, foraging behaviours were significantly more suppressed by lethal human activities than by active non-lethal interactions ($\beta = -1.141 \pm 0.529$, $t_{34} = -2.155$, $p = 0.038$, figure 5). The magnitude of behavioural effects on vigilance behaviour due to lethal human interactions was significantly higher that of active non-lethal interactions ($\beta = 2.359 \pm 0.983$, $t_{46} = 2.398$, $p = 0.02$, figure 5). There was no significant difference in the magnitude of interactions between active and passive non – lethal human interactions. There were no significant differences in the effect of human interactions on movement behaviours across the three types of interactions (Appendix D, figure 5).

IV. Discussion

Humans occupy multiple niches across almost every ecosystem. As predators, humans are more deadly than most other predators in both marine and terrestrial systems because they can target multiple trophic levels simultaneously and can extract animals at a faster rate than natural predators (Darimont et al. 2015). Humans also occupy natural spaces for seemingly benign activities such as resource extractions, tourism, hiking, and so on. Thus, humans can be predators in the classic sense, but their non-lethal activities, such as their presence in the environment or modification of the environment, can also be perceived as threatening. The mere presence of humans has been shown to alter animal behaviour, a phenomenon considered under the risk disturbance hypothesis (Frid and Dill, 2002). Understanding how animals perceive and respond to humans in their environments is vital for successful management of animal populations as well as the management of ecosystems they inhabit. The review and meta-analysis presented here covers a wide range of studies both geographically and taxonomically over the past three decades (Figure 2, Appendix A).We find that the magnitude of effects on movement, foraging and vigilance behaviours of wild animals depends significantly on the type of human interaction with lethal human-wildlife interactions creating the greatest and only overall significant effects on behaviours compared to both active and passive non-lethal interactions (Figure 5).

1. Lethal interactions: hunting, fishing, etc.

Humans have hunted other for a majority of their evolutionary history (Treves and Naughton-Treves 1999). In this context, hunting includes fishing, and trapping that result in removal of prey individuals through direct human intervention. Darimont et al.'s (2015) analysis revealed that humans have killed a larger biomass of prey species than most other predators in their respective ecosystems. The efficiency and scale at which humans can kill prey adds to their perceived fierceness, a predator trait (Wirsing et al. 2021). Thus, prey should respond to human hunters very strongly (Clinchy et al. 2016; Crawford et al. 2022). Clinchy et al. (2016) showed that in areas where badgers are hunted, badgers respond to playbacks of human voices by significantly reducing their foraging activity. Our meta-analysis showed that, as expected, lethal interactions had a significant and adverse effect on both foraging and vigilance behavior of animals across taxa and geographical locations. In line with the foraging – vigilance trade off (Brown and Kotler 2004), our metanalysis shows that animals significantly reduced foraging and significantly increased vigilance in response to human hunters. We find an overall larger magnitude of effect on vigilance rather than foraging (Figure 5), but this is most likely because fewer studies have reported the effects of lethal interactions on foraging behavior (Figure 3).

The behavioral response to lethal interactions was largest for large game species such as deer (*Dama dama*), elk (*Cervus* elaphus) and moose (*Alces alces*), whereas the response of terrestrial predators, such as puma (*Puma concolor*), hyena (*Crocuta crocuta*) and badgers (*Meles meles*), was limited (Suraci et al. 2019; Clinchy et al. 2016; Pangle and Holekamp 2010). Across prey species, the type of response was varied. Pecorella et al. (2016) showed that fallow deer (*Dama dama*) were more vigilant and foraged less in areas where culling was allowed than where culling was not allowed in Maremma Regional Park (Italy). Large ungulates such as Sable antelope (*Hippotragus niger*) and greater Kudu (*Tragelaphus stepsiceros*) also showed large increases in vigilance in the areas around Hwange National Park (Crosmary et al. 2012). Fallow deer showed a proportional decrease in foraging as vigilance increased (Pecorella et al. 2016), however, this trade-off is not always proportional. Red deer (*Cervus elaphus*) in the Scottish Highlands showed a disproportionate increase in vigilance behaviors relative to the decrease in foraging behavior in response to lethal interactions (Jayakody et al. 2008). Conversely, Moose (*Alces alces*) showed a larger decrease in foraging behavior than increase in vigilance (Bhardwaj et al. 2022). Notably, roe deer (*Capreolus capreolus*) showed large changes in movement behavior as opposed to foraging and vigilance (Benhaiem et al. 2008; Picardi et al. 2019).

2. Active non-lethal disturbance

According to the risk disturbance hypothesis, animals are expected to perceive non-lethal human disturbance similarly to the threat of predation (Frid and Dill 2002). For instance, bird species have been found to reduce foraging and increase vigilance in response to pedestrians in urban parks of Madrid (Fernández-Juricic et al. 2001). These behavioural changes are akin to how birds would respond to a natural predator, suggesting that human presence is perceived as a threat. Thus, animals may respond to human disturbances in the same way that they do to mitigate predation risk from natural predators. Multiple studies have sought to test the risk disturbance hypothesis across contexts. Price (2008), in a review, showed that human disturbance in the form of pedestrians alters the flight, foraging and vigilance behaviours of multiple bird species. Stansell et al. (2022) showed that dark-eyed juncos (*Junco hyemalis*) are more shy in urban areas than in their wild habitat.

However, the relative magnitude of perceived risk from lethal humans, and non-lethal humans may greatly differ (Mols et al. 2022). Our analysis shows variation across studies in terms of the magnitude and direction of observed effects for both types of non-lethal interaction with humans, but the effects of active interactions were small for most studies. In addition, lethal interactions with humans elicited the greatest magnitude of effects across outcomes. We hypothesize that this could be attributed to the divergent ways in which animals perceive benign humans in their environment (Figure 1, Smith et al. 2021).

In some cases, the presence of humans may benefit some species by altering interactions between them; female grizzly bears with cubs have been observed using areas with recreational human activity to avoid depredation by aggressive males (Ladle et al. 2019). In particular, they may influence the interactions between predators and prey (Moller 2008; Shannon et al. 2014; Proudman et al. 2021). For example, humans may deter predators by their mere presence and create safe havens for prey who are ambivalent to human presence to forage. This is known as the human shield hypothesis (sensu Berger 2007). However, lack of data across trophic levels makes it difficult to test this hypothesis (Reimers, Lund, and Ergon 2011; Ward et al. 1997; Uchida and Blumstein 2021).

In addition, a large number of studies in our analysis showed no significant effect of active non-lethal interactions on foraging (n = 10) and vigilance (n = 9) behavior, i.e., the effect sizes were close to 0. We hypothesise that this subdued response to humans may be attributed to habituation as a function of frequency of interaction. Many studies have pointed to substantial habituation to tourist interactions, such as with mammals in the African Savannah (Knight 2009), killer whale and Hector's dolphin interactions with whale watchers (Bejder et al. 1999, Williams et al. 2002) and penguin interactions with researchers (Shelton et al. 2004). More specifically, Uchida and Blumstein (2021) showed that yellow bellied marmots (*Marmota flaviventer*) in highly disturbed forests grew habituated to humans after repeated exposure and reduced their flight initiation distances; however, marmots in groups that were habituated gained less body mass over the duration of the study. On the other hand, mammal population densities are on the whole higher near human settlements, indicating that the benefits of associated resources may outweigh the negative effects of exposure (Tucker et al, 2021). Overall, there is a need to examine both the immediate effects of non-lethal human disturbance as well as the long-term positive or negative fitness consequences of such exposure.

3. Passive non-lethal interactions

Humans are the most elaborate ecosystem engineer on the planet, completely altering environments to make it more suitable for themselves. Predation risk is highly dependent on whether animals perceive these environments as safe or threatening (Wirsing et al. 2021). Van der Kolk et al. (2024) found that various shore birds altered their flight responses based on the frequency of airplanes over their nesting areas, with intermittent disturbance having the greatest negative effect. Similarly, multiple studies have highlighted the negative effects of ship sonar on cetacean behavior (see Harris et al. 2018 for a meta-analysis and review).

