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Applied ecology of fear: A meta-analysis on the potential of facilitating human-wildlife coexistence through nonlethal tools

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Abstract

1. The term "applied ecology of fear" was recently introduced to describe the growing research field that applies the theory of the ecology of fear to manage wildlife behaviour. The management goal is to drive targeted species spatially and temporally away from areas of human interest by inducing cues from real or simulated predators to reduce human-wildlife conflict.
2. We aimed to quantify, through a meta-analysis, if prey anti-predator response would vary among field trials versus pen-based studies, predator cue types, predator hunting style and prey feeding type, and be stronger in response to larger predators relative to the prey's size. We also explored what studies found in terms of wildlife habituation to cues.
3. We used species belonging to the Cervidae family as a case study since deer are among the group of species with the highest degree of human-wildlife conflict. We retrieved 114 studies from online databases and collected information from 39 of those studies that fitted our research scope.
4. We found that acoustic cues more frequently led to an anti-predator response in deer than olfactory or visual cues. Neither predator hunting strategy nor deer feeding strategy or type of study (free-ranging or pen-based animals) influenced the extent to which deer responded to cues. Deer more frequently responded to cues that belonged to a larger predator relative to their size. Habituation was reported in less than one-third of the studies, with a study period ranging from 1 to 90 days, and occurred as soon as 7 days after the start of the study on average.
5. Our meta-analysis suggested that acoustic cues hold most potential as a tool to manage deer behaviour. These findings support the development of applied ecology of fear tools that introduce predator cues to reduce human-wildlife conflicts. Major knowledge gaps remain that limit the effective use of such tools in wildlife management and future research should focus on improving our understanding of habituation to cues, on comparing the effectiveness of different types of cues,

on simultaneously using a combination of cue types, and on testing cues at spatial–temporal scales of actual land-uses.

KEYWORDS
Cervid, consumer-resource interactions, habituation, landscape of fear, predation, predator cues, wildlife behaviour, wildlife management

1 | INTRODUCTION

Several wildlife species are increasing in numbers and expanding in range across large areas of the northern hemisphere, including multiple deer species and certain large carnivores (Côté et al., 2004; Ramirez et al., 2018; Weber & Gonzalez, 2003). This wildlife comeback has many positive consequences, including contributions to biodiversity and a diverse set of ecosystem processes (Bakker & Svenning, 2018). This comeback, however, can also challenge human-wildlife coexistence, particularly in areas that are densely populated by humans, and the social and monetary costs associated with human-wildlife conflict can be significant (Linnell et al., 2020). At the same time, views on wildlife and wildlife management are changing. One of such changes is a shift towards more ecocentric worldviews, focused on human-wildlife mutualism—including animal welfare—leading to increasing calls for nonlethal wildlife management tools (van Eeden et al., 2017). Moreover, hunting alone is not always successful in reducing negative interactions between humans and wildlife (Sudharsan et al., 2006; Takatsuki, 2009). There has thus been an increasing interest in how we can more effectively manage wildlife behaviours to reduce human-wildlife conflict (Cromsigt et al., 2013; Gaynor et al., 2021).

The "ecology of fear" (Brown et al., 1999) describes how the risk of predation affects anti-predator behaviour in prey species across spatial and temporal scales, triggering behavioural responses in individuals, demographic processes at the population level and ultimately the effects prey animals have on their environments (Clinchy et al., 2013; Laundré, 2010; Zbyryt et al., 2018). Gaynor et al. (2021) introduced the "applied ecology of fear" framework that integrates "ecology of fear" theory into wildlife conservation and management practices. Applied ecology of fear capitalizes on the fear that prey species have for real or simulated predators to manage risk avoidance behaviours in prey species proactively, such as patterns of habitat selection, movement and foraging (Gaynor et al., 2019). The management goal of applied ecology of fear is to change animal behaviour in such a way that it reduces human-wildlife conflicts, for example by driving animals away from areas of human interest. One example of such applied ecology of fear is the development of nonlethal tools to manage wildlife behaviour by introducing predator cues to the environment to deter deer from production land (Gaynor et al., 2021).

Prey can assess predation risk through a diversity of cues, by detecting predators visually or by hearing (acoustic cues) or smelling (olfactory cues) them even when they are not present in the direct vicinity. Diverse experimental work has indeed confirmed anti-predator responses to these visual cues (Stankowich & Coss, 2007), olfactory cues (Chabot et al., 1996; Kuijper et al., 2014), and acoustic cues (Li et al., 2011; Widén et al., 2022). However, different types of cues likely vary in their effectiveness in inducing anti-predator responses for diverse reasons. For example, environmental conditions, such as rain, light availability and structural cover, can limit or enhance how prey species sense a certain type of cue in the environment. Experience of prey interacting with predators may also shape the strength with which prey respond to different cues (Berger et al., 2001). Moreover, even if prey sense a cue, this does not always lead to an anti-predator response since prey continuously face a trade-off between anti-predator behaviour and other essential behaviours such as the need for foraging when an individual is in a poor health condition (Clare et al., 2023; Gaynor et al., 2019).

Functional traits of predator and prey are likely both important drivers of how effectively predator cues elicit anti-predator behaviour in prey (Apfelbach et al., 2005; Hettena et al., 2014). Two key hypotheses were previously formulated: the predator–prey body mass ratio hypothesis and the predator type hypothesis (Schmitz, 2017; Tsai et al., 2016). The body mass ratio hypothesis suggests that prey will respond more strongly to larger predators, and that cues from predators of similar size to the prey will elicit weaker anti-predator responses as they are seen as a reduced threat (Tsai et al., 2016). The predator type hypothesis suggests that the responses of prey species will depend on the type of predator that preys upon them, that is the hunting strategy that their main predator employs (Hirt et al., 2020). Hirt et al. (2020) separated predators into three hunting strategies: those that sit-and-wait to ambush prey (ambush predators), those that pursue their prey (pursuit predators) and those that hunt prey in groups (group hunting). The latter two predator types both follow their prey across larger distances and can jointly be referred to as coursing predators. We expect that prey species that are preyed upon by ambush predators will rely more on olfactory and acoustic cues to sense a predator hiding in dense vegetation. Instead, prey species that are more vulnerable to coursing predators (i.e. pursuit predators or group hunters, sensu, Hirt et al., 2020) will rely more on visual cues to sense a predator roaming in an open environment (Schmitz, 2017). In addition to predator hunting type, prey feeding type may also influence the type of cue prey is most responsive to. For example, it has been suggested that herbivores that predominately graze in open habitats may be adapted to using visual cues, whereas those that browse in wooded habitats with reduced visibility may rely more on acoustic or olfactory cues (Leuthold, 2012).

