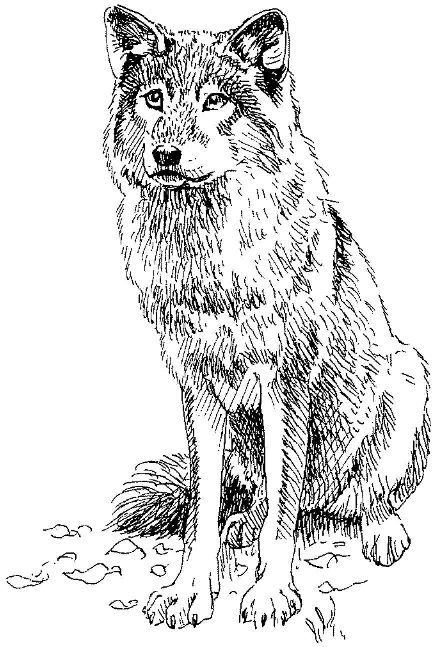

Effectiveness of behaviour-based interventions in reducing livestock depredation by wolves (*Canis lupus*)

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Abstract: Sustainable coexistence between wolves (*Canis lupus*) and humans primarily relies on the availability of effective mitigation practices to reduce livestock depredation by wolves. As a result of wolf recovery, domestic animal losses have been rising, despite the broad implementation of both lethal and nonlethal management efforts. This growing conflict of interest between livestock activities and wolf conservation requires an evidence-based insight into the effectiveness of nonlethal livestock protection interventions. Therefore, in this systematic review, we synthesised the evidence available on the effectiveness of behaviour-based interventions in reducing livestock depredation by wolves. We systematically searched Scopus and Web of Science and screened for literature in a specialised systematic map database created by Snijders et al. (2019). We retrieved 2825 publications, of which 16 articles (and their 31 corresponding studies) were included in the review after the screening process. We used relative risk ratios (RR) and standardised mean differences (SMD) as measures of the intervention effect size and subsequently performed a meta-analysis. Our study revealed a worrying lack of published empirical evidence on nonlethal behaviour-based interventions, at least in the English language, despite their broad application in practical management efforts. Nevertheless, most interventions included in the review, particularly fladry, demonstrated high effectiveness in deterring wolves from approaching- or predating livestock and bait carcasses. The limited size of the evidence base did not allow exploration of the factors that may further moderate the effect size. Knowing these so-called effect moderators could lead to more tailor-made practical recommendations on when and where to employ which type of behaviour-based intervention. Overall, our results suggest that behaviour-based nonlethal measures could be a promising mitigation tool, provided that more research supports these findings. Therefore, we strongly recommend scientists, conservation practitioners and management authorities to collaborate and to further research nonlethal interventions, especially investigating efficacy in real depredation scenarios. A more evidence-based approach to human-wolf conflict is essential in building a viable future for wolves, livestock and pastoral activities.

Keywords: wolves, *Canis lupus*, human-wildlife conflict, livestock, predation, nonlethal, systematic review, meta-analysis.

Introduction

Livestock depredation by wolves (*Canis lupus*) poses a considerable threat to human-wolf coexistence, putting both human livelihoods and wolf conservation at risk (Khan et al. 2019, Kusi et al. 2020). Since the 1990s, wolves are making a strong comeback across the European and North American mainland and are adapting to a wide range of different environments (Mech 1995, Reinhardt et al. 2019), including highly anthropogenic landscapes such as the Netherlands and Bel-

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gium (Chapron et al. 2014, Van Den Berge 2019, Jansman et al. 2021). With wolves living closer to human settlements (Ronnenberg et al. 2017) and wolf populations expanding both in numbers and distribution (Andersen et al. 2015), the prevalence of conflict with livestock activities is increasing considerably (Iliopoulos et al. 2009, Hosseini-Zavarei et al. 2013, Torres et al. 2015, Bocci et al. 2017, Meuret et al. 2017, Khorozyan & Heurich 2022). For centuries, the primary method used to (attempt to) reduce depredation was culling predators, which resulted in the near extinction of wolves in large parts of their historical range (Young & Goldman 1944, Mech 2017). Recently, studies have shown that killing wolves may be ineffective in the long-term and can even lead to counter-productive effects by increased wolf reproduction efforts the subsequent year or territory colonisation by adjacent wolf packs (Wielgus & Peebles 2014, Treves et al. 2016, Lennox et al. 2018, Grente 2021). Although lethal control remains part of wolf management, livestock depredation is increasingly managed through nonlethal methods that aim to protect livestock and support wolf conservation (Shivik et al. 2003, Gehring et al. 2006, Stone et al. 2017).

Nonlethal strategies to deter wolves from livestock are predominantly based on theories regarding animal behaviour (Wilkinson et al. 2020, Blackwell et al. 2016, Miller & Schmitz 2019) and aim to manipulate wolf behaviour and distribution in such a way that it prevents wolves from attacking or approaching domestic animals (hereafter *depredation*) (Smith et al. 2000, Eklund et al. 2017). Underlying behavioural theories include the carnivore landscape of fear and the optimal foraging theory (Brown et al. 1999, Blackwell et al. 2016, Wilkinson et al. 2020). According to the landscape of fear hypothesis (LOF), prey animals change their behaviour and distribution based on the presence of predators to optimise their tradeoff strategy between food provisioning and safety (Bleicher 2017, Wilkinson et al. 2020). Similarly to how wolves can change the behaviour and distribution of prey species such as elk (Creel & Christianson 2008, Laundré et al. 2014), humans can be perceived as apex predators that influence the landscape of fear of carnivores (Smith et al. 2017). Wild wolves have a natural fear of humans and show high avoidance behaviour (Carricondo-Sanchez et al. 2020, Versluijs et al. 2022), except for rare cases of bold, habituated wolves (Gese et al. 2021). By simulating human presence around livestock (e.g. guarding dogs, lights and sounds), behaviour-based nonlethal measures can elicit avoidance behaviour resulting in top-down cascading effects that reduce damage to livestock (Frid & Dill 2002, Laundré et al. 2010). Moreover, the optimal foraging theory (OF) states that – for an individual to optimise their fitness – they must select a feeding strategy that is the lowest in cost and the highest in benefits (MacArthur & Pianka 1966). Based on OF theory, wolves are confronted with a tradeoff between the costs of hunting (spending energy, risk of injury and death) and feeding on prey with high caloric rewards. Because most livestock species have lost their anti-predator behaviour through domestication (Flörcke & Grandin 2013) and are in good physical condition, livestock depredation tends to be a high-benefit and low-cost resource strategy (Wilkinson et al. 2020). Additionally, the energy a predator requires to detect prey kept in predictable locations (i.e. livestock) is low (Sih 2005). Therefore, the cost of predating on livestock is low, at least when human retribution is also low. Nevertheless, costs for predators can be increased through protection measures. Behaviour-based intervention methods aim to artificially increase the cost of livestock depredation and shift the balance negatively in order to persuade predators to shift to a more profitable prey type (Haswell et al. 2019). Eliciting the behaviourally mediated effects predicted by LOF and OF hypotheses is done using disruptive and aversive stimuli (deterrents and repellents) designed to heighten the perceived risk and cost of approaching or predating on domestic animals.

Turbo Fladry barrier used to protect sheep from wolves in the Netherlands. This nonlethal tool combines both disruptive (fladry strips) and aversive (electrified wires) stimuli to keep wolves from trespassing into pastures and from predating on livestock. *Photo: Van Bommel Faunawerk.*

Aversive and disruptive stimuli are unpleasant to the animal and may cause pain, discomfort or fear (Shivik & Martin 2000). Typically, *disruptive stimuli* (deterrents) are used to induce fear, making use of *neophobia* (the fear of new) to prevent or change a specific behaviour (Shivik & Martin 2000), whereas aversive stimuli make use of unpleasant experiences or pain to elicit a negative association with an undesirable behaviour. The major difference is that aversive stimuli rely on negative experiences and can become more effective with learning (i.e. with repeated exposures to the negative stimulus), whereas disruptive stimuli rely solely on novelty and are only efficient when learning (or habituation) does not occur (Shivik et al. 2003). Examples of disruptive stimuli are fladry, the radio-activated guard box (RAG), fox lights and range riders. Aversive stimuli interventions can include conditioned taste aversion (CTA), turbo fladry, electric fences, shock collars and nonlethal projectiles (Shivik 2003, Appleby et al. 2017). Some interventions combine disruptive and aversive stimuli, such as livestock guarding dogs (LGD) that can elicit fear by barking (simulated human presence) and may represent a real risk of injury or death to wolves when they attack. Disruptive stimuli disrupt predatory behaviour by inducing a startle or fright response in the animal, discouraging it from approaching further (Shivik 2004) and can come in the form of chemical, visual, acoustic, or physical cues, or a combination thereof (Smith et al. 2000, Shivik 2004). The major issue related to disruptive stimuli interventions is *habituation* to the stimuli (Musiani et al. 2003). Due to the absence of negative consequences of the stimulus, the initial fear fades over time, resulting in decreased intervention effectiveness (Shivik & Martin 2000). *Aversive stimuli* can induce direct negative experiences and thereby disrupt behaviour but can also be used for aversive conditioning. By pairing a behaviour (such as approaching livestock) with an aversive stimulus (such as an electric shock from a collar) a strong learned association is created between the performed behaviour and the unpleasant stimulus by means of *positive punishment* (Rossler et al. 2012). If true conditioning is acquired, the animal shows the aversion even when the unconditioned stimulus (e.g. shock) is absent (Snijders et al. 2019), making conditioning a promising tool for mitigating predation conflicts. However,