By altering habitats, human development alters the distribution of risk in the landscape. For example, roads can clear away thickets or other cover that ambush predators use thus making it "safer" for some prey species. Thus, one would expect prey species to congregate around roads and invest more in foraging. We see evidence for this in guancos (*Lama guanicoe*) and mice (*Peromyscus leucopus*) (Cappa et al. 2017; Grignolio et al. 2011). Mehlhoop et al. (2002) showed that moose (*Rangifer tarandus*) in Norwegian forests avoid human infrastructure in areas where hunting is permitted. On the other hand, Cappa, Giannoni, and Borghi (2017) showed that guancos (*Lama guanicoe*) in large groups were less vigilant and foraged closer to roads in an

Argentine wildlife reserve and thus may perceive roads as beneficial. Widespread habitat alteration has also led to temporal shifts in activity of multiple taxa globally (Gaynor et al. 2018).

Conflict with predator species can also make human settlements safe spaces for consumers to forage (eg. wild boar, Podgorski et al. 2013). Conversely, development may also open up habitats making it more difficult for prey individuals to escape predation (Smith, et al. 2016). Human development may also pose a direct threat to animals, especially in the case of conflict with livestock or roadkill (Loss et al. 2015, van der Kolk et al. 2024, Harris et al. 2018). Across 468 mammal species, Tucker et al (2021) find an increase in population densities near human settlements, and speculate that more resources and lower competition/predation may lead to this pattern. However, they do caution that while some species may get benefits, many others be negatively affected and decline. Similarly, our meta-analysis found considerable variation across studies on the effect of passive interactions on foraging, vigilance and movement behaviors (Figure 4). Thus, the response of animals to passive interactions with roads and human settlements may be highly context and species dependent.

4. Context dependence of the behavioural effects human interactions on animals

Animals can make mistakes in how they respond behaviourally to human interactions (Smith et al. 2021), by overreacting or underreacting. Animals can overreact to non-lethal interactions leading to high energy investment and even chronic stress responses (e.g. (Blumstein 2003; Nunes et al. 2019; Westekemper et al. 2018; review: Larson et al. 2016). On the other hand, misunderstanding lethal interactions can lead to the death of the individual. Thus, there are a number of contingencies that may apply to the expression of risk avoidance and mitigation behaviours. For example, the openness of the habitat, predator traits such as habitat domain, hunting mode and fierceness, and prey body state are some important variables to consider (Schmitz et al. 2001, Wirsing et al. 2021). While all of these also apply to the human predator, there may be some additional considerations for a predictive framework (Smith et al. 2024).

i. Trophic level

Human hunters can augment existing predation risk from natural predators, create new predation risk or both depending on which animals they target (Supplementary Table B2). Hunters tend to disproportionately target predatory and larger species for their higher social and economic value. For example, marine apex predators such as sharks, barracuda and tuna are highly valuable in fish markets compared to consumer species such as sardines (Pauly et al. 1998; Jackson et al. 2001). Similarly, in many developed countries large herbivores such as deer are hunted for sport or culling (Pecorella et al. 2016). Thus, interactions with humans may be perceived differently across trophic levels.

When humans target top predators, they create new risk that these animals have not previously experienced. Predators may or may not be equipped to respond to new threats leading to many extirpations (e.g. Wolves in Yellowstone (Laundré, Hernández, and Altendorfet al. 2001), bears in Alaska (Merkle et al. 2013), puma in California and Florida (Nickel et al. 2021)). Thus, predators must respond as naive prey when targeted by humans. The severity and direction of the response may be proportional to the extent and duration of persecution by humans. Predators may be overly cautious around human hunters leading to greater missed opportunities. Alternatively, predators may not be cautious enough around humans leading to greater direct mortality (Smith et al. 2021). The direct removal of predator individuals and their behavioural responses to the risk of the human super-predator may have beneficial effects for consumers effectively subtracting predation risk for these animals (e.g. mesopredator release and population explosions of large herbivores, see Terbourg et al. 2015).

The majority of studies we found in our search focused on lower trophic levels and not predators (Appendix A). This may be because it is particularly difficult to observe foraging and vigilance behaviours in predators (but see Smith et al. (2017) for examples of human disturbance effects on *Puma concolor* foraging behaviour). We were unable to test our hypotheses regarding predator behavioural responses to humans in this meta – analysis, however, we highlight this as an important topic for future research. Incorporating other behaviours such as movement and habitat selection may allow us to gain further insights into how predators themselves respond to the threat of predation.

Humans may also compete with top predators by targeting consumers (eg. deer hunters in California). This may have a multiplicative effect on predation risk perceived by consumer individuals. Consumers may have fewer safe habitats to forage and thus may experience a higher energy cost of anti-predator strategies. There may also be mutualisms between predators and humans creating areas of higher predation success (corralling) or even subsidizing predator energy costs (cattle depredation). In a majority of studies, humans were not the only predator present. For example, humans compete with puma in the Santa Cruz Mountains of California, with wolves in parts of north America, and with bears in the arctic. Thus, hypotheses about multiplicative effects of human predation risk and competition with top predators may be testable in the field.

In some cases, humans may target multiple trophic levels simultaneously. Trawl fishing, for example, is particularly non-selective. It is difficult to determine the effects of such ubiquitous predation risk. Suraci et al. (2019) tested effects of lethal human interactions across multiple trophic levels in the Santa Cruz Mountains and found evidence for a behavioural cascade. To our knowledge, no other study has simultaneously tested behaviours across multiple trophic levels.

ii. Body mass

As with predators, larger animals may also be disproportionately targeted for economic reasons and as trophies. Larger and healthy animals are rarely targeted by predators and thus have little reason to invest in anti-predator behaviour. Thus, we expected the magnitude of effects to increase with the body mass of the study animal. This, however, was not the case in our analysis as the change in effect size was negligible across outcomes.

iii. History

The disproportionate targeting of apex predators has led to the local extirpation of many species in the global north. Though conservation efforts have led to the creation of no-take and no-hunting zones in the past few decades, a history of hunting may still affect how animals perceive humans in their environment (Clinchy et al. 2016). For example, pPlayback experiments of extirpated predators indicates that fear may persist across generations (Clinchy et al. 2016). However, the degree of response by animals may depend on a number of factors, starting from their own responses (whether innate or learned), nature of hunting, duration of hunting cessation, which species were historically targeted and the nature of current human interactions. Repeated exposure and learned tolerance may also play a role in response attenuation (Uchida and Blumstein, 2021). Thus, it may be worthwhile to investigate whether the animal response over time to the cessation of human activity, both lethal and non-lethal.

5. Using fear of humans for management

The fear of human hunters can also be valuable tool for conservation and management. Miller and Schmitz (2019) proposed a framework for reducing the conflict between large carnivores (*Panthera tigris*) and cattle herders in central India. They showed that by utilizing tigers' intrinsic fear of humans in the central Indian landscape and common human signs such as traps, fences and scents, conflict can be significantly reduced. Blackwell et al. (2016) proposed using fear induced by periodic playbacks of human noises to deter animals from roads and reduce the toll of road kill. Gaynor et al. (2021) proposed an applied ecology of fear framework for using non-consumptive behavioural effects of the human super predator for conservation and management. If indeed non-lethal cues work best when reinforced by actual lethal actions, a combination of human cues and periodic and regulated hunting may offer a viable model for the management of wild populations and the reduction of conflict.