Prey may become less responsive to predator cues when exposed to the cue very frequently; this process is known as habituation (Apfelbach et al., 2005). From an evolutionary perspective, habituation allows prey to filter irrelevant and repetitive information from their environment to reduce energy expenditure on anti-predator behaviours and to relocate that energy to other essential behaviours, such as foraging and reproduction (Rankin et al., 2009). Studies on habituation report contrasting findings, for example during a field experiment with wild white-tailed deer they did not habituate after continuous exposure to wolf urine for 35 days; whereas in a captive study elk or wapiti in pens habituated to coyote urine after only 2 days (Andelt et al., 1992; Palmer et al., 2021). The main drivers of habituation are the characteristics of the exposure to the cue and the traits of the predator emitting and the prey receiving the cue (Blumstein, 2016). Traits like body mass, sex, age, degree of sociality and temperament are known to explain to a certain extent the variation in habituation since they modulate the resource acquisition and predator avoidance trade-off (Blumstein, 2016). Other factors mediating habituation are the duration and frequency at which the cue is emitted, whether there are lethal consequences for the prey if not reacting to the cue, and the extent to which prey is experiencing other stressors, such as food stress (Blumstein, 2016; Smith et al., 2021). Habituation is an important research topic for the applied ecology of fear as it determines the effectiveness of nonlethal management tools.

We are unaware of studies that systematically reviewed the response of prey to visual, olfactory and acoustic cues. Such a systematic analysis is necessary for a more effective application of risk cues in wildlife management and for identifying knowledge gaps (Smith et al., 2020). Here, we focus on species of the Cervidae family as a prime species group for applied ecology of fear, as several deer species are strongly increasing across large parts of their native range in the northern hemisphere leading to human-wildlife conflicts in these regions (Côté et al., 2004; Linnell et al., 2020; Martin et al., 2020; Ramirez, 2021; Ramirez et al., 2023). Similarly, several deer species are increasing as non-native species across significant parts of the southern hemisphere, including Australasia, Southern Africa and South America, where they were originally introduced for hunting and now have many undesired impacts (Castley et al., 2001; Davis et al., 2016; Flueck, 2010). We aimed to quantify, through a meta-analysis of the global literature: (I) how deer respond to different types of experimentally induced predator cues, (II) how predator hunting strategy affects how deer respond to cues (predator type hypothesis), (III) how deer feeding type affects how deer respond to cues (prey feeding type hypothesis), (IV) if individual predator–prey body mass ratio modulates anti-predator responses in deer (body mass ratio hypothesis) and (V) how long it takes for deer to habituate to predator cues.

2 | MATERIALS AND METHODS

We searched two online literature databases (Scopus & Web of Science) for scientific publications on the behavioural responses of deer to experimentally induced predator cues (visual, olfactory, acoustic) across all ecosystems worldwide (February 4th 2023). We used all combinations of the following search criteria: "(artificial or simulate or fake or mock or synthetic or imitation or human or man-made) and (deer or cervid or ungulate) and (sound or audio vocalization or bark or growl or grunt roar or howl or sight or visual or aural or model or poster or billboard or smell or olfactory or scent or aroma or trace) and (cue or clue or signal or display or playback or hint or trial) and (response or behaviour or behavior or vigilance or visitation or flee or flight or escape or fight or forage or walk or browse or graze or damage or habituate)". The search did not include geographical restrictions and therefore, potentially, included studies on deer outside their native range. We retrieved 114 articles after deleting duplicates. For our meta-analysis, we used the Preferred Reporting Items for Systematic reviews and Meta-Analysis (PRISMA) guidelines. These are standardized guidelines for systematically gathering, processing, and reporting information through systematic reviews (Page et al., 2021).

We excluded 84 articles during the screening process since they were out of the research scope by reading the titles and abstracts (see Appendix S1: Figure S1 for exclusion criteria). When evaluating the remaining literature by reading the content of the articles, we excluded an additional 11 articles, but we retrieved 20 new articles that were listed in the bibliography lists of the screened publications. The most common exclusion criteria were articles that were not peer-reviewed or that were written in other languages than English, articles on species that did not belong to the Cervidae family, and articles on a topic that deviated too much from our defined scope; for example, articles on intra-specific communication and on responses to non-predator chemical or naturally occurring cues. The exclusion process yielded a final total of 39 peer-reviewed publications (see Appendix S1: Data Source S1), from which we extracted the following information: authors, study location, type of study (field trial or captive study), predator species, type of cue (olfactory, visual, acoustic), type of deer population (wild or captive), deer species and behavioural responses (Table 1). Predators and deer were also grouped into functional types (see Appendix S1 for the species in each group: Tables S1 and S2). Predators were grouped into hunting strategies following the classification of Hirt et al. (2020) (i.e. ambush predators or coursing predators, including pursuit predation and group hunting), while deer were grouped into feeding types (i.e. browsers, intermediate, grazers). The latter feeding strategy, grazers, was finally excluded from this categorization because it grouped only one species. Yet, this species was kept for the rest of the analyses that did not contrast deer feeding types. We distilled separate values for each response for studies that presented results for multiple large predators (including humans) and deer species. For example if one study tested the response of three deer species

TABLE 1 List and description of anti-predator behaviours used in the 39 studies synthesized in the results section. That is at least one of the 39 studies used one of the below response variables as a proxy for deer antipredator response when exposed to predator cues.