Livestock guardian dog (LGD) guarding sheep in a mobile fence enclosure, Veluwe, the Netherlands. *Photo: Van Bommel Faunawerk.*

a recurrent issue related to aversive stimuli is the phenomenon of *extinction*, where – without frequent re-exposure to the stimulus - the learned association fades over time (Appleby et al. 2017). Another drawback is *confounding* of the (conditioned) association, resulting, for example, in an individual acquiring an aversion to humans instead of the targeted behaviour (here approaching or attacking livestock), as seen in studies on dingos (*Canis lupus dingo*) (Appleby et al. 2017). To optimise the association between actual predation behaviour (attack) and a negative (aversive or disruptive) stimulus, it is therefore important that nonlethal tools are as highly behaviourally contingent as possible and deter/repel the predator at the moment of attack initiation (Breck et al. 2002).

To conclude, through behaviour-based intervention methods, wolves are confronted with a behavioural tradeoff between the risk of illness, injury or even death and the benefits of feeding. When used correctly, nonlethal intervention methods can thus decrease the motivation for depredating livestock. But what does it mean to use them correctly? Despite the wide implementation of protection measures, livestock depredation remains a considerable issue (Meuret et al. 2017). Therefore, it is crucial to better understand how effective these interventions are and under what circumstances they are worthwhile (Bruns et al. 2020). Gaining this knowledge can contribute to more evidence-based and adaptive approaches to wolf-livestock conflicts, with the ultimate goal of a better coexistence between wolves and humans (Stone et al. 2017, van Eeden et al. 2018).

Therefore, in this systematic review, we explored the literature to investigate if and to what extent behaviour-based interventions were able to reduce livestock depredation by wolves. Moreover, we researched whether certain interventions were more effective than others at limiting depredation events. Based on the theories of optimal foraging (OF) and landscape of fear (LOF) (MacArthur & Pianka 1966, Brown et al. 1999), we predicted that behaviour-based interventions would effectively reduce *depredation* events by increasing the (perceived) cost or risk of livestock predation and that interventions inducing a higher (perceived) cost or risk would be more effective. Finally, we hypothesised that a wide range of environmental factors could affect the effectiveness by shifting the cost-benefit ratio in favour of livestock depredation (e.g. low wild prey availability (Bocci et al. 2017, Janeiro-Otero et al. 2020)) (Wilkinson et al. 2020), but were unable to test this due to a limited number of articles in the evidence base (*n*=16). Ultimately, with this review, we hope to divulge evidence-based information that can support stakeholders in choosing appropriate livestock protection measures and inform future research in human-wolf coexistence.

Methods

Following systematic review methodology, we framed the primary research question *'What is the effectiveness of behaviour-based interventions in reducing livestock depredation by wolves (*Canis lupus*)?'* around a PICO structure (Livoreil et al. 2017): *Population* (wild wolves), *Intervention* (behaviour-based methods), *Comparator* (no or any non-behaviour-based intervention) and *Outcome* (livestock depredation).

Literature search

Search strategy

To identify and retrieve as much evidence as possible on the effectiveness of livestock protection measures, we searched multiple platforms, including two bibliographic databases: Web of Science (WoS Core Collection) and Scopus (both accessed through the Wageningen University and Research Library institutional subscriptions). Searches were performed on 14 September 2021 (WoS) and 1 October 2021 (Scopus); hence any relevant study published in these databases beyond this date was not considered in this review. We also accessed the specialist Zotero database of Snijders et al. (2019), comprising articles from their Systematic Map *'Effectiveness of animal conditioning in reducing human-wildlife conflicts'*. We searched the following Zotero subfolders: *Personal Communication, Google Scholar, Bibliographic databases* and *Specialist Websites* using the full-text search tool on 30 September 2021.

Search string

Within the Zotero database (Snijders et al. 2019), we searched each subfolder at the full-text level using the search terms "*wolf*", "*wolves*", and "*canis lupus*". In WoS and Scopus, we searched articles on the title and abstract level using a search string in English constructed from the PICO elements *population, intervention* and *outcome* and containing the search terms:

> _wolf OR wolves OR "canis lupus"_ AND _condition* OR aversi* OR disrupt* OR repel* OR nonlethal OR non-lethal OR learn* OR train* OR avoid* OR "negative reward" OR punish* OR reinforce* OR habituat* OR protect* OR "livestock guard* dog" OR "livestock protection dog" OR LGD OR LPD OR collar* OR herd* OR shepherd OR "human presence" OR "range rider" OR fenc* OR fladry OR CTA or "conditioned taste avers*" OR capture_ AND _predat* OR depredat* OR attack* OR kill* OR conflict* OR loss* OR livestock OR domestic OR sheep OR cattle OR "farm animal" OR cow OR lamb OR approach OR movement OR calf OR calves_

To estimate the comprehensiveness of the search, we proofed the outcomes with five priorly established benchmark articles: Hawley et al. 2009, Gehring et al. 2010a, Lance et al. 2010, Rossler et al. 2012, Stone et al. 2017 and Iliopoulos et al. 2019. We tested the search string in Web of Science Core Collection on 9 September 2021, and results retrieved all five benchmark publications.

Inclusion criteria and study selection

We used CADIMA (version 2.2.3.), a free online tool for systematic reviews (Kohl et al. 2017, https://www.cadima.info/index.php) to perform our article selection and data extraction.

For an article to be included in the review, it had to conform to the key elements of the study question (PICO), which we translated into the following selection criteria: 1. *Population*: all subspecies of wolves (*Canis lupus*) that are free-ranging or captive at the time of the intervention. Studies on captive wolves were taken into consideration up until the data extraction phase as to ensure having sufficient studies in case insufficient data was available on free-ranging wolves; 2. *Intervention*: all non-lethal intervention methods that are behaviour-based and have as a goal: OR the conditioning of wolves against depredation through learned associations with intervention stimuli OR the blocking of depredation behaviour (attack and precursor behaviour) at the moment of intervention either by hindering (deterrents) or averting the behaviour (repellents) of the target (and non-target) individuals OR a combination thereof; 3. *Comparator*: no intervention OR any other intervention that is not behaviour-based and has as goal to reduce livestock depredation by wolves, this could be, for example, translocation or lethal control; 4. *Outcome*: all quantitative measures for livestock (or domestic animal) depredation OR quantitative measures for precursor behaviours that could lead to depredation (e.g. approaching livestock or trespassing a barrier).

We first screened all recovered articles on the title and abstract level before performing full-text screenings on selected publications (Figure 1). In addition to the PICO-based criteria, we excluded studies that did not present any (primary) quantitative data, such as qualitative studies (e.g. interviews), modelling studies or reviews.

Data extraction and study validity-assessment

From each selected study, we first extracted relevant meta-data. Subsequently, quantitative data on the effectiveness of intervention methods were extracted from the article's main text when available or was extracted from figures using WebPlotDigitizer version 4.5. (Rohatgi 2021, https://apps.automeris.io/wpd/). For articles where data was relevant, but no measure of variance was given, we contacted the authors requesting raw data (n=3). Studies for which the missing data could not be retrieved were excluded from the quantitative analysis but included in the narrative synthesis, and corresponding findings were discussed in a separate qualitative analysis (see results).

We performed a critical appraisal to assess the validity of the studies in the evidence base (see Figure 3 caption for appraisal criteria). The outcome of the study validity assessment was not used to exclude additional studies from the quantitative synthesis, as the sample size was already limited, but rather to give context to the evidence.