V. Conclusions

The effects of natural animal predators on prey have been studied and debated for many decades (Lotka 1920; Sih 1984; Dill, Heithaus, and Walters 2003; Steneck 2012; S.L. Lima et al. 2021). It is clear that through their consumption of prey, natural predators create a dangerous environment to which prey respond (Lima and Dill 1990; Laundré 2010). Thus, a wide range of anti-predator responses have evolved and are induced in animals to minimize the probability of being killed (Lima and Dill 1990). Recent evidence suggests that the fear of predators itself even without direct threat of being killed changes prey responses (i.e. non-consumptive effects of predators), with potential consequences to fitness (Schmitz, Beckerman, and O'Brien 1997; Heithaus et al. 2008; Hawlena and Schmitz 2010; Clinchy, Sheriff, and Zanette 2013; Heithaus et al. 2008; Sheriff et al. 2020; Michael Clinchy, Sheriff, and Zanette 2013).

We have presented an extensive synthesis of the available literature on the effect of human interactions on animal behaviour. Our general conclusions and suggestions for future research are listed below:

1. While lethal interactions with humans have a profound effect on animal behaviour, there is mixed evidence of such effects from non-lethal interactions.
2. There is considerable variation in the response of animals to non-lethal interactions that has yet to be disentangled. Factors such as frequency of interactions, history of hunting, and trophic level may attenuate the response of animals to human disturbance.
3. The effects of human interactions on animal fitness and movement would be an important consideration for the management of wild populations.
4. Future research may benefit from contrasting humans as lethal predators with natural predators in the same space and across trophic levels, given the potential for compounding effects on animals and ecosystems.

Acknowledgments

Funding for this research was provided by the Prime Ministers Research Fellowship () to SD with some support from DBT-Wellcome Trust India Alliance grant (IA/I/19/2/504639) to MT. We would like to thank Dr. Nitya Mohanty and Dr. Daniel Noble for their invaluable inputs during the drafting of this manuscript.

References

Atwood, TB., Madin, EMP, Harborne, AR, Hammill, E., Luiz, OJ., Ollivier, QR., Roelfsema, CM., Macreadie, PI., and Lovelock, CE.. 2018. "Predators Shape Sedimentary Organic Carbon Storage in a Coral Reef Ecosystem." *Frontiers in Ecology and Evolution* 6 (August):110. https://doi.org/10.3389/fevo.2018.00110.

Bejder, L., S. M. Dawson, and J. A. Harraway. 1999. "Responses by Hector's Dolphins to Boats and Swimmers in Porpoise Bay, New Zealand." *Marine Mammal Science* 15 (3): 738–50. https://doi.org/10.1111/j.1748-7692.1999.tb00840.x.

Benhaiem, S., Delon, M. , Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.J.M., Morellet, N., and Verheyden, H.. 2008. "Hunting Increases Vigilance Levels in Roe Deer and Modifies Feeding Site Selection." *Animal Behaviour* 76 (3): 611–18. https://doi.org/10.1016/j.anbehav.2008.03.012.

Benson, JF, Mahoney, PJ, and Patterson, BR. 2015. "Spatiotemporal Variation in Selection of Roads Influences Mortality Risk for Canids in an Unprotected Landscape." *OIKOS* 124 (12): 1664–73. https://doi.org/10.1111/oik.01883.

Berger, J. 2007. "Fear, Human Shields and the Redistribution of Prey and Predators in Protected Areas." *BIOLOGY LETTERS* 3 (6): 620–23. https://doi.org/10.1098/rsbl.2007.0415.

Bhardwaj, M., Lodnert, D., Olsson, M., Winsvold, A., Eilertsen, S.M., Kjellander, P., and Seiler, A.. 2022. "Inducing Fear Using Acoustic Stimuli—A Behavioral Experiment on Moose (Alces Alces) in Sweden." *Ecology and Evolution* 12 (11). https://doi.org/10.1002/ece3.9492.

Blackwell, BF, DeVault, TL , Fernandez-Juricic, E, Gese, EM, Gilbert-Norton, L, and Breck, SW. 2016. "No Single Solution: Application of Behavioural Principles in Mitigating Human-Wildlife Conflict." *Animal Behaviour* 120:245–54.

https://doi.org/10.1016/j.anbehav.2016.07.013.

Blumstein, DT. 2003. "Flight-Initiation Distance in Birds Is Dependent on Intruder Starting Distance." *Journal of Wildlife Management* 67 (4): 852–57. https://doi.org/10.2307/3802692.

Boyle, S.A., and Samson, F.B. 1985. "Effects of Nonconsumptive Recreation on Wildlife: A Review." *Wildlife Society Bulletin (1973-2006)* 13 (2): 110–16.

Brown, CL, Hardy, A.R., Barber, J.R., Fristrup, K.M., Crooks, K.R., and Angeloni, L.M. 2012. "The Effect of Human Activities and Their Associated Noise on Ungulate Behavior." *PLOS One* 7 (7). https://doi.org/10.1371/journal.pone.0040505.

Brown, J.S., and Kotler, B.P. 2004. "Hazardous Duty Pay and the Foraging Cost of Predation: Foraging Cost of Predation." *Ecology Letters* 7 (10): 999–1014. https://doi.org/10.1111/j.1461-0248.2004.00661.x.

Cappa, FM, SM Giannoni, and CE Borghi. 2017. "Effects of Roads on the Behaviour of the Largest South American Artiodactyl (Lama Guanicoe) in an Argentine Reserve." *ANIMAL BEHAVIOUR* 131:131–36. https://doi.org/10.1016/j.anbehav.2017.07.020.

Chamberlain, A.A., Hovick, S.M., Dibble, C.J., Rasmussen, N.L., Van Allen, B.G., Maitner, B.S., Ahern, J.R., et al. 2012. "Does Phylogeny Matter? Assessing the Impact of Phylogenetic Information in Ecological Meta-analysis." *Ecology Letters* 15 (6): 627–36. https://doi.org/10.1111/j.1461-0248.2012.01776.x.

Cinar, O., Nakagawa, S., and Viechtbauer, W. 2022. "Phylogenetic Multilevel Meta-analysis: A Simulation Study on the Importance of Modelling the Phylogeny." *Methods in Ecology and Evolution* 13 (2): 383–95. https://doi.org/10.1111/2041-210X.13760.

Clinchy, M., Sheriff, M.J., and Zanette, L.Y. 2013. "Predator-Induced Stress and the Ecology of Fear." *Functional Ecology* 27 (1): 56–65. https://doi.org/10.1111/1365-2435.12007.

Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C., and Macdonald, D.W. 2016. “Fear of the Human ‘Super Predator’ Far Exceeds the Fear of Large Carnivores in a Model Mesocarnivore.” *Behavioral Ecology* 27 (6): 1826–32.

Crawford, D.A., Conner, L.M., Clinchy, M., Zanette, L.Y., and Cherry, M.J. 2022. “Prey Tells, Large Herbivores Fear the Human ‘Super Predator.’” *Oecologia* 198 (1): 91–98. https://doi.org/10.1007/s00442-021-05080-w.

Crosmary, W.G., Makumbe, P., Cote, S.D., and Fritz, H. 2012. “Vulnerability to Predation and Water Constraints Limit Behavioural Adjustments of Ungulates in Response to Hunting Risk.” *Animal Behaviour* 83 (6): 1367–76. https://doi.org/10.1016/j.anbehav.2012.03.004.

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E., and Wilmers, C.C. 2009. “Human Predators Outpace Other Agents of Trait Change in the Wild.” *Proceedings of the National Academy of Sciences* 106 (3): 952–54. https://doi.org/10.1073/pnas.0809235106.

Darimont, C.T., Fox, C.H., Bryan, H.M., and Reimchen, T.E. 2015. “The Unique Ecology of Human Predators.” *Science* 349 (6250): 858–60. https://doi.org/10.1126/science.aac4249.

Darimont, C.T., Cooke, R., Bourbonnais, M.L., Bryan, H.M., Carlson, S.M., Estes, J.A., Galetti, M., et al. 2023. “Humanity’s Diverse Predatory Niche and Its Ecological Consequences.” *Communications Biology* 6 (1): 609. https://doi.org/10.1038/s42003-023-04940-w.