Response name	Response description	Presence of anti-predator response
Behaviour	Variation in behaviour such as vigilance, snorting, tail flagging & stamping	Increase in behaviour incidence
Crop damage	Variation in crop damage	Decrease in crop damage
Diel activity	Variation in daily activity pattern compared to baseline activity	Increase or decrease in activity
Fleeing behaviour	Variation in incidence of flee	Increase flee incidence
Foraging	Variation in foraging time, food consumption or food selection. Some studies reported crop damage as a proxy for foraging	Decrease foraging time & quality
Heart rate	Variation in heart rate compared to baseline	Increase or decrease in heart rate
Patch use	Variation in time spend at a specific patch compared to baseline	Increase or decrease utilization
Visitation	Variation in visitation to a specific site or visitation span	Decrease in visitation

(roe, red & fallow deer) to wolf cues, we extracted three individual responses, one for each of the deer species. The same procedure was followed for responses to multiple predator species. Given the wide array of statistical analyses and responses presented in the articles, we did not use the exact effect sizes of the response (these were also not always reported). Instead, we classified each response in each study as either the presence of an anti-predator response to a predator cue (the deer displayed an anti-predator response) or the absence of such a response (see Table 1 for this classification). A binary approach allowed us to directly compare studies with a wide range of experimental methods, from captive to wild deer populations and from quantifying cardiac rhythms to feeding behaviour. We used a *p*-value of <0.05 as a threshold value to separate anti-predator responses from no responses.

We used 10 chi-square tests to investigate how deer respond to different types of cues. The chi-square tests were constructed with contingency tables and by setting anti-predator behaviour by deer (as yes vs. no) as response and cues from predators as the predictor, clustered by type of cue, type of study, predator hunting strategy, deer feeding type and a combination that grouped predator hunting strategy and deer feeding type with type of cue. We controlled for variables with small sample sizes by omitting those with <4 samples from all analyses. Type I error was not controlled for in the set of models given that we had clear hypotheses for each of our research questions and by adjusting the *p*-values, the likelihood of type II error increases. Chi-square tests are also inherently conservative in their estimates, reducing the probability of type I error (Narum, 2006). To test whether individual predator–prey body mass proportion affects anti-predator responses in deer, we calculated the metabolic body mass proportion (MBP). We calculated the MBP as the proportional metabolic body mass of each individual predator to each individual deer species for each of the trials in the systematic literature review by applying the following formula: $MBP_{species} = MB_{predator}/MB_{prey}$, where $MB_{species} = m_{species}^{0.75}$ (Kleiber, 1947). We used metabolic mass instead of body mass as metabolic mass better reflects the energetic needs of a species. Average body mass was sourced from Hirt et al. (2020) for predators and Pérez-Barbería and Gordon (2001) for deer, supplemented with other scientific references for species that were lacking in those two studies (see Appendix S1: Tables S1 and S2 for a reference per species). We ran a logistic regression model with the anti-predator behaviour as a response (as yes vs. no) and MBP and cue type (visual, olfactory, acoustic) plus the interaction between these variables as predictors. A *p*-value <0.05 was used as a threshold for a significant relationship between response and predictors and all given coefficients were standardized. We described habituation patterns reported in the pool of studies by extracting information related to the number of days when habituation occurred. The package "lme4, version 1.1–23" was used for modelling (Bates et al., 2015) and the packages "ggplot2, version 3.3.2" and "circlize, version 0.4.15" for plotting the relationships (Gu et al., 2014; Wickham & Winston, 2016). All statistical analyses were conducted in R 4.0.2 (R Core Team, 2013).

3 | RESULTS

3.1 | Geographical distribution of studies and main species

Twenty-eight out of the 39 studies used olfactory cues, 11 used acoustic cues and five visual cues. Only five studies compared different cue types within the same study (two studies compared acoustic and visual cues, one study olfactory and acoustic cues and one study all three cues). Most studies assessed individual deer responses and not the responses of the whole group. Studies were conducted in 12 different countries (13 territories, including Greenland) and the number of studies conducted per territory ranged between 1 and 23 (Figure 1). The studies simulated 13 predator species and analysed the behavioural responses of 11 deer species (Figure 2a,b respectively).

3.2 | Effectiveness of cues clustered by type

The 39 studies resulted in 256 independent tests of, the presence or absence of, behavioural responses of deer to single predator cues (Figure 3a,–b respectively, Appendix S1: Tables S3–S5 and Figure S2). No experiments tested responses to a combination of

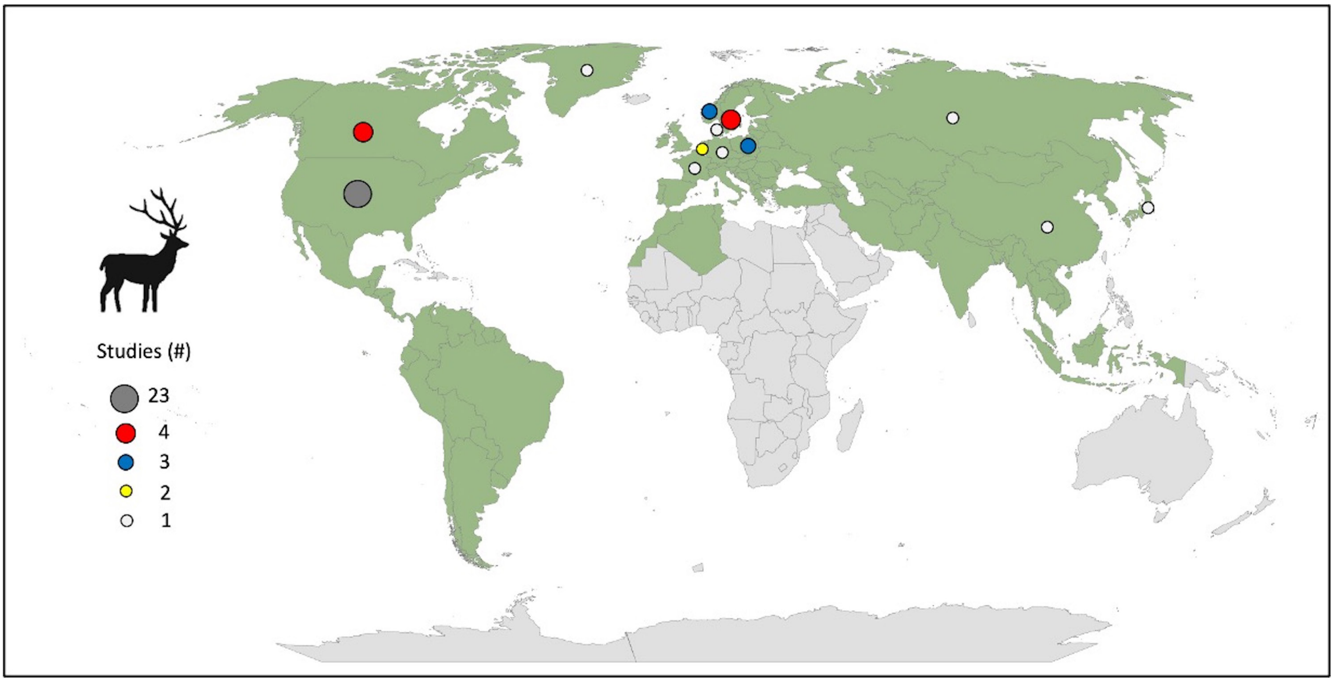

FIGURE 1 The number of studies conducted in 12 countries (13 territories) across the northern hemisphere. The approximate natural distribution of deer (excluding introductions) at the country level is shown in green colour.

