






REVIEW

Protecting wild bird nests against predators: A systematic review and meta-analysis of non-lethal methods

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Abstract

1. Implementing effective, affordable and ethical conservation management will be crucial for minimising future biodiversity losses. Such management requires reliable foundational evidence to help managers make informed choices about how to address the needs of their target species. Unfortunately, such evidence is still lacking for many species and management scenarios.
2. One major global challenge is improving the reproductive success of threatened species in the context of predation. We conducted a systematic review and meta-analysis of in situ experiments that used non-lethal methods to protect bird nests against predators, with the aims of summarising global trends in nest protection efforts, comparing the effectiveness of different protection measures and informing future research and management. We considered peer-reviewed studies in English.
3. We detected a large geographic and taxonomic bias in the evidence base with 58% of articles conducted in North America and 76% on ground-nesting birds. Less than 3% of articles involved taxa listed as Endangered or Critically Endangered and 51% of study units lasted just a single breeding season.
4. Nests protected with exclosures, fences and guards were more likely to be successful than their unprotected controls. Interventions involving deterrents, conditioned taste aversion, chemical camouflage and diversionary feeding did not have a significant positive effect on nest success, but the interventions in these categories were less common and more diverse in nature.
5. *Synthesis and applications.* To increase their conservation value, future non-lethal nest protection experiments should whenever possible clearly state overall aims, take place over multiple seasons, use a comparable control and test non-lethal protection methods independently of lethal predator control. Greater focus is required on under-studied taxa such as cup-nesting songbirds and birds in South America, Africa and Asia, and novel protection techniques such as deterrents and chemical camouflage. Practitioners should consider the evidence we synthesise here when deciding whether non-lethal nest protection approaches are optimal

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for their study system, to increase conservation success and reduce ethical and financial costs.

KEYWORDS

avian conservation, breeding success, hatching success, nest predation, nest survival, predator exclusion, wildlife conservation

1 | INTRODUCTION

The breeding period is a time of particular vulnerability for many organisms and low rates of breeding success can threaten the persistence of populations. For many species, predation is a prominent cause of breeding failure (Ibáñez-Álamo et al., 2015; Kats & Ferrer, 2003). While predation is a natural ecosystem process, anthropogenic habitat changes and exotic species introductions can drastically alter the composition of predator communities (Ritchie & Johnson, 2009), putting pressure on vulnerable prey populations (Doherty et al., 2016). For threatened species facing elevated predation risk, devising effective ways to reduce predation rates will be crucial for minimising future extinctions (Doherty et al., 2016). In the face of persistent global biodiversity loss (Ceballos et al., 2017), implementation of effective, evidence-based conservation has become a priority (Sutherland et al., 2004). Implementing conservation actions based on robust evidence offers high confidence that desired outcomes can be achieved and ensures effective utilisation of limited conservation funds (Cook et al., 2017). Evidence-based conservation practices can also facilitate the ethical refinement of management actions (Doherty & Ritchie, 2017).

For birds—among the most well-studied animals—eggs, chicks and breeding adults are often susceptible to predation (Ibáñez-Álamo et al., 2015). The nesting period is therefore a key focus for managers around the world seeking to implement evidence-based conservation to boost avian breeding success. Managers may attempt to achieve this via the provision of artificial nest sites (e.g. Mänd et al., 2005) and good quality habitat/resources required for nesting (e.g. Narango et al., 2017), exclusion of livestock or people from nesting areas (e.g. Berger-Geiger et al., 2019) or through predator control or exclusion (Smith et al., 2010, 2011). The impact of nest predators can be reduced using both lethal and non-lethal techniques. Lethal control involves the trapping, shooting, poisoning or otherwise killing of target predators to reduce their abundance or remove them from breeding areas. This can be an effective strategy in reducing nest predation rates (Smith et al., 2010) but can also be ethically and politically contentious and may result in unintended impacts on non-target species (Doherty & Ritchie, 2017). In such instances, non-lethal nest protection measures may be more ethical and, depending on the approach used, less labour-intensive (Doherty & Ritchie, 2017). Protecting bird nests from predators using non-lethal methods often involves the use of physical barriers such as fences, guards and cages to discourage or prevent predators from

entering a nesting site (Smith et al., 2011). However, an increasing number of studies are exploring alternative nest protection methods that manipulate the behaviour of nest predators, such as deterrents (e.g. Liu & Liang, 2021), chemical camouflage (e.g. Norbury et al., 2021) and conditioned taste aversion (e.g. Tobajas et al., 2020).

We conducted a systematic review and meta-analysis of peer-reviewed, experimental studies of non-lethal nest protection for wild birds, with two major aims:

1. To provide a global overview of research on non-lethal wild bird nest protection in order to detect knowledge gaps and provide guidelines for future research.
2. To examine the efficacy of non-lethal nest protection methods as a means of increasing wild bird nesting success and test whether system-specific factors such as nest position and predator taxon have any detectable influence on their effectiveness.

2 | MATERIALS AND METHODS

2.1 | Criteria for the inclusion or exclusion of studies

We established strict inclusion and exclusion criteria in order to identify relevant studies for our meta-analysis. We included only peer-reviewed studies available in English that were conducted in situ. Studies were only included if they tested the effectiveness of non-lethal nest protection, aimed specifically at protecting bird nests from wild predators and provided nest success data in terms of daily nest survival rate (DSR) or apparent nest success (i.e. failed or succeeded). We excluded articles if they involved any form of lethal predator control, protected nests from threats other than predation, did not measure nest fate as a binomial outcome or did not contain a suitable control. We considered a suitable control to be a control group that closely replicated the conditions of the treatment group without major confounding factors. We did not consider changes in nest productivity for this analysis, as nest success was the more commonly reported measure in the literature.