Davis, D., Banks, S., Birtles, A., Valentine, P., and Cuthill, M. 1997. “Whale Sharks in Ningaloo Marine Park: Managing Tourism in an Australian Marine Protected Area.” *Tourism Management* 18 (5): 259–71. https://doi.org/10.1016/S0261-5177(97)00015-0.

Del Hoyo, J., Elliott, A., and Sargatal, J. 1992. *Handbook of the Birds of the World*. Vol. 1. Lynx

Edicions: Barcelona. http://www.aviornis.nl/uploads/media/Parelhoenders_in_Handbook_of_the_Birds_of_the_World_01.pdf.

Dill, L.M., Heithaus, M.R., and Walters, C.J. 2003. “Behaviorally Mediated Indirect Interactions in Marine Communities and Their Conservation Implications.” *Ecology* 84 (5): 1151–57. https://doi.org/10.1890/0012-9658(2003)084[1151:BMIIIM]2.0.CO;2.

Estes, J.A., Brashares, J.S., and Power, M.E. 2013. “Predicting and Detecting Reciprocity between Indirect Ecological Interactions and Evolution.” *The American Naturalist* 181 (Suppl 1): S76–99. https://doi.org/10.1086/668120.

Fernández-Juricic, E., Clavijo, M., Jiménez, M.D., Asensio, E., and Lucas, E. 2001. “Bird Tolerance to Human Disturbance in Urban Parks of Madrid (Spain): Management Implications.” *In Ecology of Urban Environments*. https://doi.org/10.1007/978-1-4615-1531-9_12.

Foo, Y.Z., O’Dea, R.E., Koricheva, J., Nakagawa, S., and Lagisz, M. 2021. “A Practical Guide to Question Formation, Systematic Searching and Study Screening for Literature Reviews in Ecology and Evolution.” *Methods in Ecology and Evolution* 12 (9): 1705–20. https://doi.org/10.1111/2041-210X.13654.

Frid, A., and Dill, L.M. 2002. “Human-Caused Disturbance Stimuli as a Form of Predation Risk.” *Conservation Ecology* 6 (1). https://doi.org/10.5751/ES-00404-060111.

Gaynor, K.M., Cherry, M.J., Gilbert, S.L., Kohl, M.T., Larson, C.L., Newsome, T.M., Prugh, T.R., Suraci, J.P., Young, J.K., and Smith, J.A.. 2021. “An Applied Ecology of Fear Framework: Linking Theory to Conservation Practice.” *Animal Conservation* 24 (3): 308–

21. https://doi.org/10.1111/acv.12629.

Harrer, M., Cuijpers P., Furukawa, T.A., and Ebert, D.D.. 2021. *Doing Meta-Analysis With R: A Hands-On Guide*. 1st ed. Boca Raton, FL and London: Chapman & Hall/CRC Press. https://www.routledge.com/Doing-Meta-Analysis-with-R-A-Hands-On-Guide/Harrer-Cuijpers-Furukawa-Ebert/p/book/9780367610074.

Harris, C.M., Thomas, L., Falcone, E.A., Hildebrand, J., Houser, D., Kvadsheim, P.M., Lam, F.P.A., et al. 2018. “Marine Mammals and Sonar: Dose-Response Studies, the Risk-Disturbance Hypothesis and the Role of Exposure Context.” *JOURNAL OF APPLIED ECOLOGY* 55 (1): 396–404. https://doi.org/10.1111/1365-2664.12955.

Hawlena, D., and Schmitz, O.J.. 2010. “Herbivore Physiological Response to Predation Risk and Implications for Ecosystem Nutrient Dynamics.” *Proceedings of the National Academy of Sciences* 107 (35): 15503–7. https://doi.org/10.1073/pnas.1009300107.

Heithaus, M.R., Wirsing, A.J., Thomson, J.A., and Burkholder, D.A.. 2008. “A Review of Lethal and Non-Lethal Effects of Predators on Adult Marine Turtles.” *Journal of Experimental Marine Biology and Ecology* 356 (1–2): 43–51. https://doi.org/10.1016/j.jembe.2007.12.013.

Herberstein, M.E., McLean, E.L., Wolff J.O., Khan M.K., Smith K., Allen A.P., et al. 2022. “AnimalTraits - a Curated Animal Trait Database for Body Mass, Metabolic Rate and Brain Size.” *Scientific Data* 9 (1): 265. https://doi.org/10.1038/s41597-022-01364-9.

Jeremy, J.B.C., Kirby, M., Berger W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., et al. 2001. “Historical Overfishing and the Recent Collapse of Coastal Ecosystems.” *Science* 293 (5530): 629–37. https://doi.org/10.1126/science.1059199.

Jayakody, S., Sibbald, A.M., Gordon, I.J., and Lambin, X.. 2008. “Red Deer Cervus Elephus Vigilance Behaviour Differs with Habitat and Type of Human Disturbance.” *WILDLIFE BIOLOGY* 14 (1): 81–91. https://doi.org/10.2981/0909-6396(2008)14[81:RDCEVB]2.0.CO;2.

Knight, J. 2009. “Making Wildlife Viewable: Habituation and Attraction.” *Society & Animals* 17 (2): 167–84. https://doi.org/10.1163/156853009X418091.

Ladle, A., Avgar, T., Wheatley, M., Stenhouse, M.B., Nielsen, S.E., and Boyce, M.S.. 2019. “Grizzly Bear Response to Spatio-Temporal Variability in Human Recreational Activity.” *JOURNAL OF APPLIED ECOLOGY* 56 (2): 375–86. https://doi.org/10.1111/13652664.13277.

Courtney L., Reed, S.E., Merenlender, A.M., and Crooks, K.R.. 2016. “Effects of Recreation on Animals Revealed as Widespread through a Global Systematic Review.” *PLOS ONE* 11 (12): e0167259. https://doi.org/10.1371/journal.pone.0167259.

Laundré, J.W. 2010. “Behavioral Response Races, Predator–Prey Shell Games, Ecology of Fear, and Patch Use of Pumas and Their Ungulate Prey.” *Ecology* 91 (10): 2995–3007. https://doi.org/10.1890/08-2345.1.

Laundré, J.W., Hernández, L., and Altendorf, K.B.. 2001. “Wolves, Elk, and Bison: Reestablishing the ‘Landscape of Fear’ in Yellowstone National Park, U.S.A.” *Canadian Journal of Zoology* 79 (8): 1401–9. https://doi.org/10.1139/z01-094.

Lima, S.L., Gámez, S., Arringdale, N., and Harris, N.C. 2021. “Vigilance Response of a Key Prey Species to Anthropogenic and Natural Threats in Detroit.” *Frontiers in Ecology and Evolution* 9. https://doi.org/10.3389/fevo.2021.570734.

Lima, S.L., and Dill, L.M. 1990. “Behavioral Decisions Made under the Risk of Predation: A Review and Prospectus.” *Canadian Journal of Zoology* 68 (4): 619–40. https://doi.org/10.1139/z90-092.

Lintulaakso, K. 2021. “MammalBase — Database of Traits, Measurements and Diets of the Species in Class Mammalia.” Zenodo. https://doi.org/10.5281/ZENODO.7462864.

Lipsey, M.W., and Wilson, D.B. 2001. *Practical Meta-Analysis*. Applied Social Research Methods Series, v. 49. Thousand Oaks, Calif: Sage Publications.

Loehr, J., Kovanen, M., Carey, J., Hogmander, H., Jurasz, C., Karkkainen, S., Suhonen, J., and Ylonen, H.. 2005. “Gender- and Age-Class-Specific Reactions to Human Disturbance in a Sexually Dimorphic Ungulate.” *CANADIAN JOURNAL OF ZOOLOGY* 83 (12): 1602–7. https://doi.org/10.1139/Z05-162.