Quantitative synthesis methods

Because each study reported its intervention effectiveness using different outcome measures, we standardised the outcomes between studies by using two types of effect sizes, relative risk ratios (RR) and standardised mean differences (SMD):

Relative risk ratio (RR)
Whenever possible, we used relative risk ratios (RR) to express the effectiveness of livestock protection measures. RR was defined as the ratio between the likelihood of depredation occurring in the intervention group (livestock protection) compared to the likelihood of depredation occurring in the control group (no protection measure) (see Figure 4 caption for RR-value interpretation) and was calculated based on the following formula:

$$Relative\ risk\ ratio\ (RR) = \frac{a/(a+b)}{c/(c+b)}$$

where a is the number of depredated units in the treatment group, b is the number of non-depredated units in the treatment group ('survival' measure), c is the number of depredated units in the control group, and d is the number of non-depredated units in the control group (based on Eklund et al. 2017).

For studies that reported a measure of trespassing rather than a number of depredated animals, we calculated a survival measure as: *b = outcome measure events outside – outcome measure events inside protected area*.

Throughout the study, we defined *depredation* as both (1) animals being predated upon, resulting in injuries and/or death and (2) the performance of precursor behaviours that could lead to an attack: approaching livestock, trespassing on intervention areas.

When appropriate, we transformed the RR into a more user-friendly measure giving the percentage of risk reduction associated with a given intervention:

$$Relative\ risk\ reduction\ (RRR) = 100\% * (1 - RR)$$

Standardised Mean Difference (SMD)
Some studies did not report any measure for the number of non-depredated units (b) required to obtain a RR. For the studies that reported a mean and variance instead, we calculated a standardised mean difference between control and treatment groups following the formula:

$$SMD = \frac{\bar{x}_1 - \bar{x}_2}{SD_p}$$

where $\bar{x}_1$ is the mean of the intervention and $\bar{x}_2$ the mean of the control and is the pooled standard deviation (see Figure 5 caption for SMD-value interpretation).

Handling of complex data structures

To avoid mistakes with complex data structures and to stay as close as possible to true values, we decided not to transform the data with additional statistical analyses. For example, in studies with a BACI design, we only used before-after data and did not transform BACI to control-impact, in order to minimise the risk of non-intended (environmental) variables between study groups. Moreover, in studies that reported multiple time points (several years), we either counted each year as a study (when considered as independent data) or used only one year for the effect size calculation. When, for example, two before years (n-1 and n-2) and one intervention year (n) was reported, we took the before year that was closest to the intervention year (n-1) to minimise annual variations.

Statistical methods

Because we found no truly robust way of converting between standardised mean differences and risk ratios (Viechtbauer 2022), we decided to use SMD and RR studies in two separate analyses. Data analysis was performed in R version 4.1.2 using the *metafor* package (Viechtbauer 2010). Throughout the study, we used two-sided tests with a significance threshold of $P<0.05$.

Risk ratios
We used the *escalc(measure =RR)* function to calculate the log *risk ratios* (RR) of the intervention effectiveness. This *metafor* function automatically corrected zero cell errors by adding a ½ correction to all the cells, this was important because some studies did not observe any depredation events, especially under intervention. After calculating the RR for each study, we fitted a random effects model (REM) using the *rma* function to obtain the summary effect size of all behaviour-based intervention studies. Further-

more, we did a meta-regression on the moderator *intervention* to investigate differences between interventions. Finally, we performed a subgroup analysis for *fladry* and *biofence* because they differed significantly (P=0.0001) and we wanted to gain better insight into the impact of biofence on the overall effect size.

Standardised mean differences
To calculate the standardised mean difference between control and intervention groups and thus the magnitude of the intervention effect, we used the *escalc(measure =SMD)* function. This function automatically corrected small sample sizes, transforming the outcomes into corrected and more accurate *Hedges g* effect sizes. Subsequently, we fitted a random effects model to get the summary effect size of all interventions and studies. Because of the small number of studies (n=6), we did not perform any meta-regressions to investigate effect modifiers on this dataset.

Results

Narrative synthesis of the evidence base

The initial search across bibliographic databases and the Zotero database (Snijders et al. 2019) retrieved 4292 articles, 2825 after duplicate removal (Figure 1). We included fifty articles based on title and abstract, of which 47 articles were retrievable in full text. Finally, this yielded 16 articles: Breck et al. 2002, Musiani et al. 2003, Shivik et al. 2003, Schultz et al. 2005, Hawley et al. 2009, U.S. Fish and Wildlife Service 2009, Davidson-Nelson & Gehring 2010, Gehring et al. 2010a, Lance et al. 2010, Rigg et al. 2011, Rossler et al. 2012, Salvatori & Mertens 2012, Ausband et al. 2013, Stone et al. 2017, Iliopoulos et al. 2019, Samelius et al. 2021. These sixteen articles represented 31 studies (multiple studies per article) which were used in the narrative synthesis to represent the evidence base as a whole. Finally, we included 18 studies out of ten different publications in the quantitative synthesis (meta-analysis), and excluded thirteen studies from seven articles from the quantitative synthesis but included these in a qualitative synthesis (non-statistical exploration of study results). The full list of excluded studies (n=13) with corresponding criteria for exclusion from the meta-analysis can be found in the supplementary materials (Table S1[1]).

The evidence base for the effectiveness of animal behaviour-based interventions in free-ranging wolves was small (n=16 publications, n=31 studies, Figure 1). Moreover, the number of studies on interventions protecting living livestock was also limited, with more than half of the studies testing precursor and consumption behaviours rather than attacks on livestock (n=17 vs n=14, Figure 2c). The evidence base comprised twice as many studies on disruptive stimuli compared to aversive stimuli (n=16 vs n=8, Figure 2a), while seven studies investigated intervention methods that combined both aversive and disruptive stimuli, such as livestock guarding dogs (LGDs), and electrified fladry. Fladry was studied more frequently than other interventions (n=9, Figure 2b), followed by shock collars (n= 4), LGD's (n=4) and electric fences (n=4).

Finally, the geographical areas of the studies were strongly skewed towards North American countries, most importantly the U.S. (n=16, Figure 2d) followed by Canada (n=4). In Europe, ten studies were conducted on behaviour-based interventions from a total of three publications. For Asia, we found only one article, in Mongolia.

Critical appraisal
Overall, a high number of studies (n=19) from the evidence base allowed the evaluation of nonlethal tools in a real-life setting, with only one-third of studies being performed on units

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[1] https://www.zoogdiervereniging.nl/publicaties/2023/lutra-66-1-2023