2.2 | Systematic review

We used two search platforms for our literature search: *Web of Science (WoS)* and *Scopus*. We used the software *Covidence (Veritas*

Health Innovation, 2023) to streamline the review process. For WoS we searched for 'Topic' within 'All Databases' (WoS Core Collection, Current Contents Connect, KCI-Korean Journal Database, MEDLINE and SciELO Citation Index) and for Scopus we searched 'Title, Abstract, Keywords'. We searched for literature on both platforms on the 10th of October 2023, using a search string designed to capture all relevant literature (Appendix S1).

2.3 | Article screening

Excluding duplicates, our search identified 1297 unique articles, which passed two-stage screening (Figure S1). All articles underwent double title/abstract screening by DG and RC. During abstract screening, we reached agreement on inclusion or omission of 93% of articles. We assessed the remaining articles ($n=86$) further until an agreement was made whether to include or exclude. Accepted articles and articles we were still uncertain met the inclusion criteria after title/abstract screening advanced to the full-text review. A total of 180 articles entered full-text screening. During full-text screening, we excluded a further 113 articles. The primary reasons for exclusion were the presence of some lethal predator control ($n=30$), the absence of a suitable measurement of nest success ($n=16$) and the absence of a suitable control group ($n=16$; Figure S1 and Appendix S3). Additionally, we excluded parts of some relevant articles due to their lack of suitability for the meta-analysis. We deemed 67 articles to fulfil all our inclusion criteria (Figure S1).

During the literature screen, we flagged five relevant review articles (Beauchamp et al., 1996; Franks et al., 2018; Hartway & Mills, 2012; Scopel & Diamond, 2017; Smith et al., 2011) and searched their reference lists for articles not found in the structured literature search. We also searched the reference and citation lists of the papers identified as suitable for our review in Covidence between the 12th and 13th of October 2023. We identified 13 articles for inclusion through citation searching, bringing the total number of articles included in our meta-analysis to 80 (Figure S1, Appendix S2).

2.4 | Data extraction and effect size calculation

We extracted data manually for 80 articles that met all inclusion criteria. Whenever possible, we separated article components that presented data on different prey families, different interventions or used notably different methods. We refer to these components within an article as 'study units' throughout the analysis. To provide a general overview of the literature, we extracted the country in which the study took place, details of treatment and controls in terms of protection measures implemented and sample sizes, as well as relevant notes on study design and additional comments/assumptions. We extracted quantitative data to calculate an effect size (log odds ratio) and corresponding sampling variance for each study unit. See Appendix S1 for further detail regarding effect size calculations.

We predicted that five moderator variables would impact the effectiveness of non-lethal nest protection interventions and extracted information accordingly (Table S1):

2.4.1 | Prediction 1—Intervention type

We predicted that physical barriers preventing predator access to nests from all directions would be more effective than those which only prevent access from a single direction and those that do not physically prevent access at all (Prediction 1a). We categorised each non-lethal nest protection intervention as either a physical intervention (enclosure, fence, guard) or a behavioural intervention (deterrent, conditioned taste aversion [CTA], diversionary feeding [DF] or chemical camouflage [CC]). Two interventions that did not fit into these categories (Mulder et al., 2021; Stojanovic et al., 2019) were grouped as 'other'. We defined an enclosure as a physical barrier aiming to prevent predator access from all directions, a fence as a physical barrier attempting to prevent the horizontal movement of predators (accompanied by live-trapping and translocation for four studies) and a guard as a physical barrier attempting to prevent vertical movement through climbing. Behavioural interventions aimed to discourage nest predation by manipulating predator behaviour but did not physically block their access to nests. We defined a deterrent as an intervention that attempts to immediately discourage predators from preying on a nest, conditioned taste aversion as an intervention which involved conditioning predators to avoid consuming eggs, diversionary feeding as the use of supplementary food to divert predators away from nests and chemical camouflage as the use of misleading odours to confuse olfactory predators into perceiving nests as unprofitable. Furthermore, we predicted that electrified fences would have a stronger effect than non-electrified fences (Prediction 1b) and therefore recorded whether fences were electrified or not. Because just one study involved electrified enclosures (Maslo & Lockwood, 2009), we only analysed the efficacy of electrification for fences.

2.4.2 | Prediction 2—Nest position

We predicted that position of nests would influence the effectiveness of interventions; specifically, that protection of ground nests would be more effective than of nests in other locations, based on the challenges associated with protecting less accessible nests (Major et al., 2015). To test this, we recorded the nest position for each study unit as a three-level factor: ground, elevated or cavity. We defined a ground nest as any nest that was established on the ground; an elevated nest as any nest elevated off the ground but exposed to predators (e.g. cup nests); and a cavity nest as a nest that is also off the ground but established in cavities such as tree hollows or nest boxes. One study included nests from multiple positions (Cocquelet et al., 2019), and therefore we excluded it from the analysis of this moderator.

2.4.3 | Prediction 3—Predator taxon

We predicted that the predator taxon being targeted by an intervention would influence the effectiveness of the intervention method. To test this, we categorised each study as focusing on one of five different predator taxa: mammals, birds, reptiles, crustaceans or multiple (protecting against more than one predator taxon).

2.4.4 | Prediction 4—Experiment type (artificial/natural)

We predicted that artificial nest experiments could exhibit different results to experiments focused on real nests, based on the divergence of results from artificial and natural nests in previous studies (Moore & Robinson, 2004; Weston et al., 2017). To test this, we defined each study unit as either artificial or natural based on the nature of the experiment. One study combined artificial and natural nests (Crabtree & Wolfe, 1988), and therefore we excluded it from the analysis of this moderator.