Loss, S.R., Will, T., and Marra, P.P. 2015. “Direct Mortality of Birds from Anthropogenic Causes.” *Annual Review of Ecology, Evolution, and Systematics* 46 (Volume 46, 2015): 99–120. https://doi.org/10.1146/annurev-ecolsys-112414-054133.

Lotka, A.J. 1920. “Analytical Note on Certain Rhythmic Relations in Organic Systems.” *Proceedings of the National Academy of Sciences* 6 (7): 410–15. https://doi.org/10.1073/pnas.6.7.410.

Madin, E.M.P., Gaines, S.D., Madin, J.S., and Warner, R.R. 2010. “Fishing Indirectly Structures Macroalgal Assemblages by Altering Herbivore Behavior.” *The American Naturalist* 176 (6): 785–801. https://doi.org/10.1086/657039.

Mehlhoop, A.C., Van Moorter, B., Rolandsen, C.M., Hagen,, D. Granhus, A., Eriksen, R., Ringsby, T.H., and Solberg, E.J. 2022. “Moose in Our Neighborhood: Does Perceived

Hunting Risk Have Cascading Effects on Tree Performance in Vicinity of Roads and Houses?" *ECOLOGY AND EVOLUTION* 12 (4). https://doi.org/10.1002/ece3.8795.

Merkle, J.A., Robinson, H.S., Krausman, P.R., and Alaback, P.. 2013. "Food Availability and Foraging near Human Developments by Black Bears." *JOURNAL OF MAMMALOGY* 94 (2): 378–85. https://doi.org/10.1644/12-MAMM-A-002.1.

Mikolajewicz, N., and Komarova, S.V. 2019. "Meta-Analytic Methodology for Basic Research: A Practical Guide." *Frontiers in Physiology* 10 (March):203. https://doi.org/10.3389/fphys.2019.00203.

Miller, JRB, and Schmitz, OJ. 2019. "Landscape of Fear and Human-Predator Coexistence: Applying Spatial Predator-Prey Interaction Theory to Understand and Reduce Carnivore-Livestock Conflict." *BIOLOGICAL CONSERVATION* 236:464–73. https://doi.org/10.1016/j.biocon.2019.06.009.

Moller, AP. 2008. "Flight Distance of Urban Birds, Predation, and Selection for Urban Life." *BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY* 63 (1): 63–75. https://doi.org/10.1007/s00265-008-0636-y.

Moller, AP. 2012. "Urban Areas as Refuges from Predators and Flight Distance of Prey." *BEHAVIORAL ECOLOGY* 23 (5): 1030–35. https://doi.org/10.1093/beheco/ars067.

Moller, AP, Grim T., Ibanez-Alamo JD, Marko, G, and Tryjanowski, P. 2013. "Change in Flight Initiation Distance between Urban and Rural Habitats Following a Cold Winter." *BEHAVIORAL ECOLOGY* 24 (5): 1211–17. https://doi.org/10.1093/beheco/art054.

Mols, B, Lambers, E, Cromsigt, JPGM Kuijper, DPJ, and Smit, C. 2022. "Recreation and Hunting Differentially Affect Deer Behaviour and Sapling Performance." *OIKOS* 2022

(1). https://doi.org/10.1111/oik.08448.

Montero-Quintana, AN, Vazquez-Haikin, JA, Merkling, T, Blanchard, P, and Osorio-Beristain, M. 2020. "Ecotourism Impacts on the Behaviour of Whale Sharks: An Experimental Approach." *ORYX* 54 (2): 270–75. https://doi.org/10.1017/S0030605318000017.

Nakagawa, S, Lagisz, M, Jennions, MD, Koricheva, J, Noble, DWA, Parker, TH, Sánchez-Tójar, A, Yang, Y, and O'Dea, RE. 2022. "Methods for Testing Publication Bias in Ecological and Evolutionary Meta-Analyses." *Methods in Ecology and Evolution* 13 (1): 4–21. https://doi.org/10.1111/2041-210X.13724.

Nevin, OT, and Gilbert, BK. 2005. "Measuring the Cost of Risk Avoidance in Brown Bears: Further Evidence of Positive Impacts of Ecotourism." *BIOLOGICAL CONSERVATION* 123 (4): 453–60. https://doi.org/10.1016/j.biocon.2005.01.007.

Newey, P. 2007. "Foraging Behaviour of the Common Myna (Acridotheres Tristis) in Relation to Vigilance and Group Size." *EMU* 107 (4): 315–20. https://doi.org/10.1071/MU06054.

Nickel, BA, Suraci, JP, Nisi, AC, and Wilmers, CC. 2021. "Energetics and Fear of Humans Constrain the Spatial Ecology of Pumas." *Proceedings of the National Academy of Science of the United States of America* 118 (5).

Noble, D.W. A., Pottier, P, Lagisz, M, Burke, S, Drobniak, SM, O'Dea, RE, and Nakagawa, S. 2022. "Meta-Analytic Approaches and Effect Sizes to Account for 'Nuisance Heterogeneity' in Comparative Physiology." *Journal of Experimental Biology* 225 (Suppl_1): jeb243225. https://doi.org/10.1242/jeb.243225.

Noble, D.W.A., Lagisz, M, O'dea, RE, and Nakagawa, S. 2017. "Nonindependence and Sensitivity Analyses in Ecological and Evolutionary Meta-analyses." *Molecular Ecology*

26 (9): 2410–25. https://doi.org/10.1111/mec.14031.

Nunes, JACC, Blumstein, DT, Giglio, VJ, Barros, F, and Quimbayo, JP. 2019. “Reef Fish Antipredator Behavior in Remote Islands Does Not Reflect Patterns Seen in Coastal Areas.” Ethology, Ecology and Evolution 31 (6): 557–67. https://doi.org/10.1080/03949370.2019.1636141.

O’Dea, R.E., Lagisz, M, Jennions, MD, Koricheva, J, Noble, DWA, Parker, TH, Gurevitch, J, et al. 2021. “Preferred Reporting Items for Systematic Reviews and Meta-analyses in Ecology and Evolutionary Biology: A PRISMA Extension.” *Biological Reviews* 96 (5): 1695–1722. https://doi.org/10.1111/brv.12721.

Ordiz, A, Stoen, OG, Saebo, S, Sahlen, V, Pedersen, BE, Kindberg, J, and Swenson, JE. 2013. “Lasting Behavioural Responses of Brown Bears to Experimental Encounters with Humans.” Journal of Applied Ecology50 (2): 306–14. https://doi.org/10.1111/1365-2664.12047.

Oriol-Cotterill, A, Valeix, M, Frank, LG, Riginos, C, and Macdonald, DW. 2015. “Landscapes of Coexistence for Terrestrial Carnivores: The Ecological Consequences of Being Downgraded from Ultimate to Penultimate Predator by Humans.” *OIKOS* 124 (10): 1263–73. https://doi.org/10.1111/oik.02224.

Ouzzani, M, Hammady, H, Fedorowicz, Z, and Elmagarmid, A. 2016. “Rayyan—a Web and Mobile App for Systematic Reviews.” *Systematic Reviews* 5 (1): 210. https://doi.org/10.1186/s13643-016-0384-4.

Page, MJ., McKenzie, JE, Bossuyt, PM, Boutron, I, Hoffmann, TC, Mulrow, CD, Shamseer, L, et al. 2021. “The PRISMA 2020 Statement: An Updated Guideline for Reporting Systematic

Reviews.” *BMJ* 372 (March):n71. https://doi.org/10.1136/bmj.n71.

Pangle, WM, and Holekamp, KE. 2010. “Lethal and Nonlethal Anthropogenic Effects on Spotted Hyenas in the Masai Mara National Reserve.” Journal of Mammology 91 (1): 154–64. https://doi.org/10.1644/08-mamm-a-359r.1.

Papouchis, C.M., Singer, F.J., and Sloan, W.B. 2001. “Responses of Desert Bighorn Sheep to Increased Human Recreation.” *Journal of Wildlife Management*. https://doi.org/10.2307/3803110.