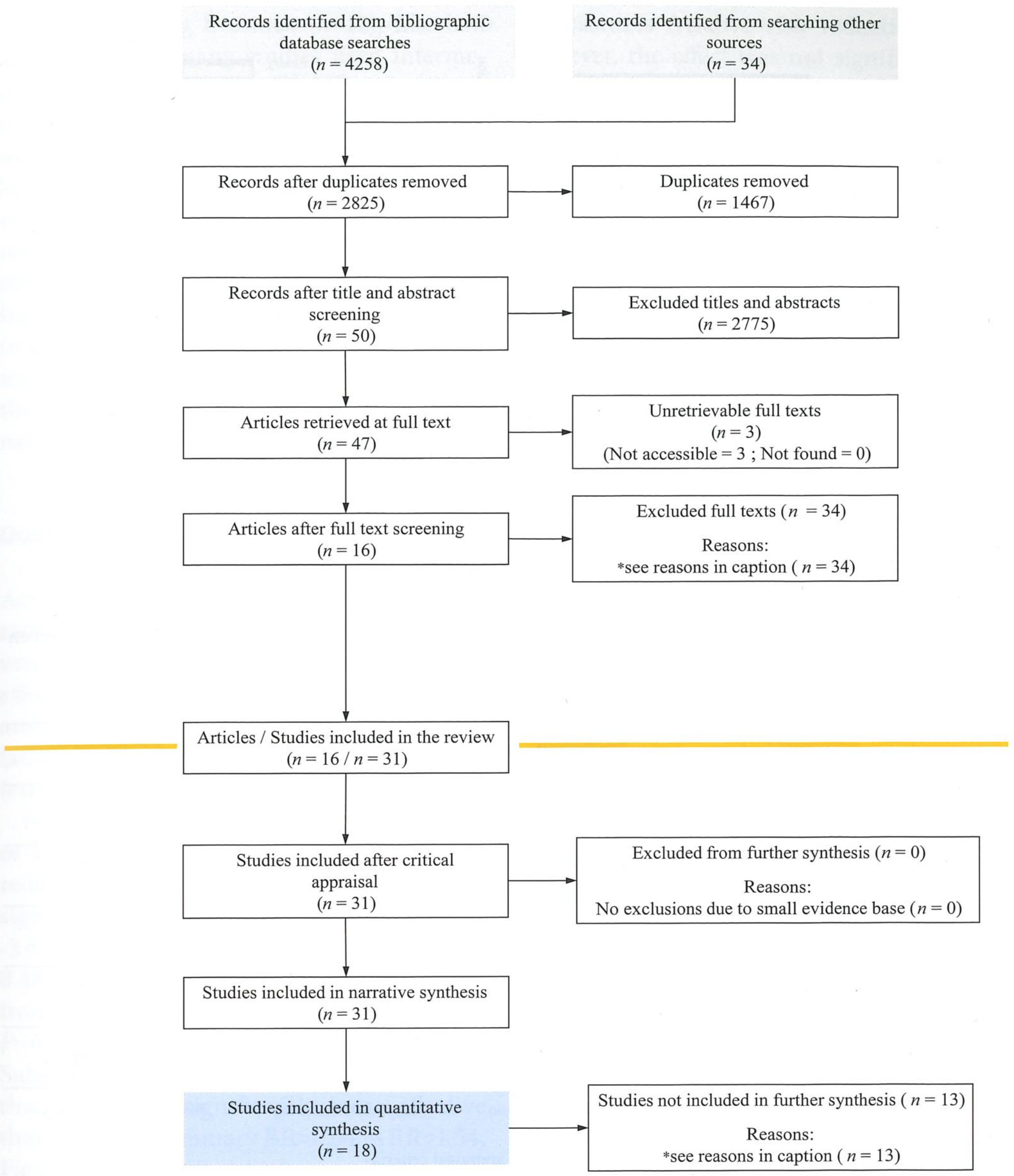

Figure 1. Flow diagram of the systematic search in WoS, Scopus and the Zotero databases from Snijders et al. (2019) with the subsequent inclusion/exclusion of articles at all stages of the review. Reasons for exclusion from the review were the following: 1. *Reasons for exclusion at full text: Population: study on captive wolves (n=7), Intervention: no appropriate intervention (n=8), Comparator: no appropriate control (n=17), Outcome: no appropriate outcome measure (n=11), Full text untranslatable (n=1), Full text duplicate of other study (n=3), note: some articles were excluded based on multiple criteria. 2. Reasons for exclusion from quantitative synthesis: lack of variance measure (n=7), no quantitative measure for before intervention (n=1), unreliable or lacking control group (n=4), combination of multiple interventions (n=1). Studies with corresponding reasons for exclusion can be found in the supplementary materials (Table S1[1]).

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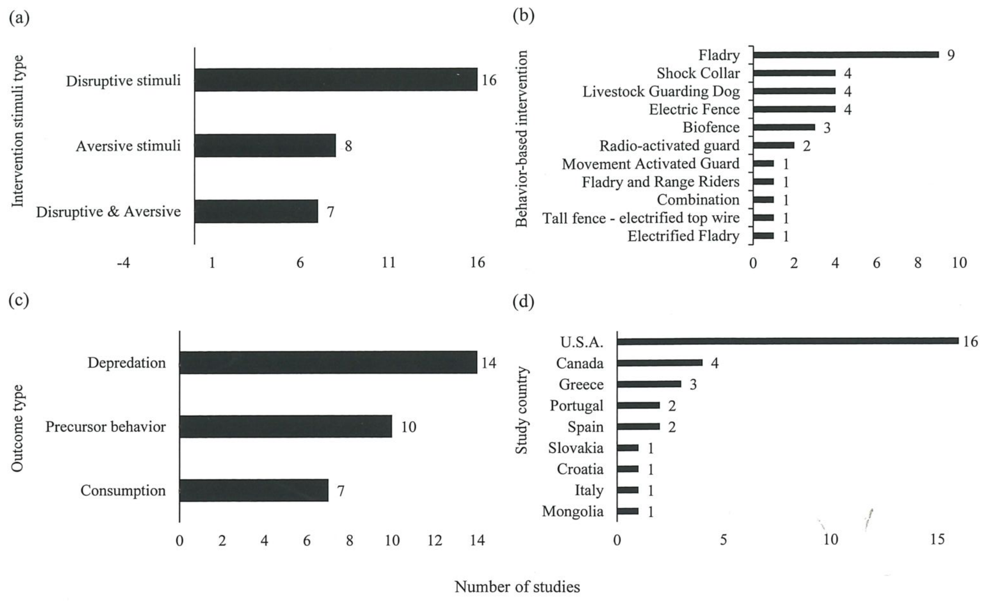


Figure 2. Number of studies in the evidence base categorised by (a) intervention stimuli type, (b) type of intervention, (c) study outcome type and (d) study country (*n*=31 studies from *n*=16 articles).

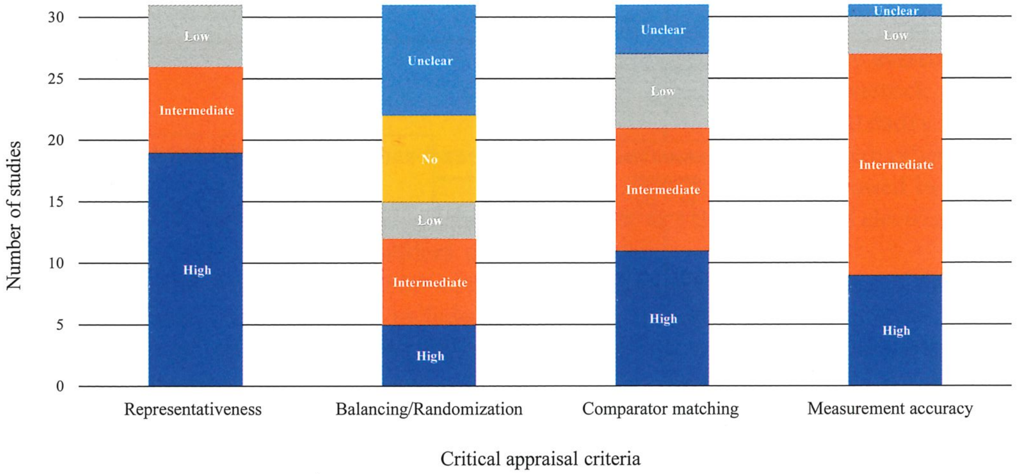


Figure 3. Study validity assessment outcomes per appraisal criteria. Each bar contains the cumulative number of studies in each category, totalling 31 studies (*n*=16 articles). Representativeness indicates how representative the study is in demonstrating an interventions' ability to reduce livestock depredation by wolves; Balancing/randomisation (selection bias) indicates if intervention units were balanced and/or randomised in a way that allowed minimisation of any pre-treatment differences between study groups; Comparator matching (performance bias) indicates how the comparator group/period was matched with the treatment group/period in terms of variables other than intended and whether they differed enough in intended variables; finally, measurement accuracy represents whether the study outcome was measured following a method that could truly measure the effect of the treatment. High scores represent a better study validity for the specific question, whereas Low, Unclear or No scores indicate that the studies did not perform well for the corresponding criteria.

other than living livestock (*n*=12), like bait sites. However, many studies used intermediate or low-accuracy measurement methods to quantify depredation events (n=21), such as track swaths and large-scale self-reported losses. Nevertheless, nine studies used highly robust measurement methods, such as VHF telemetry and verified depredations to measure outcomes. Although randomisation or high balancing of study groups was scarce (*n*=5), high or intermediate comparator matching was present in over two-thirds of the studies (see Figure 3 caption for the explanation of the critical appraisal criteria).

Quantitative synthesis

Across all studies included in the relative risk-ratio random effects model (*n*=12), behaviour-based nonlethal tools had high overall effectiveness (relative risk reduction= 82%) and significantly reduced depredation events (attack- and precursor behaviours) by wolves (estimate= -1.7290, df=11, *P*= 0.004, Figure 4).

Furthermore, we found a strong effect of intervention type on the effectiveness of reducing depredation, with biofence differing significantly from fladry (Fladry: estimate= -3.6341, df=2, *P*<0.0001; Biofence: estimate= 0.4851, df= 2, *P*=0.1450, Figure 4) but not from turbo fladry (estimate= -1.6891, df=2, *P*=0.222).

Subsequent subgroup REM analyses showed that fladry was significantly more effective than biofence (summary RR=0.04 vs RR=1.54, Figure 4). Fladry had high overall effectiveness (relative risk reduction= 96%) and significantly reduced livestock depredation across the eight studies included in the analysis (estimate= -3.1543, df=7, *P*<0.0001). Whereas the use of biofence increased the trespassing rate of wolves into a pack exclusion area, leading to a counter-productive effect of this particular intervention (estimate= 0.4348, df=2, *P*=0.4256). Finally, turbo fladry apparently reduced the trespassing of wolves into six cattle pastures (relative risk reduction= 70%), however, the effect was not significant (estimate= -2.2040, df=0, *P*=0.3361).

To summarise the overall effectiveness of nonlethal tools presented in studies reporting means, we fitted a random effects model on standard mean differences. In alignment with results presented in Figure 4, the nonlethal measures proved to be highly effective (Hedges g= |-1.19|> 0.8, Figure 5) in reducing depredations by free-ranging wolves, with a significantly lower average number of depredation events in intervention groups (estimate= -1.1870, df=5, *P*=0.0046).