2.4.5 | Prediction 5—Prey family

We predicted that the focal prey species could affect the effectiveness of nest protection due to differences in life histories. Thus, we controlled for bird family in our analysis. Some studies focused on multiple bird species/families and therefore we could not always assign a single family value for analysis. For artificial nest experiments, we considered the species and family information not to be applicable (N/A).

We recorded four additional methodological covariates to ensure that differences in approach did not explain the variation in effect sizes between studies. These were study duration (number of breeding seasons); whether nest success was defined as a binary outcome (apparent nest success) or a rate (e.g. DSR); the period over which nest success was measured (e.g. incubation period); and nest failure definition (whether all causes of nest failure were considered, or only failures due to predation). When this information was not explicitly stated by the authors, we deduced the most logical value where possible. Where this was not possible, we set this covariate to N/A.

2.5 | Data analysis

Our complete data set consisted of 104 effect sizes (study units) from 80 articles. As not all variables were available for all study units, to test some predictions we divided the data into subsets (Table S1). We used R v4.3.1 (R Core Team, 2022) for all data analysis. We used the package metafor v4.4.0 (Viechtbauer, 2010) to calculate effect sizes for each of our study units in the form of log odds ratios and corresponding sampling variances (see Appendix S1 for

further details). We then fitted a random-effects model (null) and mixed-effect models for these data, containing variables of interest as single explanatory variables (intervention type, nest position, target predator taxon, experiment type and prey family). For a subset of study units that involved fences, we tested the effect of electrification using a mixed-effects model. Chi-squared tests revealed a lack of independence between moderators (Table S2), so we did not fit multivariate models to avoid multicollinearity (Graham, 2003). We determined the most parsimonious model through comparison of corrected Akaike information criterion (AICc) values, with the lowest AICc value as the best fit to the data (Burnham et al., 2011). We fitted additional mixed-effect models to determine whether study duration, nest success measurement type (binary or rate), nesting period measured or failure definition had a measurable impact on effect sizes.

To ensure our results were not biased by particular nuances of the study set, we analysed two additional data sets. These contained no more than two study units per article (achieved by combining similar interventions or prey families where necessary, $n=92$), and all study units except those focused on piping plovers *Charadrius melodus* ($n=89$), as this species was disproportionately represented in the global data set. To conduct a sensitivity analysis, we used the `leave1out()` function in the package metafor (Viechtbauer, 2010), which tests the effect of excluding any one study unit on the overall model estimates. The analysis can be reproduced using the information, code and data available at <https://doi.org/10.5281/zenodo.10703166> (Gautschi et al., 2024).

3 | RESULTS

3.1 | Global trends of non-lethal bird nest protection research

The 80 articles included in the meta-analysis involved study sites in 20 countries and one overseas territory (Figure 1a). Over half (46) were conducted in North America. Nearly a third (31%) of articles involved plover species (family *Charadriidae*), with 13 articles focusing on piping plovers *Charadrius melodus*. The nests of a further 21 families (Figure 1b) and 64 species were represented in the meta-analysis, of which only the giant ibis *Thaumatibis gigantea* is listed as Critically Endangered and only the saffron-cowled blackbird *Xanthopsar flavus* as Endangered according to IUCN criteria (IUCN, 2022). Only three species are Vulnerable, while all others are either Near Threatened ($n=4$) or Least Concern ($n=56$, Table S3).

Most articles (76%) were published in the 21st century. The median treatment duration for study units was one season (range 1–18 seasons, Figure 1c), and the median sample size of the treatment group was 41.5 nests (range: 5–6767, Figure 1d). Median control sample size was 56.5 nests (range: 5–4538, Figure 1d).

Enclosures and fences were the most commonly used nest protection measures (Figure 2a). Five articles tested more than one type of predator intervention method, either together ($n=2$) or separately