Pauly, D, Christensen, V, Dalsgaard, J, Froese, R, and Torres, F. 1998. “Fishing Down Marine Food Webs.” *Science* 279 (5352): 860–63. https://doi.org/10.1126/science.279.5352.860.

Pecorella, I, Ferretti, F, Sforzi, A, and Macchi, E. 2016. “Effects of Culling on Vigilance Behaviour and Endogenous Stress Response of Female Fallow Deer.” Wildlife Research 43 (3): 189–96. https://doi.org/10.1071/WR15118.

Picardi, S, Basille, M, Peters, W, Ponciano, JM, Boitani, L, and Cagnacci F. 2019. “Movement Responses of Roe Deer to Hunting Risk.” Journal of Wildlife Management 83 (1): 43–51. https://doi.org/10.1002/jwmg.21576.

Podgorski, T, Bas, G, Jedrzejewska, B, Sonnichsen, L, Sniezko, S, Jedrzejewski, S, and Okarma, H. 2013. “Spatiotemporal Behavioral Plasticity of Wild Boar (Sus Scrofa) under Contrasting Conditions of Human Pressure: Primeval Forest and Metropolitan Area.” Journal of Mammology 94 (1): 109–19. https://doi.org/10.1644/12-MAMM-A-038.1.

Price, M. 2008. “The Impact of Human Disturbance on Birds: A Selective Review.” *Australian Zoologist* 34:163–96. https://doi.org/10.7882/fs.2008.023.

Proudman, NJ, Churski, M, Bubnicki, JW, Nilsson, JA, and Kuijper, DPJ. 2021. “Red Deer

Allocate Vigilance Differently in Response to Spatio-Temporal Patterns of Risk from Human Hunters and Wolves." *Wildlife Research* 48 (2): 163–74. https://doi.org/10.1071/WR20059.

R Core Team. 2024. "R: A Language and Environment for Statistical Computing." Manual. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rainer, F. and Pauly, D. 2010. "FishBase." Fisheries Centre, University of British Columbia Los Baños, Philippines.

Reimers, E, Lund, S, and Ergon, T. 2011. "Vigilance and Fright Behaviour in the Insular Svalbard Reindeer (Rangifer Tarandus Platyrhynchus)." *Canadian Journal of Zoology* 89 (8): 753–64. https://doi.org/10.1139/Z11-040.

Sbragaglia, V, Morroni, L, Bramanti, L, Weitzmann, B, Arlinghaus, R, and Azzurro, E. 2018. "Spearfishing Modulates Flight Initiation Distance of Fishes: The Effects of Protection, Individual Size, and Bearing a Speargun." *ICES Journal of Marine Sciences* 75 (5): 1779–89. https://doi.org/10.1093/icesjms/fsy059.

Schmitz, OJ, Beckerman, AP, and O'Brien, KM. 1997. "Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Trophic Interactions" *Ecology* 78 (6).

Shannon, G, Angeloni, LM, Wittemyer, G, Fristrup, GM, and Crooks, KR. 2014. "Road Traffic Noise Modifies Behaviour of a Keystone Species." *Animal Research* 94:135–41. https://doi.org/10.1016/j.anbehav.2014.06.004.

Shelton, E. J., J. E. S. Higham, and P. Seddon. "Habituation." *penguin research and ecotourism: some thoughts from left field. New Zealand Journal of Zoology* 31, no. 1 (2004): 119.

Sheriff, MJ., Peacor, SD, Hawlena, D, and Thaker, M. 2020. "Non-consumptive Predator Effects on Prey Population Size: A Dearth of Evidence." Edited by Jean-Michel Gaillard. *Journal of Animal Ecology* 89 (6): 1302–16. https://doi.org/10.1111/1365-2656.13213.

Sih, A. 1984. "The Behavioral Response Race Between Predator and Prey." *The American Naturalist* 123 (1): 143–50. https://doi.org/10.1086/284193.

Smith, J.A., Wang Y, and Wilmers, CC. 2016. "Spatial Characteristics of Residential Development Shift Large Carnivore Prey Habits." *Journal of Wildlife Management* 80 (6): 1040–48. https://doi.org/10.1002/jwmg.21098.

Smith, JA., Gaynor, KM, and Suraci, JP. 2021. "Mismatch Between Risk and Response May Amplify Lethal and Non-Lethal Effects of Humans on Wild Animal Populations." *Frontiers in Ecology and Evolution* 9 (March):604973. https://doi.org/10.3389/fevo.2021.604973.

Smith, JA., McDaniels, ME, Peacor, SD, Bolas, EC, Cherry, MJ, Dorn, NJ, Feldman, OK, et al. 2024. "Population and Community Consequences of Perceived Risk from Humans in Wildlife." *Ecology Letters* 27 (6): e14456. https://doi.org/10.1111/ele.14456.

Stansell, HM, Blumstein, DT, Yeh PJ, and Nonacs P. 2022. "Individual Variation in Tolerance of Human Activity by Urban Dark-Eyed Juncos (Junco Hyemalis)." *Wilson Journal of Ornithology* 134 (1): 43–51. https://doi.org/10.1676/21-00001.

Steneck, RS. 2012. "Apex Predators and Trophic Cascades in Large Marine Ecosystems: Learning from Serendipity." *Proceedings of the National Academy of Sciences* 109 (21): 7953–54. https://doi.org/10.1073/pnas.1205591109.

Suraci, JP, Clinchy, M, Zanette, LY, and Wilmers, CC. 2019. "Fear of Humans as Apex Predators Has Landscape-Scale Impacts from Mountain Lions to Mice." *Ecology Letters* 22

(10): 1578–86. https://doi.org/10.1111/ele.13344.

Suraci, JP, Smith, JA, Clinchy, M, Zanette, LY, and Wilmers, CC. 2019. “Humans, but Not Their Dogs, Displace Pumas from Their Kills: An Experimental Approach.” Scientific Reports 9. https://doi.org/10.1038/s41598-019-48742-9.

Tran, DSC, Langel, KA, Thomas, MJ, and Blumstein, DT. 2016. “Spearfishing-Induced Behavioral Changes of an Unharvested Species inside and Outside a Marine Protected Area.” Current Zoology 62 (1): 39–44. https://doi.org/10.1093/cz/zov006.

Treves, A, and Naughton-Treves, L. 1999. “Risk and Opportunity for Humans Coexisting with Large Carnivores.” *Journal of Human Evolution* 36 (3): 275–82. https://doi.org/10.1006/jhev.1998.0268.

Tucker, M. A., Santini, L., Carbone, C., & Mueller, T. (2021). Mammal population densities at a global scale are higher in human-modified areas. Ecography, 44(1), 1-13.

Uchida, K, and Blumstein, DT. 2021. “Habituation or Sensitization? Long-Term Responses of Yellow-Bellied Marmots to Human Disturbance.” *Behavioral Ecology* 32 (4): 668–78. https://doi.org/10.1093/beheco/arab016.

van der Kolk, H., Allen, M., Bruno J., and van de Pol, M. 2024. “Frequency-Dependent Tolerance to Aircraft Disturbance Drastically Alters Predicted Impact on Shorebirds.” *Ecology Letters* 27 (6): e14452. https://doi.org/10.1111/ele.14452.

Ward, C, and Low, B.S. 1997. “Predictors of Vigilance for American Crows Foraging in an Urban Environment.” *The Wilson Journal of Ornithology*.

Westekemper K., Reinecke, H., Signer, J., Meißner, M., et al. 2018. “Stay on Trails - Effects of Human Recreation on the Spatiotemporal Behavior of Red Deer Cervus Elaphus in a

German National Park." *Wildlife Biology*. https://doi.org/10.2981/wlb.00403.

Williams, Rob, Andrew W. Trites, and David E. Bain. 2002. "Behavioural Responses of Killer Whales (Orcinus Orca) to Whale-Watching Boats: Opportunistic Observations and Experimental Approaches." *Journal of Zoology* 256 (2): 255–70. https://doi.org/10.1017/S0952836902000298.