Shock collars, livestock guarding dogs and tall fences showed a very large reduction effect on trespassing behaviour and livestock depredation (Hedges g= |-1.27 to -2.94|), and the use of Movement Activated Guard reduced carcass consumption to a smaller - but still large - extent (Hedges g= |-0.87|> 0.8).

In contrast, carcass consumption rates increased by 0.38 standard deviations on bait sites protected by fladry compared to sites without fladry, indicating a small (0.2 < 0.38 < 0.5, Figure 5) but non-significant effect.

Qualitative synthesis

Thirteen studies from seven articles (see supplementary materials, Table S1) were excluded from the quantitative synthesis, representing seven different nonlethal interventions: shock collars (*n*=2), livestock guarding dogs (*n*=3), electric fences (*n*=4), radio-activated guard boxes (RAG box, *n*=2), fladry and range riders (*n*=1 with *n*=4 cases for fladry and *n*=4 cases for range riders) as well as one study on the combination of multiple intervention methods. Overall, the findings of these studies supported our quantitative synthesis results that behaviour-based nonlethal tools effectively reduce livestock depredation by wolves. More specifically, fladry was highly effective and reduced livestock killings by 100% when used in management activities to reduce depreda-

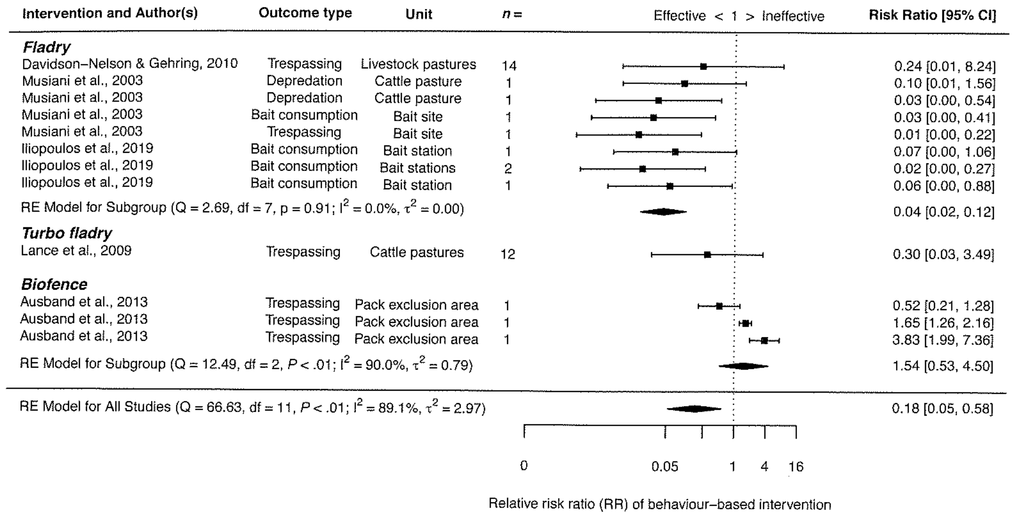


Figure 4. 95% CI interval relative risk ratio of behaviour-based intervention effectiveness to reduce livestock depredation by wolves. When RR=1, there is no difference in the risk of depredation between intervention and control groups. An RR<1 indicates that the risk of depredation is higher in the control group, with intervention effectiveness increasing as the RR gets closer to 0. Contrastingly, when R>1, the risk of depredation is higher in the intervention group, indicating a counter-productive measure.

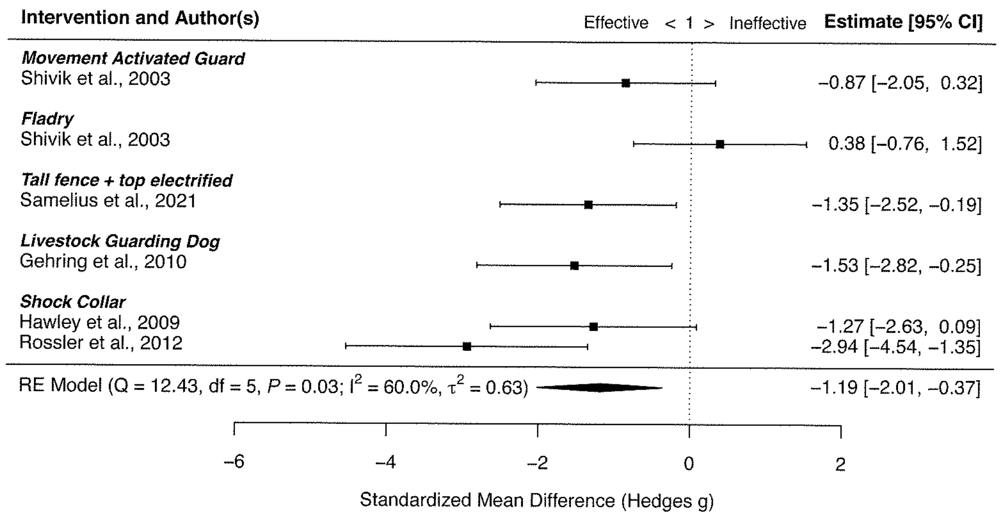


Figure 5. 95% CI interval effect size (Hedges g) of behaviour-based interventions. The sign of the effect size (g) indicates the direction of the effect, with negative values suggesting the treatment to be effective (lower mean number of depredation events in the intervention group). The amplitude of the effect can be interpreted following the rule of thumb: 0.2 = small effect, 0.5 = medium effect and >0.8 = large effect. The (absolute) value of Hedges g represents the number of standard deviations in which the intervention and control group differ.

tion in Arizona and New Mexico (n=4) (U.S. Fish and Wildlife Service 2009). Additionally, two studies suggested that shock collars effectively reduced wolf visitation to livestock farms that had previously suffered depredation. Moreover, in both studies, no livestock was killed by shock-collared wolves during the period of intervention (Rossler et al. 2012). Also, livestock guarding dogs were effective, reducing the number of killed livestock two- to threefold (n=1 and n=2 studies, respectively) (Salvatori & Mertens 2012), supporting the results from our meta-analysis (Figure 5).

Other protection measures that were not represented in the quantitative synthesis also suggested effective conflict mitigation. For example, electric fences used as part of the LIFE nature projects reduced depredations by 100% on Portuguese- (n=10) and Croatian (n=11) livestock holdings, compared to a 99% reduction in Spain (n=30) and a lower 57.80% reduction in Italy (n=239) (Salvatori & Mertens 2012). Moreover, RAG boxes efficiently detered wolves from depredating cattle in small pastures (Breck et al. 2002). Furthermore, management officials found that proactive use of range riders was effective in two out of four cases, with no attacks on livestock during the intervention (n=2), whereas two cases reported one and ten depredation incidents when range riders were active (eight months intervention), respectively (Fish and Wildlife Service 2009). Finally, a seven-year study on the adaptive use of predator deterrents and husbandry techniques in large sheep bands found that sheep depredations were 3.5 times lower in the protected area compared to the non-protected area (Stone et al. 2017).

Discussion

In this systematic review, we aimed to elucidate if – and to what extent – behaviour-based livestock protection measures are effective in discouraging wild wolves from approaching and killing livestock. The study results demonstrate that across all included studies, behaviour-based methods are highly effective at reducing livestock *depredation* by wolves, supporting our hypothesis that nonlethal tools can manipulate the (perceived) cost-benefit ratio in such a way that it deters wolves from predating on domestic livestock. Furthermore, it reinforces the application of behavioural principles in human-wildlife conflicts, as proposed by Blackwell et al. (2016). However, our study also underlines a key concern: the number of scientific publications evaluating behaviour-based protection measures against free-ranging wolves is very low (n=16), with even scarcer numbers of studies investigating interventions in actual conflict scenarios (on living livestock). This suggests that – although nonlethal methods are widely promoted – there is limited published empirical evidence to substantiate or guide the correct use of livestock protection measures.

Effectiveness of behaviour-based methods

The effect of intervention type: fladry, biofence and turbo fladry

The initial findings showed some fluctuation in effectiveness between studies within the same intervention and between different interventions. Although we could not test for the differences between aversive and disruptive stimuli interventions specifically, a meta-regression investigating the effect of *intervention* on the RR studies did demonstrate statistical differences in effectiveness between fladry, biofence and turbo fladry.