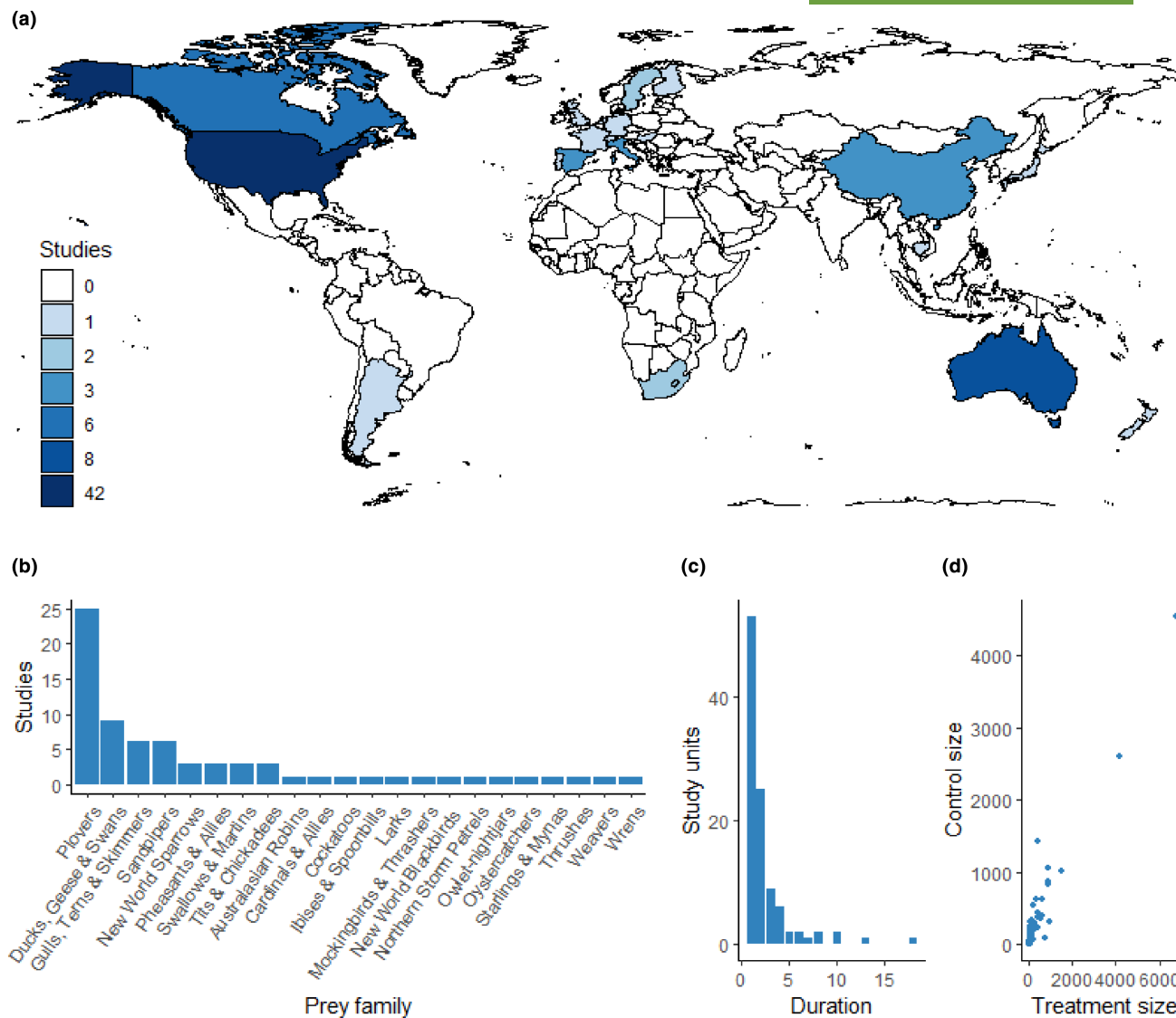


FIGURE 1 (a) Non-lethal nest protection articles included in this meta-analysis ($n=80$) by country. Note two articles involved study sites in both Canada and USA. (b) Bird prey families by the number of articles in which they are represented. (c) Study units by duration in breeding seasons ($n=104$) and (d) Control size versus treatment size (in nests) of study units ($n=104$). The information presented includes only peer-reviewed studies in English.

($n=3$). Nearly half (49%) of the articles focused on at least two predator taxa, including a combination of mammals, birds and reptiles (Figure 2b). More than three quarters (76%) of articles focused on ground-nesting birds (Figure 2c). A total of 56 articles measured the effectiveness of non-lethal nest protection interventions using natural nests, 21 conducted artificial nest experiments and three included both artificial and natural nest components (Figure 2d).

3.2 | Efficacy of non-lethal nest protection methods

Overall, non-lethal nest protection significantly improved nest success relative to unprotected control nests (model estimate=1.02; 95% CI=0.79–1.24 based on 104 effect sizes from

80 articles). Of the moderators tested, only intervention type (Prediction 1a, $n=104$ effect sizes), target predators (Prediction 3, $n=104$) and prey family (Prediction 5, $n=68$) had a significant impact on the effectiveness of non-lethal nest protection (Figure 3a,c,f). Experiment type (Prediction 4, $n=103$) and nest position (Prediction 2, $n=103$) did not have a significant impact. Treatments had a positive impact on nest success when applied to both artificial and natural nests, and when dealing with cavity, elevated and ground nests (Figure 3b,d). Enclosures were the most effective intervention in terms of increasing nest success, followed by a combination of fences and enclosures, fences, and guards. Both electric and non-electric fences showed a positive effect on nest success (Prediction 1b, $n=27$, Figure 3e). Interventions classified as chemical camouflage, conditioned taste aversion, deterrent, diversionary feeding or 'other' did not significantly improve