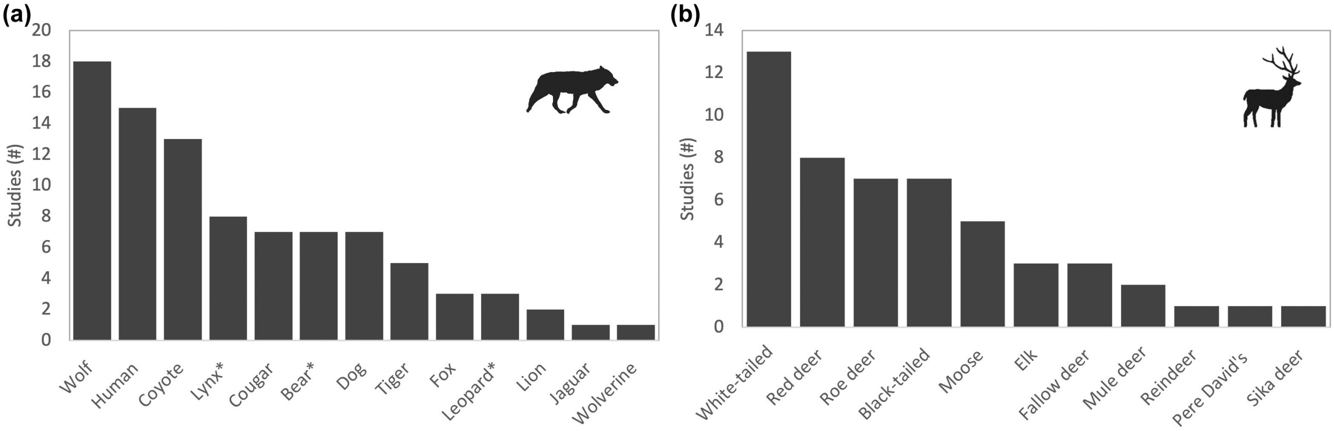

FIGURE 2 The number of studies that simulated different predator species (panel a) and the number of studies that quantified the response of different deer species (b) to predators. Species indicated by an asterisk (*) group similar species to facilitate visualization of the figure but were treated independently for the rest. Black bear, brown bear and grizzly bear were pooled as Bear; leopard and snow leopard were pooled as Leopard, and bobcat and lynx were pooled as Lynx.

cues. Twenty-eight studies experimented with wild deer in field trials (201 responses) and 11 studies looked at captive deer in pens (55 responses); yet, the type of study (field trials vs. pen-based studies) did not influence the likelihood of anti-predator responses in deer ($x^2=2.47$, $p=0.130$, Appendix S1: Figure S3). The 256 responses to predator cues were distributed across the three cue types as follows: visual (34), olfactory (133) and acoustic (89) cues from predators. Overall, there was a difference in anti-predator response to the different predator cues ($x^2=21.04$, $p<0.001$, Figure 4, Appendix S1: Figure S4), where deer responded more frequently to acoustic cues (in 85% of all acoustic cues presented) than to olfactory (60%) or visual (50%) cues.

3.3 | Effectiveness of predator cues by predator hunting strategy and deer feeding type

Hunting strategy did not influence the likelihood of overall anti-predator responses ($x^2=1.03$, $p=0.310$, Figure 5a, Appendix S1: Figure S5). Predator hunting strategy did not influence the likelihood of an anti-predator response to visual cues ($x^2=0.68$, $p=0.682$, Figure 6a, Appendix S1: Figure S6), olfactory cues ($x^2=0.05$, $p=0.861$, Appendix S1: Figure S7) and acoustic cues ($x^2=0.47$, $p=0.673$, Appendix S1: Figure S8). Deer feeding type did not influence the likelihood of deer responding to cues ($x^2=0.69$, $p=0.423$, Figure 5b, Appendix S1: Figure S9). Deer feeding type did