First, the results revealed that – across the included studies (n=12) – fladry was more effective than turbo (electrified) fladry at reducing depredation events. This goes against our hypothesis that interventions with a higher cost should be more effective, since electrified fladry induces both fear and pain (shock) compared to fladry which is solely based on neophobia. Hence, here we could conclude that our hypothesis was not supported and that stimuli type does not appear to influence depredation reduction. Alternatively, certain confounding factors could explain the unexpected result. First, the outcome measurement method might not have been appropriate enough to illustrate the difference in effects between the intervention types. During electrified fladry testing, Lance et al. (2010) measured effectiveness by track surveys (number of tracks inside- and outside of pasture), which did not allow for verifying whether wolves that had trespassed the fladry barrier had also received a shock. Without electric shock administration, electrified fladry would have exposed the animal to the same (disruptive) stimulus as classic fladry, potentially leading to similar effect sizes. Furthermore, only one fladry study evaluated similar conditions to the electrified fladry: trespassing on living livestock pastures (Davidson-Nelson & Gehring 2010). When isolating these two studies, the effectiveness is comparable (risk reduction of 70% for electrified fladry and 76% for fladry).

Secondly, fladry proved to be significantly more effective than biofence in reducing depredation and trespassing by wolves. Biofence (mimicking wolf presence by deploying wolf faeces and urine) was counter-productive and increased the number of visitations (trespasses) into the protected area, suggesting this method might not be effective at keeping wolves out of livestock pastures. This is in line with previous results by Anhalt et al. (2014), where the biofence failed to significantly manipulate wolf movements. However, here we examined the outcome measure 'number of trespass locations' instead of 'average trespass distance (km)' (unusable data due to lack of variance measure). Under natural inter-pack dynamics, wolves respect territory boundaries to avoid being killed by adjacent packs (Smith & Ferguson 2012). Nevertheless, wolves may cross boundaries without entering far into the rival pack's territory, as each added distance increases intraspecific mortality risk (Mech 1994). When considering the outcome 'average distance trespassed', wolves moved less far into the treated area, suggesting the bio boundary changed wolf behaviour to some extent by mimicking adjacent pack presence. Further research could investigate whether wolves would respond better to biofence material retrieved from dominant individuals, as in this study, authors could not control for the hierarchical origin of the scat and urine. It remains to be tested whether biofence could be a useful tool to apply in real management scenarios. Although the labour-intensive maintenance of the biofence (frequent refreshing of odour cues) might limit extensive practical applications, it could be trialed as a tool for smaller-scale interventions like deterring young dispersing wolves from livestock pastures.

To conclude, more research is needed before we can make strong inferences about the differences in effectiveness between interventions and identify the additional factors that may partly explain the observed variation in effect sizes. Such confounding factors are crucial to elucidate in future studies, as this can help build stronger guidelines for using protection measures in different depredation scenarios.

Effectiveness of disruptive and aversive stimuli interventions

Disruptive methods attempt to repel predators from livestock by making use of fear-inducing stimuli that instigate a flight response. Fladry has been used for centuries in wolf hunts and was later deployed to frighten wolves away from livestock by relying on the flapping of fladry fabric strips in the wind. In this review, fladry was the most studied intervention (n=9) and showed highly promising results as a tool to reduce trespassing behaviour and livestock depredation by wolves. Nevertheless, our second meta-analysis (SMD) revealed an apparent counter-productive, yet non-significant, effect in one of the fladry studies (Shivik et al. 2003). Here, fladry use coincided with increased carcass consumption by predators at bait sites, which unexpectedly contrasted with our hypothesis. It, however, remains unclear to what extent this study reflected the deterrence ability of fladry towards wolves, given that the study evaluated the total amount of bait consumed simultaneously by multiple predators, including raptors such as eagles. Pre-treatment food conditioning could have made bait stations an increasingly popular diversionary feeding location, leading to increased consumption during fladry treatment by flying scavengers that did not have to physically trespass the fladry barrier. This is in line with previous research findings that deterrent tests intended for one species could serve as an attractant to other species (Woodroffe et al. 2007). Although in eight out of nine studies, fladry significantly reduced depredation events, it remains a continuous visual cue with a strong risk of habituation, making treatment duration a key factor. Musiani et al. (2003) found that fladry was effective for 60 days, after which trespassing and depredation resumed, suggesting that fladry is best applied punctually during critical moments such as calving or lambing seasons. Electrified fladry proved to have the capacity to reduce trespassing (see earlier) and could provide a suitable alternative to limit habituation, provided more research is done to support this hypothesis.

Aversive stimuli such as shock collars induce discomfort or pain to prevent an individual from performing an unwanted behaviour. Shock collars emit an electric current into the neck of wolves when they trespass on a protected area, to link the act of approaching livestock (or bait) to an aversive experience. Our findings show that shock collars were highly effective in two studies included in the quantitative synthesis and proved to reduce depredation behaviour in the remaining two studies from the qualitative review. These studies were typically of high reliability thanks to the use of VHF telemetry as an outcome measure and the high balancing/randomisation between study groups. The quality of the studies and the large effect sizes represented in the SMD meta-analysis suggest that this type of aversive stimulus can strongly influence the behaviour and movement of wolves by representing an increased cost (OF) or risk to survival (LOF) as proposed by Haswell et al. (2019) and Miller & Schmitz (2019). Although shock collars have proven highly effective in these studies, its practical implementation might be limited by the financial and logistical resources required to locate and capture wolves and maintain the equipment (Rossler et al. 2012). Because of the labour-intensive aspect of collaring wolves and the relatively short-term battery life, it is doubtful that shock collars will be a cost-effective method to mitigate large-scale wolf-livestock conflicts. However, it could be a viable solution in areas where capturing- and GPS collaring are already part of management or study efforts and where depredation events are recurring in specific areas.

Electric fences are based on the same principles as shock collars and induce an aversive electric shock to wolves when they attempt to enter livestock pastures. Yet, their easy deployment might have a higher applicability in the field. Today electric fences are widely used in management efforts throughout the world. It is therefore surprising to uncover that only four studies from one single article (Salvatori & Mertens 2012) performed an empirical evaluation of the method on wild wolves, at least according to our systematic English-based search results. Overall, these studies support electric fences and suggest that this aversive and behaviourally contingent (direct consequence to an undesired behaviour) stimulus could prevent wolves from trespassing into livestock pastures. Nevertheless, in Italy, the reduction in depredation was much lower than in the other three countries (58% vs 99-100%), likely due to some livestock owners (total n=239) not keeping their entire flock inside the fences (Salvatori & Mertens

2012). It is also not excluded that wolves were able to dig under or jump over fences. Jumping was presumably the reason for Samelius et al. (2021) to set up 2-metre-high fences with an electrified top wire to protect Mongolian livestock. Their results demonstrated that tall fences can prevent further damage to livestock and that providing an initial physical barrier (energetic cost), in addition to an aversive stimulus (electrified top wire), can prevent wolves from trespassing into enclosures. Tall fences also require situation-specific use, as they are labour-intensive and cannot be used to protect large domestic flocks (Samelius et al. 2021). In addition, such tall fences could obstruct the migration routes of other wildlife. In these cases, smaller electric fences may be more applicable. But first more reported evaluations are needed.

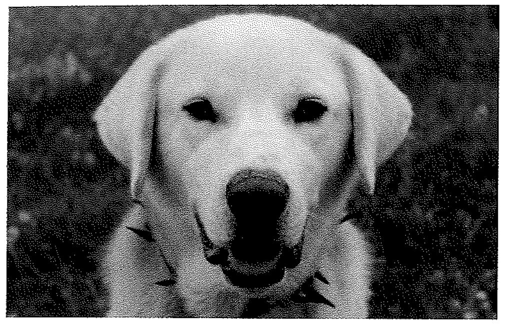
In contrast to electric stimuli, livestock-guarding dogs (LGD) have been used for millennia to protect domestic animals from wolves and other predators (Gehring et al. 2010b). Overall, guarding dogs proved a reliable measure to reduce domestic animal losses to wolves. Livestock guard dogs limited wolves killing sheep, cattle and mixed livestock in several countries but generally did not prevent depredations completely. Use of guarding dogs combines disruptive and aversive stimuli and the dogs can serve both as a warning signal to wolves (Landry et al. 2020) and pose a considerable threat to their survival if habituation occurs. Dogs can also disrupt wolf feeding on livestock carcasses, adding an additional cost to predating on LGD protected livestock. The ability of some wolves to still predate on LGD protected livestock could be attributed to age- and breed-specific traits. Indeed, livestock guarding dogs mostly become (cost-) effective starting age two, and show variation in effectiveness between breeds (Kinka and Young 2019). Moreover, when working with living protection measures, there are other parameters to consider such as individual variation in behaviour or health as well as the inter-specific interactions that might occur with other species. Guarding dogs might, for example, wander off in pursuit of wildlife (Smith et al. 2020) or attract wolves by their presence instead of repelling them (Woodroffe et al. 2017). The latter is especially true in the mating season when LGDs were seen mating with wolves, resulting in hybridisation (Kopaliani et al. 2014, Kusak et al. 2018). In areas prone to hybridisation, it might be useful to consider sterilisation, which can also reduce wandering behaviour. The effectiveness of guarding dogs in wolf territories might also be season specific, as suggested by Stone et al. (2017). Stone et al. (2017) recommend dogs should not be deployed in core-wolf areas during denning and puppy season as it could increase wolf-dog aggression with wolves attacking and killing LGDs to protect their pups. Therefore, it is important to tailor the use of guarding dogs to the context and avoid an increase in conflict.