Wirsing, AJ., Heithaus, MR, Brown, JS, Kotler, BP, and Schmitz, OJ. 2021. "The Context Dependence of Non-consumptive Predator Effects." Edited by Jonathan Chase. *Ecology Letters* 24 (1): 113–29. https://doi.org/10.1111/ele.13614.

Figures and tables

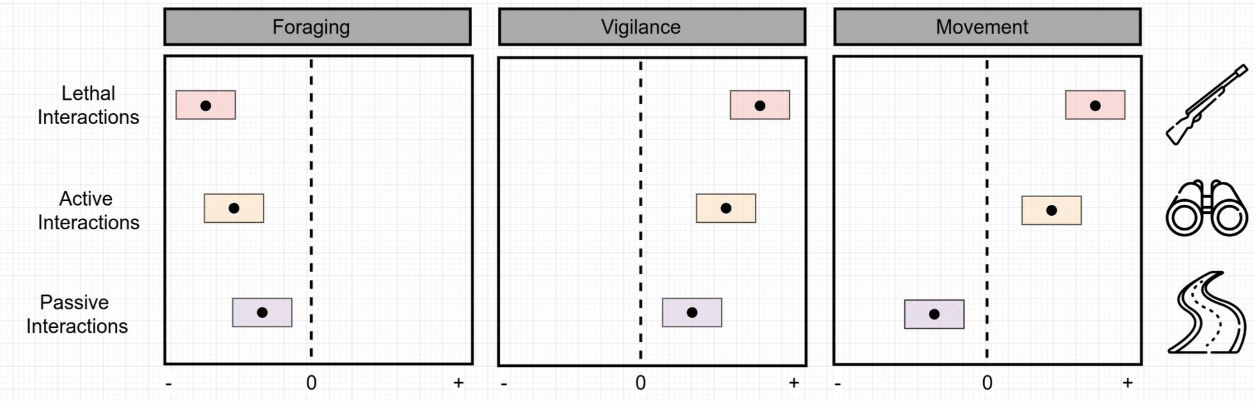
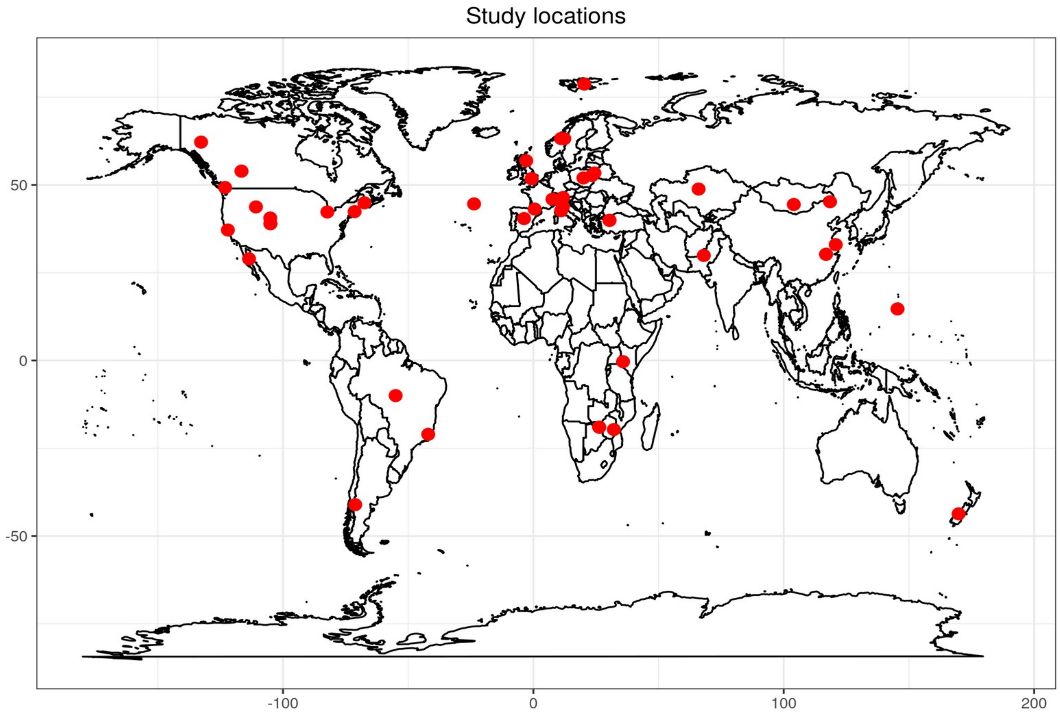


Figure 1: The different scenarios in which humans interact with animals in wild spaces and the hypothesised consequences on animal behavior. We expect a gradient of response with the strongest behavioral changes resulting from lethal interactions with humans, followed by active interactions and passive interactions. The scenarios are: a) A hunter that targets top predators (top) b) A group of ecotourists watching animals in their natural habitat (middle) c) A road cutting across a natural habitat (bottom).



945 **Figure 2:** Geographical distribution of studies included in the systematic review.

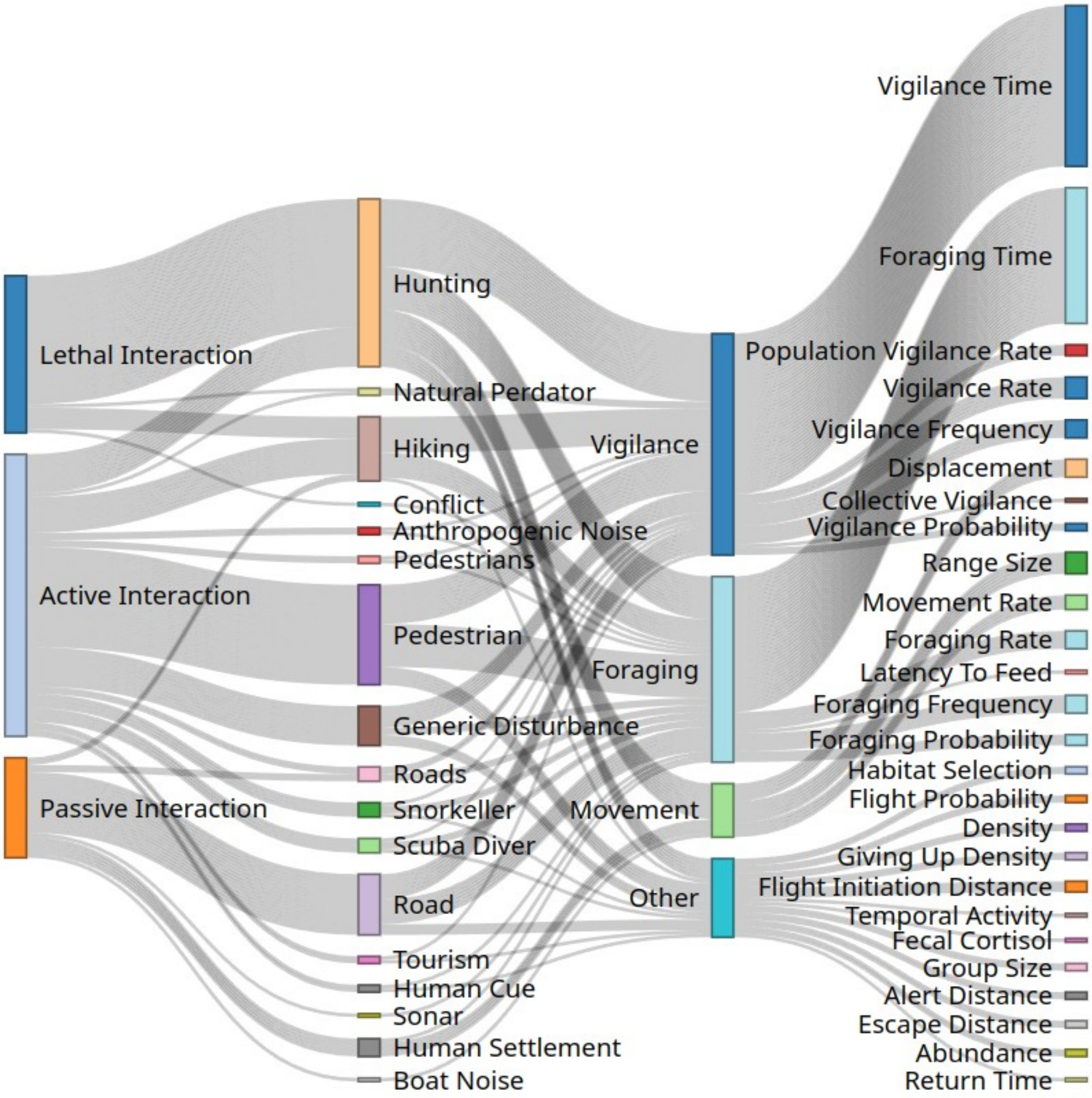


Figure 3: Distribution of included studies across type of interaction, treatment, behavior and measured outcome (in order).