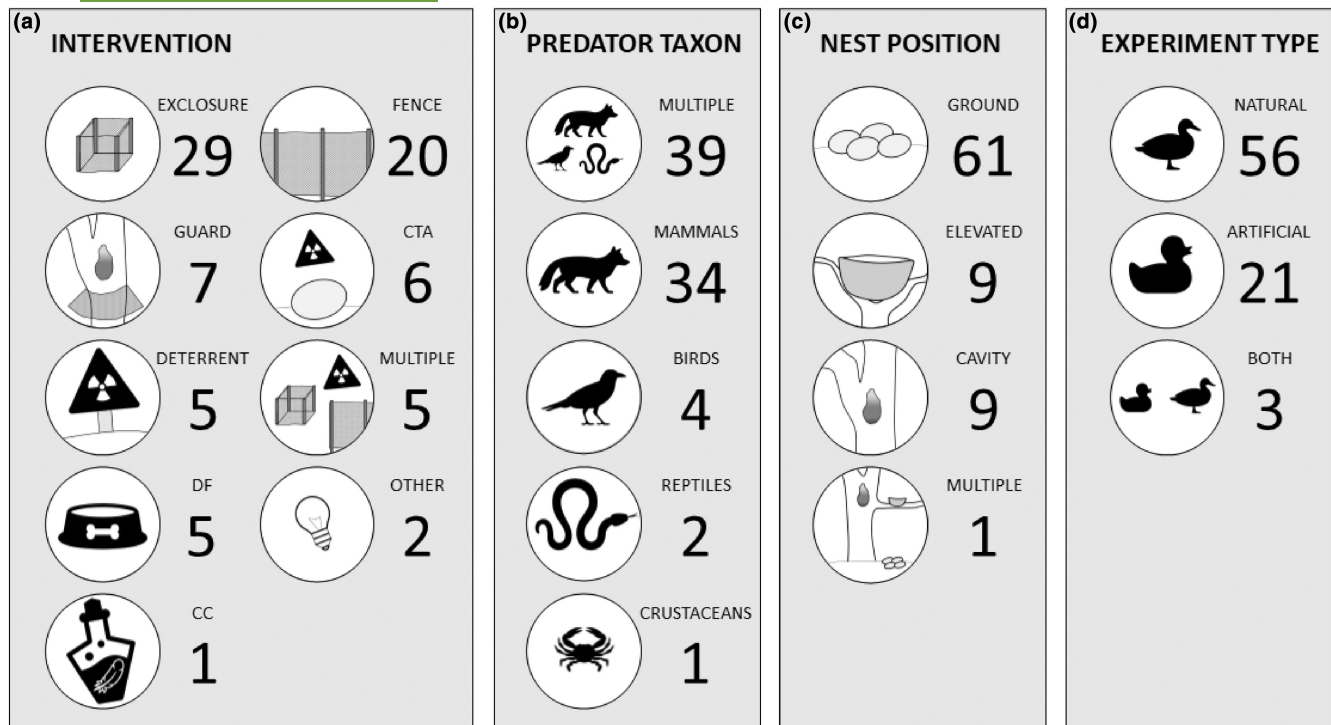


FIGURE 2 Summary of the 80 articles included in this meta-analysis showing the division of articles by (a) intervention type; (b) target predator taxon; (c) nest position; and (d) experiment type. CTA represents conditioned taste aversion; DF represents diversionary feeding; and CC represents chemical camouflage. The information presented includes only peer-reviewed studies in English.

nest success (Figure 3a, Table S4). Overall, physical interventions ($n=73$) were significantly more effective than behavioural interventions ($n=31$; Figure 4). Treatments had a significant positive impact on nests success when protecting against birds, mammals and multiple predator taxa, but not when protecting against reptiles or crustaceans (Figure 3c). Only nest treatments involving the nests of plovers (*Charadriidae*), sandpipers (*Scolopacidae*) and Australasian robins (*Petroicidae*) showed a significant positive effect on nest success (Figure 3f, Table S4). The most parsimonious model explaining nest success included intervention type as the only explanatory variable ($\Delta AICc = -29.9$, Table S5). Support for the most parsimonious model did not change when we excluded piping plover studies or excessive study units (>2) from any one article (Table S6). Methodological variables tested (study duration, nest success measurement type [binary or rate], nesting period measured and failure definition) did not have a significant impact on effect size when added to the best model (Table S7).

Our results did not vary significantly for the two restricted data sets tested (Table S6) or when using the *leave1out()* function to test the sensitivity of the model to the removal of individual studies (Table S8).

4 | DISCUSSION

Implementing conservation actions based on robust evidence can increase the success of interventions and limit costs (Sutherland

et al., 2004). Protecting breeding birds without the lethal control of predators has been an increasing area of interest in the field of wildlife management (Doherty & Ritchie, 2017; Smith et al., 2011). Therefore, we conducted a global meta-analysis to examine the efficacy of non-lethal nest protection methods. We found that articles that met our meta-analysis inclusion criteria were biased towards certain regions, species, intervention types and nest characteristics. Our results show that enclosures, fences and guards have a significant positive impact on nest success and that prey family and target predator taxon also have a significant impact on the effectiveness of non-lethal nest protection interventions. We discuss the implications of our findings for improving future research and conservation efforts.

4.1 | Trends in non-lethal bird nest protection

Most articles in our analysis involved physical barriers such as predator enclosures, fences or guards. However, nearly a quarter (24%) of the articles focused on behavioural interventions such as deterrents and conditioned taste aversion. Almost all articles (91%) focused on mammalian or mixed predator communities, with very few attempting to specifically protect nests from other taxa. This may reflect the particularly damaging impact of invasive mammalian predators on bird species (Doherty et al., 2016). However, it may also reflect an under-appreciation of the role of non-mammalian predators in nest predation (Guppy et al., 2017),