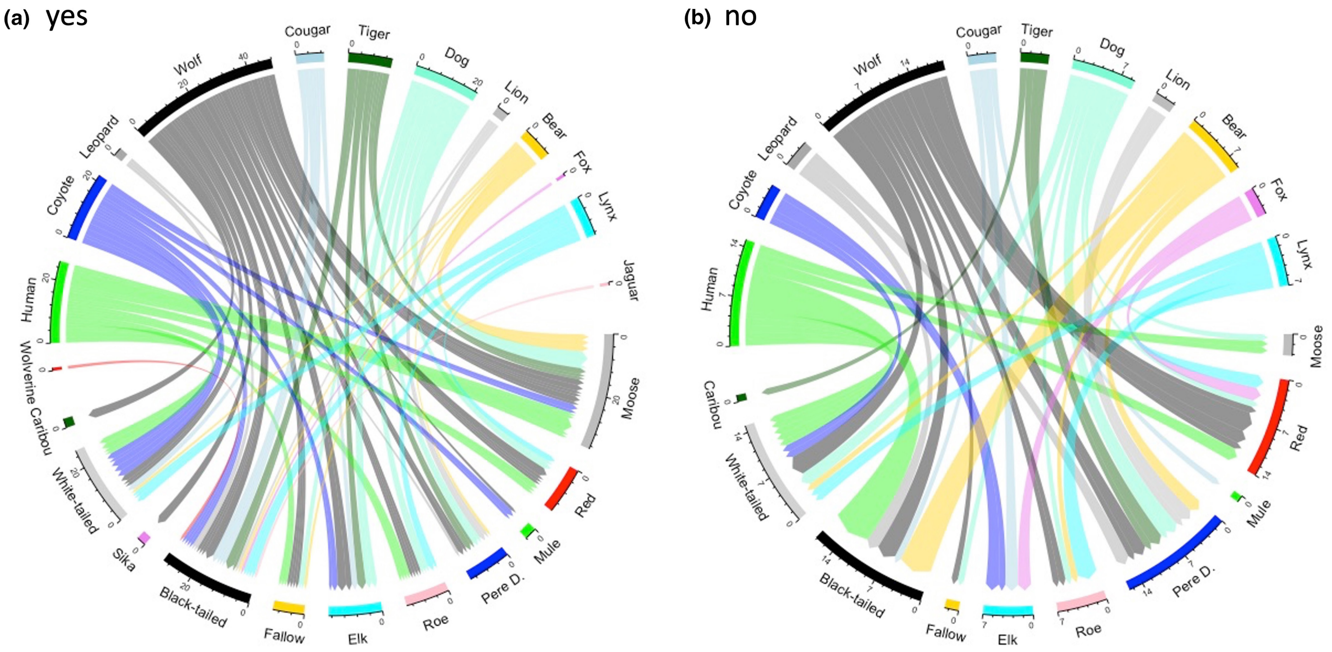

FIGURE 3 Chord diagram showing the pool of anti-predator behavioural responses of deer species to predator species, ignoring the type of cue. Anti-predator responses to visual, olfactory and acoustic cues from predators are presented in (a) and no responses in (b). Black bear, brown bear and grizzly bear were pooled as Bear; leopard and snow leopard were pooled as Leopard, and bobcat and lynx were pooled as Lynx for visualization purpose.

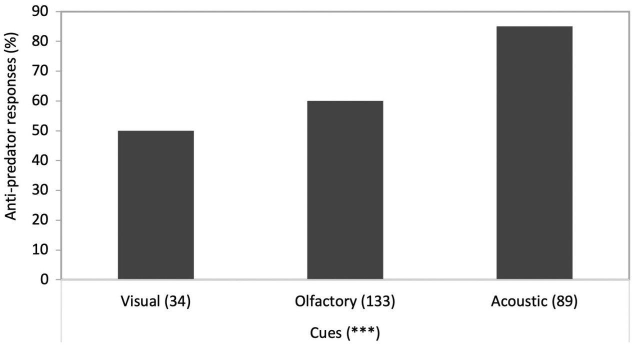

FIGURE 4 Bar graph for the percentage of anti-predator responses presented by deer to visual, olfactory and acoustic cues from predators. The number between parenthesis on the *x*-axis indicates the total number of responses. The level of significance is presented in the *x*-axis title: *p* value = ***<0.001.

not influence the likelihood of an anti-predator response to visual cues ($x^2=0.87$, $p=0.350$, Figure 6b, Appendix S1: Figure S10), olfactory cues ($x^2=0.79$, $p=0.443$, Appendix S1: Figure S11) and acoustic cues ($x^2=0.99$, $p=0.469$, Appendix S1: Figure S12) from predators.

3.4 | Anti-predator responses mediated by predator–prey body mass

Anti-predator responses to visual cues increased with predator–prey MBP ($\beta=0.75$, $p=0.05$; Table 2, Figure 7); whereas anti-predator responses to olfactory and acoustic cues had no relationship with predator–prey MBP.

3.5 | Deer habituation

Twelve studies reported on deer habituation to predator cues with contrasting results, whereas the other 27 studies did not report at all on habituation. Four of the twelve studies reported that deer habituated to predator cues after as soon as 1–10 days with an average of 7 days; the other eight studies reported that they found no habituation after an experimental period of 7–90 days with an average of 36 days.

4 | DISCUSSION

Here, we hypothesized that deer anti-predator response would vary (I) between cue types, (II) predator hunting style, (III) deer feeding type, and (IV) be stronger in response to larger predators relative to the prey's own size. We also explored (V) what studies found in terms of deer habituation to cues. Acoustic cues more frequently triggered an anti-predator response in deer than olfactory or visual cues. As hypothesized, deer responded more frequently to cues of larger predators relative to their own size. In contrast to our hypotheses, predator hunting strategy and deer feeding strategy did not influence the frequency at which deer responded to predator cues. The type of study (i.e. field vs. captive) did not influence the likelihood of anti-predator responses in deer. Only one-third of the studies analysed reported results on habituation to cues with contrasting results.

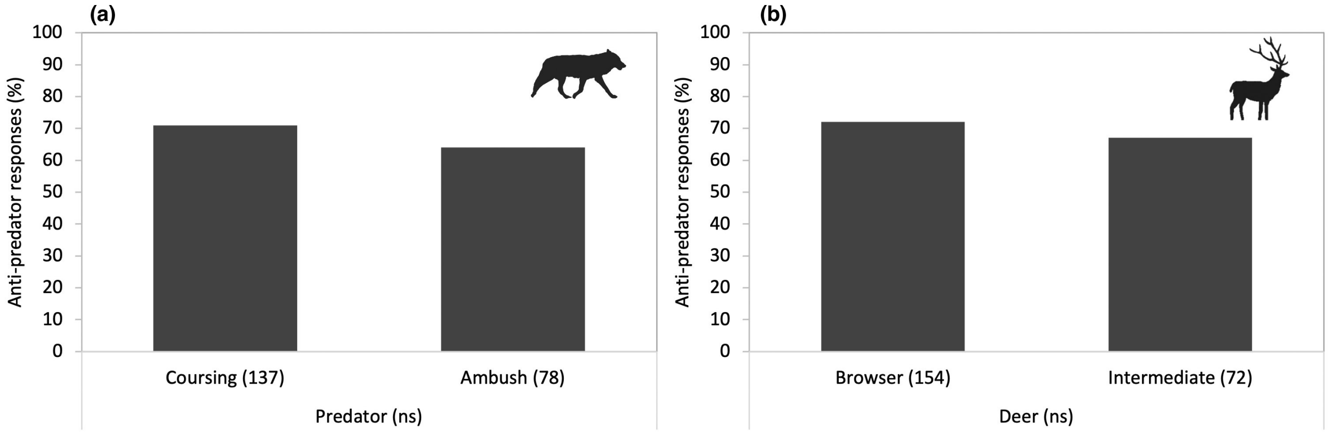

FIGURE 5 Bar graph for the percentage of anti-predator responses presented by deer to predator cues clustered by predator hunting strategy (a) and deer feeding type (b). The number between parentheses on the x-axis indicates the total number of responses. The level of significance is presented in the *x*-axis title: *p* value = not significant (ns) >0.05.