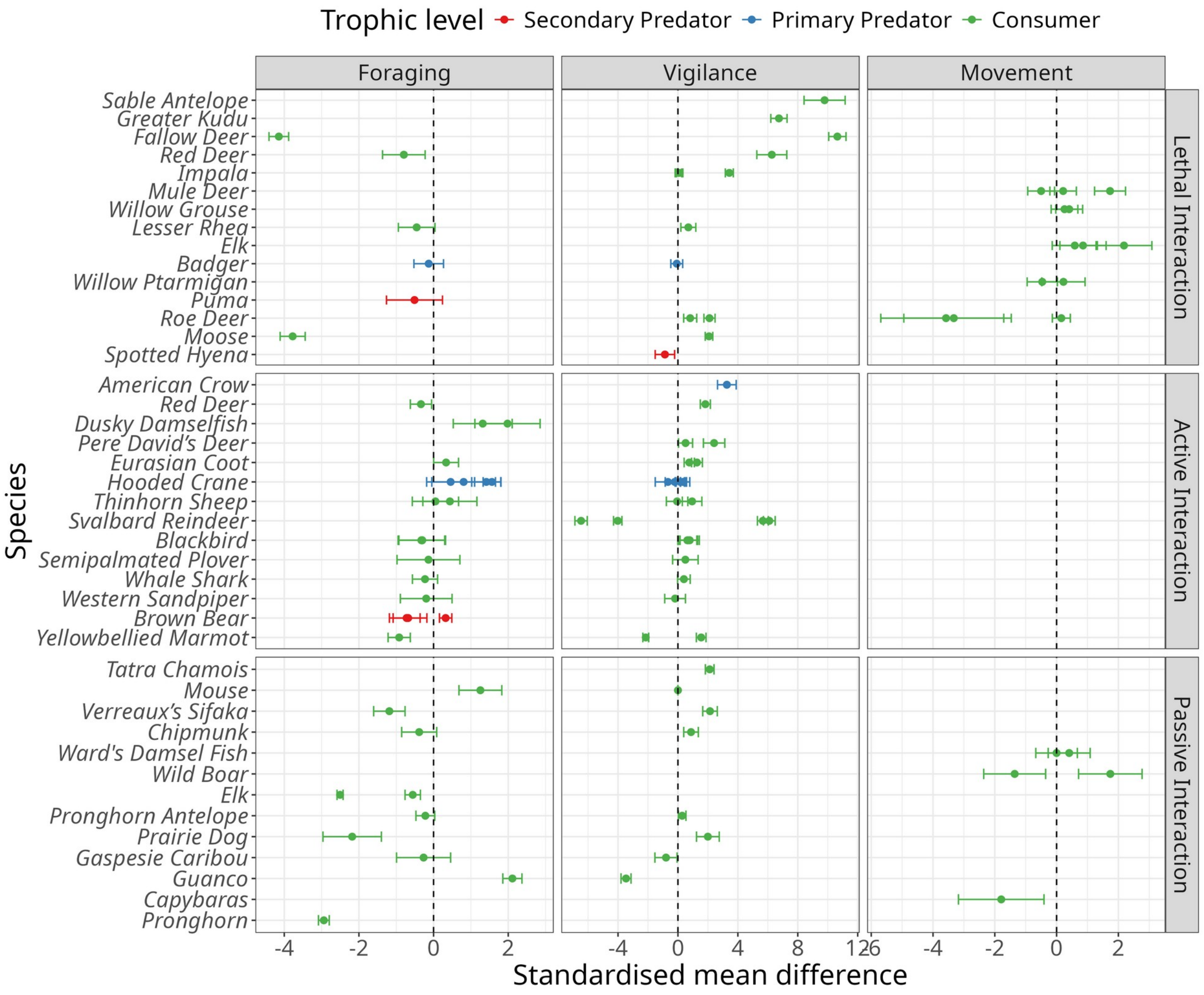


Figure 4: The effect of human disturbance (lethal, active disturbance, passive disturbance) across taxa and trophic levels. Negative values on the x-axis indicate a reduction in that behaviour, whereas positive values indicate an increase in that behaviour, relative to control conditions where no human activity is present.

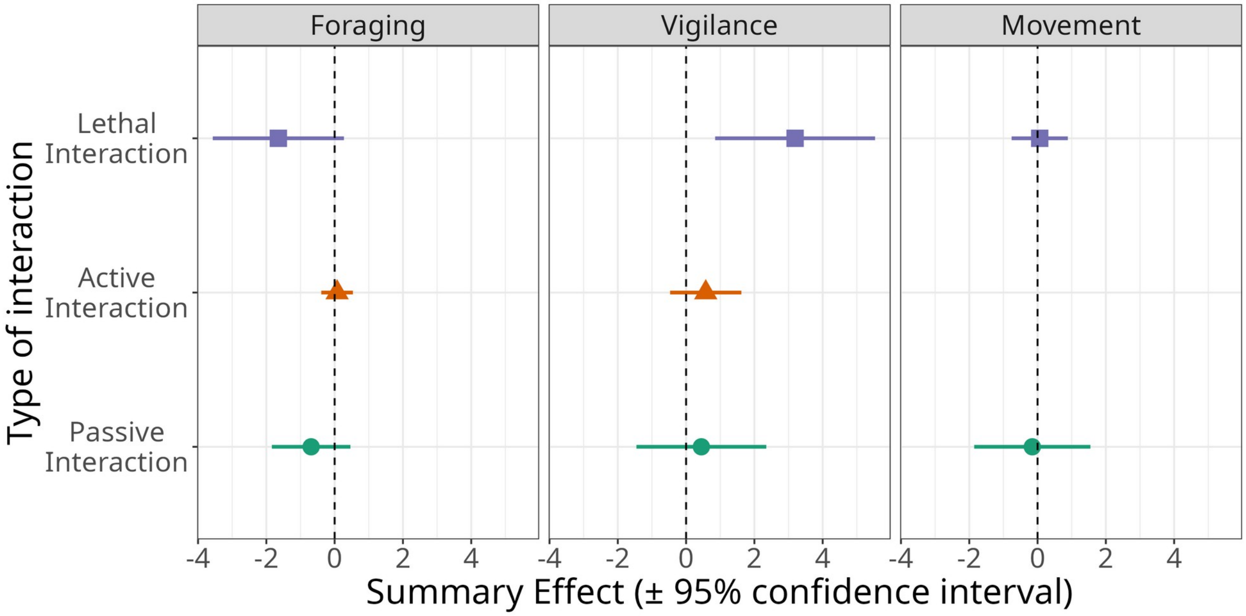


Figure 5: Summary effect of human interactions on foraging, movement, and vigilance behaviour across studies included in this meta-analysis. For movement, active disturbance was excluded due to low sample size.