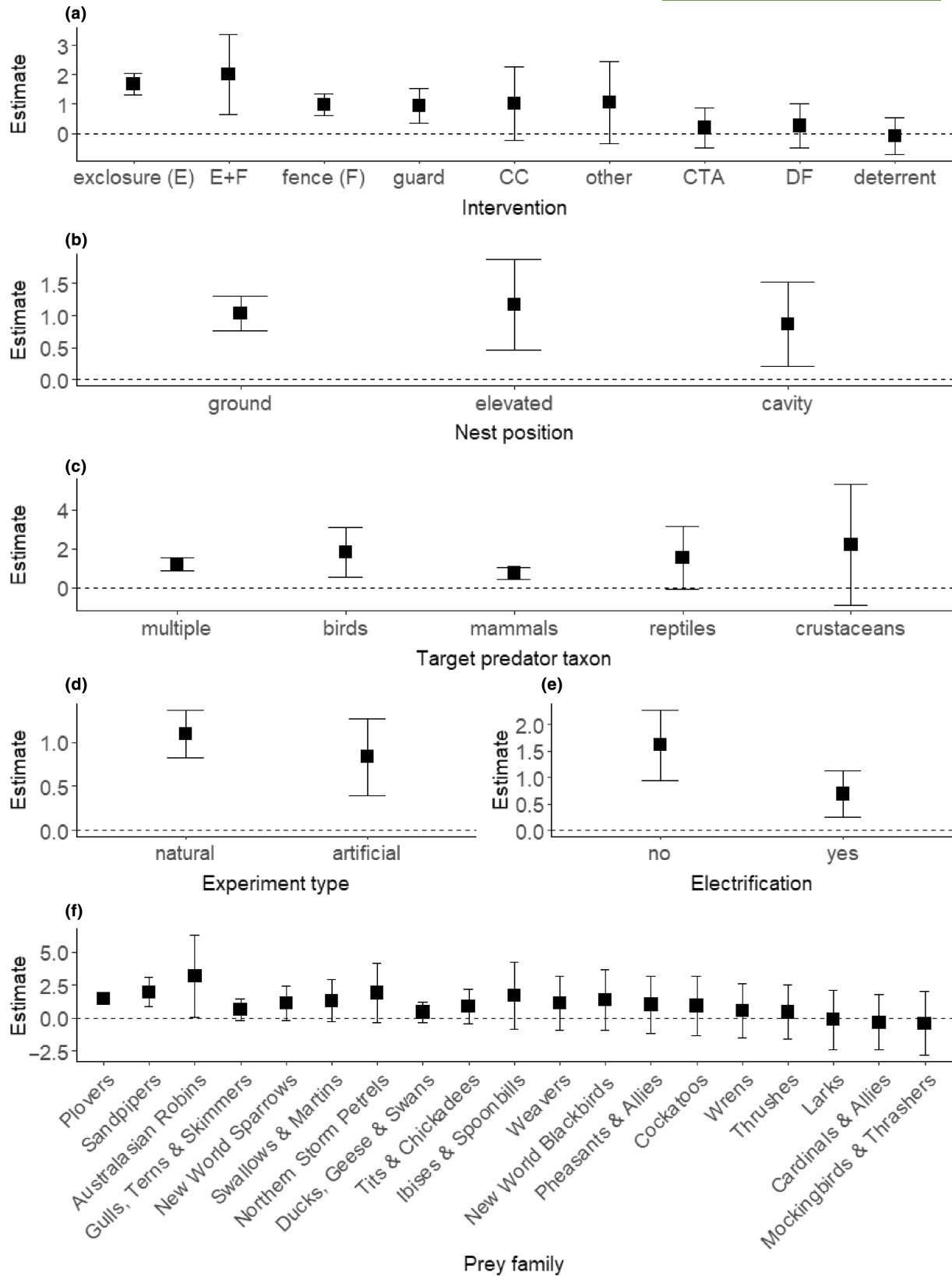


FIGURE 3 Estimated model coefficients from mixed-effect models exploring the effectiveness of non-lethal nest protection efforts. Each model contained one moderator with effect size as the response variable. (a) intervention type (study units $n=104$); (b) nest position ($n=103$); (c) target predator taxon ($n=104$); (d) experiment type ($n=103$); (e) electrification of fences ($n=27$); and (f) nesting prey family ($n=68$). Error bars represent 95% confidence intervals. Zero is indicated by the dashed line and error bars that do not overlap zero indicate a significant positive or negative effect.

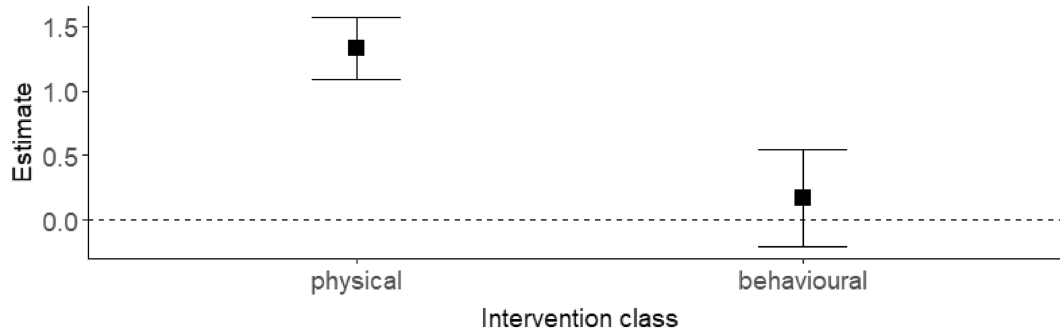


FIGURE 4 Estimated model coefficient from a mixed-effect model exploring the effectiveness of non-lethal nest protection efforts by intervention class; physical interventions ($n=73$) and behavioural interventions ($n=31$). Error bars represent 95% confidence intervals. Zero is indicated by the dashed line and error bars that do not overlap zero indicate a significant positive or negative effect.

or the increased difficulty in protecting nests from such species. Furthermore, many articles did not discuss target predators in detail (e.g. Bailey & Bonter, 2017; Mulder et al., 2021), suggesting that in some cases there may have been a lack of consideration for the identity of key nest predators.

Non-lethal nest protection experiments have historically been biased towards North America, where a great deal of work has been done on two species in particular: the piping plover and snowy plover *Charadrius nivosus*. However, in the last 10 years, 24 of 31 relevant articles focused on other continents, suggesting that this spatial bias is decreasing. Nearly a third (31%) of articles involved the family *Charadriidae*, which is probably due to the long history of successful use of nest protection measures reported by researchers working on plovers (e.g., Rimmer & Deblinger, 1990). Although 22 bird families and 65 species were represented in our review, only two articles involved species listed as either Endangered or Critically Endangered by the IUCN (IUCN, 2022). This does not consider the status of local populations or subspecies, which may not be reflected in the IUCN rating. Furthermore, it is acknowledged that the articles included in this review had varying motivations. While some were clearly focused on conservation (e.g., Pucheta et al., 2018), other articles had different motives such as understanding the role of certain predators (e.g. Cocquelet et al., 2019) or examining the anti-predatory strategies employed by nesting birds (Liu & Liang, 2021). In addition, some studies used a non-threatened species to test an experimental nest protection measure intended for a conservation application (e.g. Stojanovic et al., 2019). While the poor representation of threatened species in this review is surprising, threatened species may be poor subjects for experimental studies if their small population sizes hinder statistical inference or if fear of negative outcomes prevents management action (Canessa et al., 2020).