4.1 | Acoustic playback cues are stronger in shaping deer behavioural responses

Acoustic cues were more likely to trigger an anti-predator behaviour in deer (in 85% of all acoustic cues presented) than olfactory (60%) or visual cues (50%). Only four studies directly compared the effectiveness of different types of cues within the same study (Berger et al., 2001; Espmark & Langvatn, 1985; Li et al., 2011; Padié et al., 2015). No studies looked at the effect of combining the cues simultaneously. Testing the combined effect of cues on deer behavioural responses is an important future research avenue to develop effective tools to manage deer populations through their behaviour. Similarly, there is a strong need for studies that investigate how cue intensity, duration and frequency affect responses to the cue.

4.2 | Predator–prey body ratio modulates deer behavioural responses

Our findings confirmed that the relative size of predators is an important driver of anti-predator responses in their prey (Bryce et al., 2017; Chalcraft & Resetarits, 2003). Anti-predator responses increased with MBP, that is with increasing predator size relative to the size of prey, but only when exposed to visual cues. Deer can easily assess the size of their predator visually and, by doing so, deer can adapt their response to the size of the predator. This result suggests that, when inducing artificial predator cues to the environment, using cues from larger predators in relation to deer size will increase the likelihood of triggering stronger fear responses in deer. Group size may actually influence these relationships because deer species vary in social behaviour, where some occur in large herds (e.g. fallow deer) while others are largely solitary or only occur in small groups (e.g. moose). It remains underexplored how group size affects how deer respond to cues from predators and how group size effects may interact with deer body mass. Here, it is relevant to note that larger groups also consist of variable body masses since each individual has a unique body mass associated with their age and sex (Apfelbach et al., 2005; Hamilton, 1971).

4.3 | Anti-predator behaviour in relation to type of study, predator hunting or deer feeding strategies

Neither predator hunting strategy nor deer feeding strategy explained deer anti-predator responses. The type of study (field vs. captive) likewise did not influence deer anti-predator behaviour. Here, we should emphasize the very small sample size of only 39 studies in total. This meant that sample sizes per hunting strategy, feeding type or type of study were very small. Given that the studies also varied in a large number of other variables (e.g. habitat, wild versus captive, geographic location, etc.), it is not surprising that we did not find evidence for an effect of hunting strategy, deer feeding type and type of study. Moreover, it is important to stress that our binary approach (yes or no response to predator cues) to analysing antipredator responses may have obscured more complex behavioural responses of the deer to predator cues. Future studies should explore multivariate approaches to look at the complex response of deer to cues, but for this, there is a need for larger samples than the 39 studies that we analysed. Almost two-thirds of the studies experimented with wild deer in field trials but we call for many more studies under such natural circumstances. More work is needed on how deer feeding strategy (browser vs. grazer) and predator hunting strategy (course vs. ambush) affect deer responses to predator cues. Moreover, we need more insight into how responses to cues vary across natural environments that differ in vegetation structure. Such studies would better inform the development of predator cues as deer management tools than captive studies, especially in terms of identifying what type of cue will be most effective in inducing anti-predator responses in deer with contrasting feeding types and across different environments.