The success of adaptive approaches to wolf management and blended use of nonlethal tools was demonstrated in a seven-year study by Stone et al. (2017). In this management effort, large bands of 10,000 – 22,000 transhumant sheep were protected by context-dependent use of deterrents (e.g. fladry, fox lights, starter pistols, LGDs) and adaptive husbandry practices such as fencing at night, avoiding moving sheep through wolf rendezvous sites and guarding sheep with range riders. This method resulted in 3.5 fewer sheep killed in the protected area compared to the non-protected area, and no lethal control of wolves being necessary in the protected area. This study demonstrates that nonlethal tools can efficiently reduce livestock losses even on large operations in rugged and remote areas. Although this study did not allow the identification of single-intervention effectiveness, it does point to the promising potential of combining multiple methods to manage conflict scenarios. Biologically, alternating interventions can reduce habituation and combining multiple stimuli can increase the perceived intensity of human presence and/or reduce

Foxlight on a stick used as a visual deterrent to keep wolves from approaching sheep in Idaho, USA. *Photo: Wood River Wolf Project.*

the benefits initially associated with livestock predation. Human presence, however, does not systematically provoke a strong effect: the varying success of range riders seen in management practices across New-Mexico and Arizona (U.S. Fish and Wildlife Service 2009), could indicate that fear for the human "super predator" as suggested by Smith et al. (2017) can fade over time when no negative consequences are linked to their presence. In this regard, the duration of protection measure implementation might influence the outcome. In the management efforts of the U.S. Fish and Wildlife Service (2009), losses occurred solely during longer eight months range rider interventions and not during three- and four months interventions. To counter habituation, in many management efforts, range riders also deploy deterrents upon the perception of wolves or their indices of presence (tracks, howls, GPS-positions), rendering the effect of range riders more behaviourally contingent.

Other behaviourally contingent measures in this review were the movement-activated guard (MAG) and radio-activated guard boxes (RAG). These boxes emit frightening sounds (cracker shells, pistol- and helicopter sounds) and strobe lights when (1) wolves pass in front of the box activating the movement sensor or (2) radio-collared wolves trespass an area protected by the RAG box monitor (invisible GPS monitored-line), respectively. The MAG-box reduced predator consumption on bait sites (Shivik et al. 2003), whereas RAG box efficiently repelled wolves from predating on calves (Breck et al. 2002). It is fairly certain the RAG boxes were able to increase the risk landscape for wolves, and manipulate their behaviour because when a RAG box malfunctioned, the wolves immediately killed a calf in the no-longer protected pasture. This was not due to habituation because after reparation of the box, no more depredations occurred. These scarcely studied behaviourally contin-



Young livestock guardian dog (LGD) with spiked collar used to protect sheep and goats in remote mountain village, Vikos Aoos National Park, Greece. *Photo: Thaana Van Dessel.*

gent tools would benefit further research to evaluate whether they could be used in larger-scale management efforts.

Behavioural principles as a basis for livestock protection measures

As seen earlier, most studies in this systematic review demonstrated that behaviour-based interventions were effective at decreasing wolf approaches and attacks, suggesting that nonlethal tools are, in fact, able to induce behaviourally-mediated effects that manipulate wolf behaviour and movement in a way that reduces depredation events. This review supports previous results and theoretical frameworks by Blackwell et al. (2016), Haswell et al. (2019), Miller & Schmitz (2019) and Wilkinson et al. (2020) proposing that behavioural principles – and, more specifically, the landscape of fear (Brown et al. 1999) and optimal foraging theory (MacArthur & Pianka 1966) – could be a valuable basis for human-carnivore conflict mitigation by using stimuli that heighten the perceived risk and cost associated with attacking domestic animals. It is unlikely that factors other than the interventions were responsible for increasing the cost/risk of predation between control and treatment units since, in most studies, before-after study designs were used, ensuring similar environmental- and farm conditions within one study (high and intermediate comparator matching). Nevertheless, we cannot exclude that higher hunting pressures between control and intervention study years could have affected the landscape of fear of wolves in such a way that they did not approach or predate on livestock anymore. Although we could not evaluate this, behaviourally-mediated effects due to hunting remain doubtful as most studies reported some measure of wolf presence in the area, both before and during the intervention through track surveys, GPS positions and camera traps. Controlling for wolf presence also excludes the confounder of intervention success due to wolves having deserted the area during the implementation of the intervention.

In contrast, variation in effectiveness between studies or intervention types, rather than within study, could have been influenced by a wide range of other factors that we were unable to statistically evaluate in this study due to the limited sample size. One of these factors – the availability of alternative prey sources – plays a pivotal role in the cost-benefit tradeoff between predating on wild- or domestic animals (Torres et al. 2015, Soofi et al. 2018, Werhahn et al. 2019) and could ultimately influence the effectiveness of protection measures. Nonlethal measures attempt to artificially increase the cost of livestock depredation by inducing fear, pain or a risk of injury (Haswell et al. 2019). However, how this cost is perceived (low or high) can be influenced by intrinsic motivation (hunger, pups to feed) and the obtainability of wild prey. Wild prey abundance and distribution, and the energy and risk associated with attacking wild animals (armaments, defence mechanisms), are all important parameters in evaluating the benefits of turning to (protected) livestock. Livestock is generally a low-cost and low-risk food source for wolves, as they are available in large numbers, usually under predictable distribution patterns, and exhibit low- to no antipredator behaviour (Flörcke & Grandin 2013). Although protection measures take away some of these benefits, when wild prey populations are depleted or prey are particularly risky to attack, it can become a viable foraging strategy for wolves to be bolder towards nonlethal measures and attack livestock (Torres et al. 2015). Although we could not test this, we hypothesize that the effectiveness of behaviour-based interventions will be highly dependent on the availability of wild prey as an alternative resource.

To summarise, the results from this review strongly encourage the use and further development of behaviour-based tools in wolf management, since using behavioural principles to "educate" wolves could be a promising nonlethal alternative that supports both livestock farming and wolf conservation.

The evidence base

Sustainable mitigation of human-wolf conflicts relies strongly on using nonlethal methods that can efficiently prevent wolves from killing livestock and that support the conservation of wolf populations by avoiding lethal control. The evidence gap on the effectiveness of mitigation measures unveiled in this review has strong implications for wolf management and coexistence efforts (van Eeden et al. 2018), especially when livestock owners are already doubtful or withstanding methods that do not include (lethal) removal of the predator (Scasta et al. 2017). When strongly advocated measures are ineffective, it might heighten the mistrust towards interventions and management efforts, increase negative attitudes towards wolves and potentially limit the possibility for management agencies to recommend other methods in the future (Bogezi et al. 2021). Even with the additional studies conducted in the past five years, the results of our review strongly align with the findings by Eklund et al. (2017), Miller et al. (2016) and Treves et al. (2016), who reviewed the effectiveness of protection measures against large carnivores and Bruns et al. (2020), who studied measures against wolves specifically.

Although our review strongly supports previous findings – suggesting our search methods were indeed comprehensive – we cannot rule out that our results were to some extent limited by the scope of our literature search. Especially the restriction to the English language and the limited amount of grey literature may have led us to exclude relevant studies. These factors work in concert given that grey literature is often published in the local language. Grey literature was available and retrieved through the specialist database (Snijders et al. 2019), but only one of the studies (U.S. Fish and Wildlife Service 2009) met the selection criteria and could be included in the (qualitative) review. Nonlethal methods are often implemented in larger-scale management efforts, providing valuable insights into the effectiveness of these methods, but without necessarily being scientifically reported. Hence, not having a more comprehensive inclusion of grey literature could have caused our results to be, in some degree, affected by *publication bias*, since negative results are more likely to be reported in grey literature (if at all). When considering livestock protection measures, these negative or weak study outcomes – if they occur – are critical components to effectively adjust and adapt existing mitigation tools.

Our results may also have been affected by the duration of the intervention treatments, especially for studies on disruptive stimuli that rely on fear to be effective and are at risk for wolf habituation. Since habituation occurs over time with the repeated exposure to the (disruptive) stimuli, a longer exposure time can decrease the effectiveness of the protection measure, and vice-versa (Shivik & Martin 2000). Hence, the shorter the intervention treatment duration, the higher the probability of overestimating the effectiveness of a given protection measure. In our review, most studies evaluating the effectiveness of disruptive stimuli interventions used short treatment durations of a couple of months, ranging from 16 days to six months for fladry (Shivik et al.