More than three quarters (76%) of articles focused on ground-nesting species. This trend could reflect the fact that ground-nesting birds are disproportionately in decline and threatened by predators (Ekanayake et al., 2015; McMahon et al., 2020; Roos et al., 2018) and are therefore more likely to be the subject of nest protection efforts. However, it could also reflect a bias in conservation efforts in favour of ground-nesting species, whereby

ground nests are easier to find, monitor and protect, relative to arboreal nesting species. While non-lethal nest protection for arboreal nesting species using cavities or cup nests was much less common, it appears to be increasing. Articles involving these nest types ($n=19$) were more globally distributed than those involving ground nests, with more studies taking place in Australia (32%) and Asia (26%) than North America (16%).

Nearly a third (30%) of articles used artificial nest experiments to test the effectiveness of non-lethal nest protection. Artificial nest experiments have made significant contributions to our understanding of nest predation (Major & Kendal, 1996). Some of the experiments included in our sample may not have been possible without the use of artificial nests due to the difficulty of obtaining a sufficient sample of natural nests (e.g. Canessa et al., 2020), and often provided for more suitable experimental conditions. However, the reliability of artificial nest studies in the context of comparable natural nests remains a matter of debate (Moore & Robinson, 2004; Weston et al., 2017).

Most study units (51%) were conducted over a single breeding season. This is concerning in terms of drawing evidence-based conclusions to inform management. In many environments, nest survival rates can vary annually contingent on multiple, often correlated factors including weather, vegetation growth and predator abundance cycles (Moynahan et al., 2007; Winter et al., 2005). Similarly, most treatment sample sizes were relatively small, with 73% of study units having a treatment sample of less than 100 nests. Most of the study units using natural nests used the incubation period as their preferred measurement period ($n=45$), rather than the full nesting period ($n=21$) or defined success as survival over a number of days ($n=4$). One natural nest study measured success during only the nestling stage (Pucheta et al., 2018). The artificial nest study timeframes were often based on a biologically relevant period (e.g. incubation period, Canessa et al., 2020), but this was not always the case (e.g. 6 days, Liu & Liang, 2021). Wherever possible, we included figures that reflected overall nest failures rather than only failures due to predation, as this most accurately reflects the impact of non-lethal nest protection on nest success. For example, while protection against nest predators may reduce nest predation, it may also lead to an increase in nest abandonments (Barber et al., 2010). A total of 83% of study units using natural nests presented data that considered nest failures beyond predation.

4.2 | Effect of interventions on nest success

Our results show that non-lethal physical interventions generally improve nest success for birds. Predator exclosures and fences were the most effective interventions, but combinations of the two were no more effective than either method used independently. Guards, which prevent the vertical travel of predators (and are therefore only applicable to arboreal nesting species) also significantly increased nesting success.

Overall, behavioural interventions show a positive impact on nest success, however modelled confidence limits overlapped zero. The smaller number of studies using these interventions, particularly chemical camouflage ($n=2$) and diversionary feeding ($n=5$), limited the confidence of model estimates. Conditioned taste aversion and deterrents were also diverse in nature, employing various conditioning agents and comprising scent, sound and vision-based approaches, but the number of studies that used such treatments were too small to evaluate independently. While behavioural interventions show promise (e.g. Norbury et al., 2021; Selonen et al., 2022), there is currently insufficient evidence to conclude whether they are reliable nest protection methods and the effectiveness of such approaches may be highly context-specific, for example using snake slough to deter Swinhoe's striped squirrels *Tamiops swinhoei* from nest boxes (Liu & Liang, 2021).

Target predator and prey taxa also appeared to influence the effectiveness of nest protection interventions. Efforts focused on preventing predation by reptiles or crustaceans did not show a significant positive effect on nest success, though the combined sample size was small ($n=3$). Interventions focused on protection of nests against birds, mammals or a mixed predator community were effective, but only those focused on three prey families (*Charadriidae*, *Scolopacidae* and *Petroicidae*) had a significant positive impact on nest success. This can be partly explained by the larger number of study units for *Charadriidae* ($n=26$) and *Scolopacidae* ($n=6$) allowing for narrower confidence intervals for these families. Conversely, only one study focused on the family *Petroicidae*, finding that a small number of exclosures ($n=7$) were highly effective at reducing predation (Debus, 2006). The finding that studies on other families did not show a significant positive model estimate is probably explained by the small number of study units representing other families (median: 1, range: 1–9). Surprisingly, we also found that electric fences ($n=18$) were no better at improving nest success than non-electric fences ($n=9$), with the data suggesting they may be worse. Studies involving electric fences often commented on their inability to exclude all predators in mixed predator communities and fence breaches caused by power issues (e.g. Conner et al., 2010; LaGrange et al., 1995). We recommend further experiments to refine electric fencing as a non-lethal nest protection measure.

4.3 | Study limitations

Given the varied environments in which wild bird nest protection experiments were conducted and a lack of clear methodological guidelines for nest protection experiments, the studies included in our

meta-analysis vary in their approaches. Most variation is dictated by the focal prey species, the type and position of nest used and inherent specificities of the study systems. In addition, many studies occurring as part of management actions have imperfect experimental designs. However, this does not preclude them from producing valuable insights to inform adaptive management. To avoid constraining our sample, we included studies that measured nest success in terms of daily survival rate or apparent nest success. We also accepted studies that counted only predated nests as unsuccessful, as well as studies that included all causes of failure in the control and treatment groups. Multiple periods of measurement for nest success were accepted (incubation period, full nesting period or survival over a pre-determined period). Because all these factors could influence our results, we added these variables into the most parsimonious model to determine whether they had a significant influence on the effect size for each study unit. The results suggest that these methodological variables did not explain the effectiveness reported. While consistent methodologies would make studies more comparable, we considered the inclusion of a wide variety of non-lethal nest protection studies to be of greater importance.