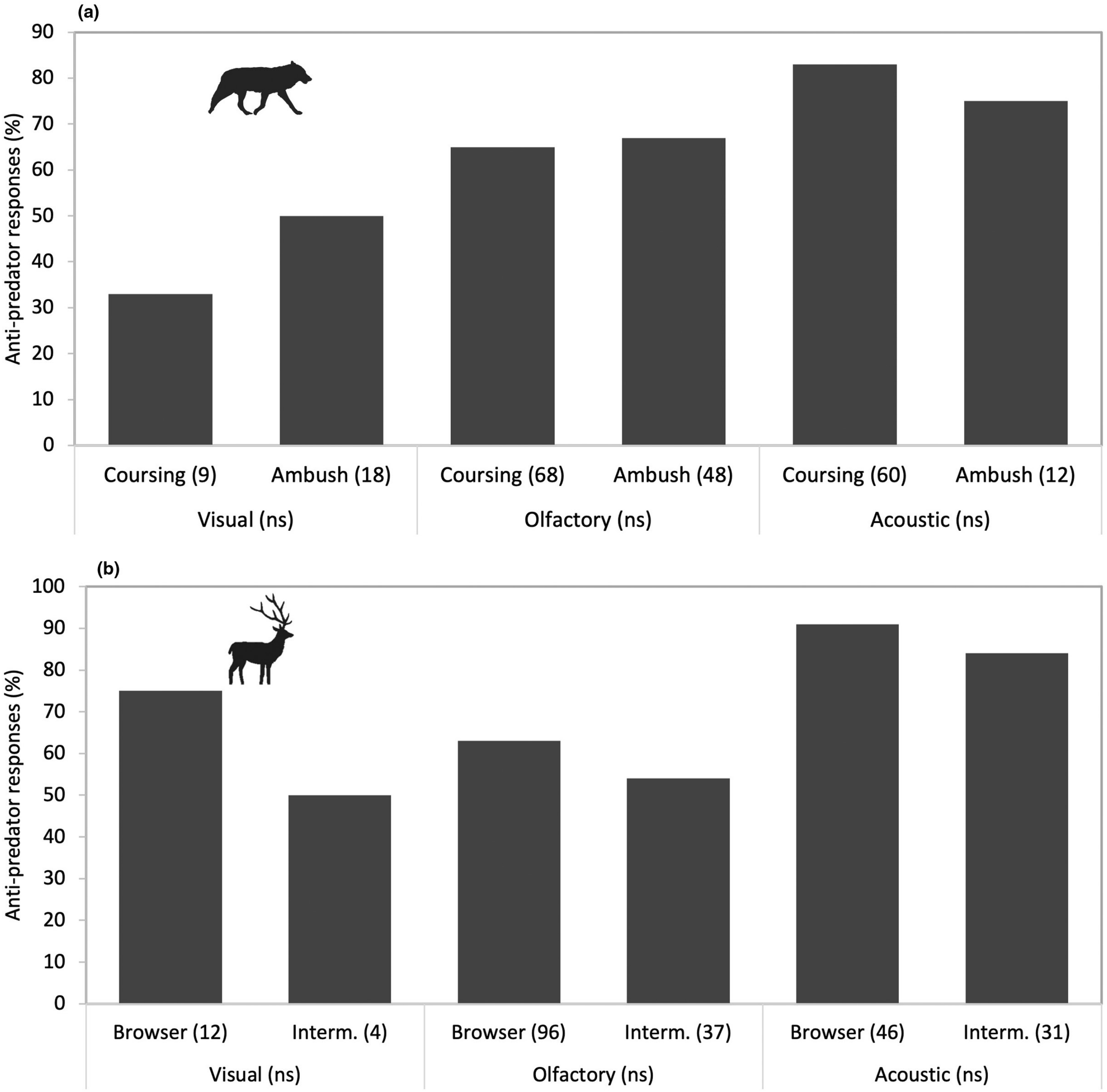

FIGURE 6 Bar graph for the percentages in deer behavioural responses to predator cues grouped by type of cue (visual, olfactory and acoustic) and predator hunting strategy (a) and deer feeding type (b). The number between parentheses on the *x*-axis indicates the total number of responses. Species with $n < 4$ were not included in the analysis. The level of significance is presented in the *x*-axis title: *p* value = not significant (ns) >0.05.

4.4 | Significant knowledge gap on habituation to predator cues

Less than one-third of the included studies reported findings on habituation to cues and those studies had contrasting results. This highlights that habituation to predator cues is an urgent field for further study. Such future studies should investigate the role of different drivers of variation in habituation levels, including the role of food shortage (Andelt et al., 1992), the quality of food (Andelt et al., 1992) the population size of the deer (Ramirez, Zwerts, et al., 2021), the type of predator cues used (Chabot et al., 1996), the dose of the cue (Prugh et al., 2019), the scheme used to induce the cue in the environment (Belant et al., 1998), the landscape matrix (Sahlén et al., 2016) and the presence of real predators in the experimental area (Blumstein, 2006). We argue that future habituation studies should focus on field trials because captive deer may be more prone to fast habituation to novel predator cues given that these deer are already habituated to humans and human infrastructure. We also found that studies that did look at habituation did so for rather short periods (a couple of weeks to months). This time span remains rather short if one considers the aim of effectively managing deer behaviour at temporal scales that are relevant to human-wildlife conflict. We thus also call for studies on habitation that span relevant time scales, such as crop growing seasons and/or multi-annual habituation.

4.5 | A geographical, predator and deer species bias

Most of the studies analysed in this research were conducted in North America and, to a lesser extent, in Europe. Our understanding of this topic is limited to these two geographical regions even though deer also have a natural distribution in South America and Asia. Moreover, deer have been introduced outside their native range, including extensive parts of the southern hemisphere, for hunting or leisure purposes and have significant impacts on the native vegetation in these regions (Coomes et al., 2003; Davis et al., 2016; Dolman & Wäber, 2008; Flueck, 2010). Thus, testing the effectiveness of predator cues in these areas will help develop nonlethal tools to manage both native and introduced deer populations. In terms of species, studies have mostly used cues from a group of widely distributed predator species (wolf, human, coyote) and less of other relevant predator species (Chapron et al., 2014; Hody & Kays, 2018). Similarly, some deer species are overrepresented (white-tailed deer, red deer, roe deer, black-tailed deer) compared to other deer species.

TABLE 2 Behavioural responses of deer to the Metabolic Body Mass Proportion (MBP) of individual predator to individual deer clustered by type of predator cue. The model's coefficient of determination (pseudo) is 0.12. The logistical regression model is accompanied by the standardized coefficients of the predictor, standard errors, *z* values and *p* values. Asterisk (*) indicates significance.

Response	Estimate	Std. error	*z* value	*p*-value
Intercept	1.49	0.31	−4.80	<0.001*
MBP (acoustic)	−0.48	0.41	−1.16	0.245
Cue (olfactory)	−0.82	0.37	−2.22	0.026*
Cue (visual)	−2.05	0.55	−3.69	<0.001*
MBP: Cue (olfactory)	0.28	0.44	0.63	0.529
MBP: Cue (Visual)	1.23	0.63	1.96	0.049*

4.6 | Our key findings and major identified knowledge gaps in relation to applying artificial predator cues in wildlife management

Changing land use, increasing human populations, and increasing populations of wildlife, such as deer, are currently going hand-in-hand in large parts of Europe and North America. As a result, these areas increasingly experience negative human-wildlife interactions (Ramirez, Jansen, den Ouden, Li, et al., 2021; Ramirez, Jansen, den Ouden, Moktan, et al., 2021). In the case of humans and deer, interactions such as crop damage, vehicle-collisions, damage to human infrastructure and the transmission of zoonotic diseases are perceived as the most problematic (Martin et al., 2020). Introducing artificial predator cues to the environment, as analysed in this study, has been suggested as a potential tool to trigger anti-predator behaviour to deter deer away from areas of human interest (see e.g. Cromsigt et al., 2013; Gaynor et al., 2021). If effective, this may help facilitate human-wildlife coexistence by keeping deer away from economically sensitive areas (e.g. croplands and forest production sites), while providing them with sufficient high-quality habitat elsewhere to maintain their well-being. Similarly, artificial predator cues may also help relieve biodiversity and certain ecological processes (e.g. plant recruitment) from high deer pressure in areas where they occur at very high densities, for example due to a lack of large carnivores. Our meta-analysis has highlighted several findings that help in the development of using artificial predator