2003: 16–29 days, Musiani et al. 2003: 60 days, Davidson-Nelson & Gehring 2010: 75 days, Iliopoulos et al. 2019: 23–165 days (per pack), U.S. Fish and Wildlife Service 2009: 180 days), 16–29 days for the Movement Activated Guard box (Shivik et al. 2003), 60–90 days for the Radio-Activated Guard box (Breck et al. 2002) and 90 days for biofence (Ausband et al. 2013). In future research, it would be useful to gain more insight into the longer-term effectiveness of these measures by evaluating livestock losses over multiple seasons, or years, if possible.

We acknowledge that field studies – especially on wolves – can be challenging and limit the possibility of achieving a golden standard in research. Therefore we would recommend further research to at least focus more on real conflict scenarios. With wolf-livestock conflict increasing in magnitude, the need for data on changes in depredation rates of living livestock is more urgent than ever. Moreover, it would be beneficial to study and further develop behaviourally contingent measures, to incorporate data on wild prey densities when evaluating protection measures, and to broaden the geographical distribution of studies, which are currently primarily aggregated in the United States. A wider and more robust evidence-base will allow for stronger reviews and meta-analyses that will have the power to unveil patterns in depredation events as well as the factors that influence them. This, in turn, could inform adaptive and context-specific implementation of protection measures that can more efficiently target unwanted wolf behaviour and reduce conflict situations.

Conclusions

The results of this systematic review demonstrate that across the available studies, the protection measures were highly effective and were able to manipulate wolf behaviour and distribution in such a way that it decreased depredation events. But the findings also revealed a considerable lack of evidence on the effectiveness of behaviour-based methods against free-ranging wolves. The current evidence base supports the hypothesis that nonlethal tools can increase the perceived cost or risk (OF and LOF) of predating on livestock, making it more beneficial for wolves to turn to alternative prey. This cost-benefit tradeoff could, however, strongly be influenced by environmental factors, as variation in effect size between different studies of the same intervention type was frequent. To better understand to what extent- and in which circumstances behaviour-based interventions are effective, there is a strong need for additional high-quality studies to fuel the evidence base. Reducing conflicts of interest between wolves and livestock activities is crucial for wolf conservation, livestock welfare and farmer livelihoods. Therefore, we urge the scientific community to support sustainable coexistence between humans and wolves by further investigating the use of behaviour-based nonlethal methods to protect domestic animals from wolf depredation.

Acknowledgements: We want to thank the authors that agreed to share their raw data (Samelius et al. 2021) and – by doing so – allowed us to include an additional study in the meta-analysis. We also thank members of the Behavioural Ecology Group (WUR) for giving constructive feedback during the process of this study. Furthermore, we want to thank our peer reviewers for their valuable input, along with Matthieu Chastel, who reviewed the original thesis. Finally, we are thankful to our fellow wolf scientists for their advice on the complex issue of human-wolf coexistence.

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Samenvatting

De effectiviteit van gedragsmatige interventies ter vermindering van predatie van vee door wolven

Om mensen en wolven (*Canis lupus*) op een duurzame manier te laten samenleven hebben we interventies nodig die effectief de predatie door wolven van vee kunnen verminderen. Doordat wolven in hun aantallen en verspreiding weer toenemen, nemen ook de verliezen van vee en huisdieren toe, ondanks de grootschalige implementatie van zowel letale als niet-letale beheersmiddelen. Het groeiende belangenconflict tussen natuurbeschermers en veehouders vereist, onder andere, een aanpak gebaseerd op feiten en wetenschappelijk gefundeerd inzicht in de effectiviteit van niet-letale beheersmiddelen. We hebben daarom een systematische review uitgevoerd en zo de beschikbare studies omtrent de effectiviteit van (dier)gedragsmatige interventies in wilde wolvenpopulaties onderzocht en samengevat. Door de kosten/baten afweging bij het wel of niet aanvallen van vee te beinvloeden kunnen gedragsmatige interventies namelijk wolven motiveren om voor alternatieve prooien te kiezen. We doorzochten systematisch academische databanken zoals Scopus en Web of Science en zochten naar literatuur in een gespecialiseerde literatuur databank gemaakt door Snijders et al. (2019). We hebben 2825 publicaties gevonden, waarvan 16 artikelen (en hun 31 gerapporteerde onderzoeken) na een screeningproces zijn opgenomen in deze review. Als maten voor de grootte

van het interventie-effect, gebruikten we zogenoemde ‘relative risk ratios’ (RR) en ‘standardized mean differences’ (SMD) en voerden vervolgens een meta-analyse uit. Ons onderzoek bracht een zorgwekkend gebrek aan gepubliceerd empirisch onderzoek naar niet-letale interventies aan het licht, althans in de Engelse taal. Dit, ondanks de wijdverspreide toepassing van deze interventies. Desalniettemin toonden onze synthese dat de meeste interventies, met name fladry, zeer effectief wolven weerhouden van het aanvallen of benaderen van levend vee of lokaas. Als gevolg van het beperkte aantal analyseerbare studies, was het niet mogelijk om factoren te onderzoeken die mogelijk de grootte van de effectiviteit van een gegeven interventie beïnvloeden. Dergelijk onderzoek zou in de toekomst kunnen leiden tot meer op maat gemaakte praktische aanbevelingen over wanneer en waar welk type interventie te gebruiken. Over het algemeen suggereren onze resultaten dat gedragsmatige niet-letale maatregelen een veelbelovend hulpmiddel kunnen zijn, op voorwaarde dat verder onderzoek onze bevindingen ondersteunt. Daarom raden we wetenschappers, natuurbeschermers en beheersautoriteiten sterk aan samen te werken en nader onderzoek te verrichten naar gedragsmatige interventies. Bovenal is ons advies om de werkzaamheid van deze interventies systematisch in reële predatiescenario’s te onderzoeken (in plaats van met lokaas). Een meer op wetenschappelijk bewijs gebaseerde benadering van mens-wolfconflicten is een essentieel onderdeel van een duurzame toekomst voor wolven, landbouwdieren en pastorale activiteiten.

Received: 16 March 2023
Accepted: 9 May 2023

Are offshore wind farms in the Netherlands a potential threat for coastal populations of noctule?

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Abstract: Offshore wind farms likely cause mortality amongst migratory bats. Yet it remains unknown whether resident coastal bat populations may be affected by offshore wind developments. We performed an analysis to assess the potential risk of offshore wind farms in the Dutch North Sea for local coastal populations of noctule (*Nyctalus noctula*). First, we assessed the potential overlap between their foraging range and areas with operational and planned offshore wind farms. Subsequently, we tracked 14 noctules from a coastal population during late summer and autumn and analysed their movements. In general, it seems unlikely that offshore wind farms in the Netherlands will significantly affect coastal populations of noctule since offshore wind developments take place beyond their regular foraging range. In some cases however, noctules do perform distant flights (‘swarm flights’), possibly in response to migrating insects. We recorded six distant foraging trips both over land and over sea with a maximum distance of 18.5 km from their roost and 12.7 km from shore. Acoustic records confirm that noctules are occasionally present in offshore wind farms at distances of 15-25 km from shore. During such an event, noctules face the risk of a collision as virtually all their flight activity occurs at heights within the rotor swept area of offshore wind turbines.

Keywords: bat mortality, energy transition, collision, barotrauma.

Introduction

The development of the offshore wind sector plays an important role in the Dutch energy transition. In 2022 a capacity of 2.5 GWH has been realized, consisting of 260 turbines in six different offshore wind farms. The installed capacity should increase to 11 GWh in 2030, which equals to 8.5% of the total energy consumption in the Netherlands and 40% of the current electricity use (Offshore Wind Energy Roadmap 2030). Offshore wind farms will therefore enable a considerable reduction in greenhouse gas emissions in the Netherlands.

Despite this environmental gain, there are biodiversity concerns at the same time: onshore wind turbines are known to cause mortality amongst bats due to collisions (Johnson et al. 2003, Bach & Rahmel 2004, Kunz et al. 2007, Arnett et al. 2008, Rydell et al. 2010, Cryan et al. 2014, Thaxter et al. 2017) and possibly barotrauma (Grodsky et al. 2011, Rollins et al. 2012, Lawson et al. 2020). Significant numbers of fatalities have been reported on land (Hayes 2013, Voigt et al. 2015, O’Shea et al. 2018), which may cause declines in local as well as migratory populations (Lehnert et al. 2014). In temperate regions most fatalities concern migratory species and occur during late summer and autumn (Rydell et al. 2010, Voigt et al. 2015, Frick et al. 2017, Rodrigues 2018). In order to reduce fatalities curtailment