For this review, we did not consider lethal nest protection or habitat manipulation measures used to reduce predation. As a result, we do not assess the efficacy of these nest protection measures here, suggesting separate meta-analyses are warranted for these approaches. We attempted to identify all available peer-reviewed literature that met our criteria; however, we probably omitted some relevant articles. For instance, due to language constraints, our search string only included English search terms and we only considered articles for which the full text was available in English, potentially overlooking some studies and/or introducing a geographical bias. The importance of breaking down language barriers is increasingly being recognised in ecology and conservation (Negret et al., 2022), so broadening our analysis across multiple languages should become more viable in the near future. We also only considered research published in peer-reviewed journals. We took this approach to ensure repeatability, but we acknowledge that this risks overlooking potentially important evidence in the grey literature (Haddaway & Bayliss, 2015) and also the potential for underrepresentation of negative findings as a result (Mlinarić et al., 2017). However, our data are available online (Gautschi et al., 2024) and could be further extended with data from other languages and grey literature.

4.4 | Conservation implications and recommendations for future research

Non-lethal nest protection is becoming an increasingly important area of research given the potential of such methods to yield longer-term and more cost-effective conservation outcomes. The applicability of our findings also extends beyond birds to other nesting taxa facing elevated predation rates such as turtles (O'Connor et al., 2017) and freshwater crocodiles (Somaweera et al., 2011). Our systematic search revealed many relevant studies that could not be included due to a lack of suitable experimental

conditions, the simultaneous use of lethal predator control or a focus on threats other than predation. To thoroughly examine the efficacy of non-lethal nest protection interventions, experiments should ideally be performed independent of lethal predator control and the treatment group should be contrasted with a comparable control group. While funding and other limitations may prevent multiple years of experimentation, we also encourage researchers to undertake longer-term studies whenever possible, as this would allow for temporal replication and greater confidence in results (Johnson, 2002).

It is encouraging to see an increasingly global distribution of peer-reviewed articles as well as more articles dealing with novel protection techniques and different species. However, there is still a need for further studies on cup and hollow-nesting birds which are currently under-represented in the conservation literature. For example, songbirds (order Passeriformes) comprise 60% of global bird diversity (Ericson et al., 2003) yet were included in only 20% of articles using natural nests in our analysis.

A crucial first step in effective nest protection is to obtain a thorough understanding of the predators posing a threat to nesting birds. Passive monitoring studies are increasingly showing that nest predator assemblages are often more diverse than may be assumed (Guppy et al., 2017). To avoid compensatory predation by other species (Ellis-Felege et al., 2012), non-lethal methods should be designed as much as possible to protect against the entire predator assemblage.

Our results provide cautious optimism for the use of non-lethal nest protection to reduce predation. Non-lethal nest protection interventions can be effective at increasing nest success and can have profound impacts on the breeding success of wild birds (e.g. Maslo & Lockwood, 2009; Norbury et al., 2021; Tan et al., 2015). Despite the value of non-lethal interventions, lethal predator control should not be discounted when considering management options (Smith et al., 2010). With either approach, managers and researchers must consider predator interventions in the context of other factors such as habitat quality and predator abundance as these are likely to interact with one another (Douglas et al., 2023). When considering the suitability of non-lethal predator control, managers and researchers should determine (i) what the exact aims of potential nest protection interventions are; and (ii) whether these techniques are suitable for their system. Managers should also consider whether nest protection efforts can be practically implemented at a sufficient scale to have a noticeable impact on the overall breeding output of a population, if that is the overall conservation goal. Alongside these considerations, our findings can contribute to evidence-based decision-making, increasing the chances of wild bird nesting success and reducing unnecessary ethical and financial costs in the process.

AUTHOR CONTRIBUTIONS

Daniel Gautschi, Ross Crates, Robert Heinsohn and Antica Čulina conceived and designed the research; Daniel Gautschi and Ross Crates conducted the title/abstract screening; Daniel Gautschi performed

the full-text screening and data extraction; Daniel Gautschi, Ross Crates and Antica Čulina conducted the meta-analysis; Daniel Gautschi, Ross Crates, Antica Čulina, Robert Heinsohn and Dejan Stojanovic wrote and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data and code are available from Zenodo <https://doi.org/10.5281/zenodo.10703166> (Gautschi et al., 2024).

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SUPPORTING INFORMATION

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

Table S1. Predictions associated with moderator variables and the sample sizes included in the meta-analysis.

Table S2. Results of Chi-square (χ^2) tests showing correlation between variables of interest. *p*-values are shown in parentheses.

Table S3. Prey species whose nests were included in the meta-analysis by 2023 IUCN Red List status.

Table S4. Estimated model coefficients from mixed effect models including moderator variables, with the log odds ratio of nest success treatments as the response variable.

Table S5. Results of mixed effect models containing moderator variables with the effectiveness of interventions in increasing nest success as the response variable.

Table S6. Results of mixed effect models containing moderator variables with the effectiveness of interventions in increasing nest success as the response variable, for restricted data sets.

Table S7. Estimated model coefficients from multivariate mixed effect models including intervention type and a single methodological variable as predictor variables and the log odds ratio of nest success treatments as the response variable.

Table S8. Estimated model coefficients produced using the `leave1out()` function in the R package `metafor`.

Figure S1. PRISMA flow diagram showing results of the literature search, title/abstract screening, full-text screening and citation search.

Appendix S1. Supplementary Methods.

Appendix S2. Reference list of articles included in the meta-analysis.

Appendix S3. Details of studies excluded during full-text review.

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