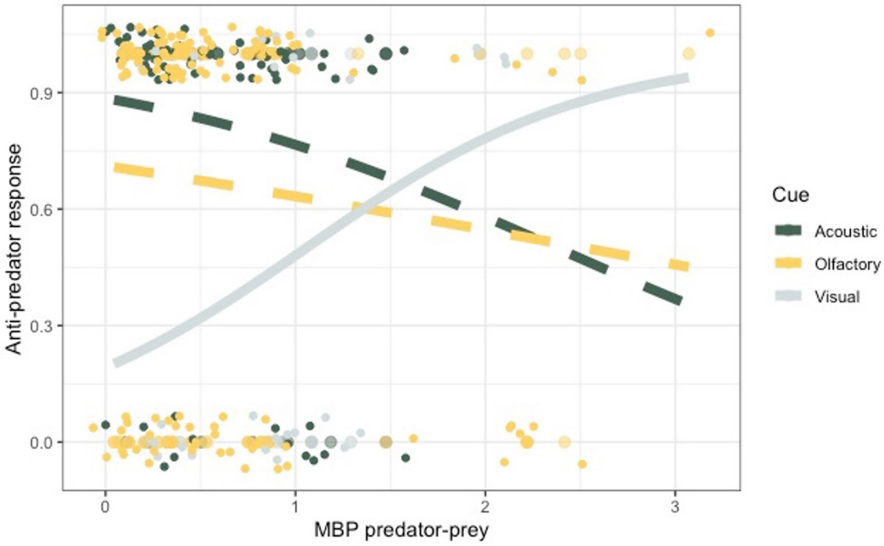

FIGURE 7 Logistic regression fits for the behavioural responses of deer to the Metabolic Body Mass Proportion (MBP) of predators to deer clustered by type of predator cue. Points depict individual values whereas solid lines indicate significant and dashed lines non-significant relationships.

cues as wildlife management tool. At the same time, it has identified major knowledge gaps that need to be responded to before the tool can be effectively applied at scale. Here we synthesize our key findings and the main knowledge gaps. The major finding of our meta-analysis is that acoustic cues from predators may be much more effective than olfactory and visual cues. Moreover, in the case of visual cues, large predator images or three-dimensional models should be favoured given that deer responded more strongly when the simulated predator was proportionally larger than their body size. Major knowledge gaps that our meta-analysis highlighted include developing a better understanding of; how deer respond to multiple types of predator cues induced simultaneously, how individuals with contrasting body size (e.g. juveniles versus adults) respond to predator cues, and how anti-predator responses vary across different land uses. However, arguably the most urgent knowledge gap is the issue of habituation, that is how long-lasting the effects of predator cues on deer are, and what drives variation in habituation. We predict that habituation can be reduced by combining predator cues (visual, olfactory, acoustic), when cue levels mimic those present in natural areas and when cues are induced to the environment dynamically (i.e. with varying intensity, duration and frequency). We also identify a major need for studies that test the use of these cues in real-life practical management situations. Most urgently, the effectiveness of cues needs to be tested at the scale of average-sized croplands and fields, or forestry plantation sites, for relevant periods (such as the full crop growing period), since most current studies were done at small experimental scales for very short periods. Such landscape-scale studies should also specifically look at the effect of the predator cues on deer redistribution across the landscape and potential spill-over effects. That is the risk that cues effectively reduce deer impacts on certain parts of the landscape (certain croplands or fields) but increase their impacts elsewhere in that landscape (e.g. other croplands or forest areas). When thinking about real-life situations, it is also relevant to consider the potential effects of the cues on the behaviour and distribution of non-target species, such as meso-carnivores or non-target herbivores that may also respond to the introduced predator cues. Future studies should also monitor and report the responses of non-target species when employing applied ecology of fear experiments.

5 | CONCLUSION

The ‘Applied ecology of fear’ is a growing field of research that seeks to develop and test non-lethal tools as part of the wildlife management kit complementing potential lethal methods. Our meta-analysis suggests that inducing acoustic cues from predators to the environment holds more promise as non-lethal tool than visual and olfactory cues. Yet, we identified major knowledge gaps that currently prevent us from applying such non-lethal tools to effectively facilitate human-wildlife coexistence. Most urgently, we need to study habituation and its drivers at spatial and temporal scales that reflect actual human land use and wildlife management settings. Future research can address this knowledge gap by setting up experiments that measure deer responses and their habituation to combinations of different types of predator cues, across different land uses at the landscape scale, and during periods that reflect the relevant human activities (e.g. multiple crop growing seasons).

AUTHOR CONTRIBUTIONS

J. Ignacio Ramirez conceived the research idea, designed the methodology, analysed the data, led the writing of the manuscript and led the acquisition of funding. Joris P. G. M. Cromsigt contributed to the designing of the methodology and data analysis. Joris P. G. M. Cromsigt, Johan Olofsson, Tim R. Hofmeester, Dries P. J. Kuijper, Matthias B. Siewert, Christian Smit and Fredrik Widemo were co-applicants for the funding acquisition, assisted with the interpretation of results and supported the writing of the manuscript. All authors critically contributed to this study and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

We, the authors, declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12322.

DATA AVAILABILITY STATEMENT

Data are already published and publicly available since the study was based on secondary data. As such, there was no local data collection. See the Supporting Information section for an overview of the data and the references of the literature used for this study.

STATEMENT OF INCLUSION

Our global meta-analysis was based on a quantitative analysis of secondary data. The research background of the authorship team broadly represents the major regions of interest in the meta-analysis, supporting the inclusion of data from peer-reviewed studies published in English and ensuring the appropriate interpretation of data and results.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Table S1. List of common names of predator species included in this study.

Table S2. List of common names of deer species included in this study.

Table S3. Information extracted from the collection of 39 studies that presented behavioural responses of deer to visual cues from predators.

Table S4. Information extracted from the collection of 39 studies that presented behavioural responses of deer to olfactory cues from predators.

Table S5. Information extracted from the collection of 39 studies that presented behavioural responses of deer to acoustic cues from predators.

Figure S1. Criteria and selection process of literature for the quantitative analysis.

Figure S2. Chord diagram showing the behavioural responses of deer species to predator species.

Figure S3. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by type of study.

Figure S4. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by type of cue.

Figure S5. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by predator hunting strategy.

Figure S6. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by predator hunting strategy and visual cues.

Figure S7. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by predator hunting strategy and olfactory cues.

Figure S8. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by predator hunting strategy and acoustic cues.

Figure S9. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by type of deer feeding strategy.

Figure S10. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by deer feeding type and visual cues.

Figure S11. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by deer feeding type and olfactory cues.

Figure S12. Contribution of the different deer anti-predator responses (1 = yes, 2 = no) to the x^2 value grouped by deer feeding type and acoustic cues.

Data Source S1. List of references from which data was extracted.

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