birds

Review

Predator-Proofing Avian Nestboxes: A Review of Interventions, Opportunities, and Challenges

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Simple Summary: On a global scale, about 20% of bird species nest in tree cavities, and many of these species will utilise artificial nestboxes. Homeowners often add nestboxes to gardens to provide new opportunities for enjoyment and engagement with nature. Nestbox schemes can also be used for conservation, especially in environments that have few natural cavities, such as open landscapes and woodlands with relatively young and even-aged trees, including plantations. However, tree-nesting birds using simple wooden nestboxes can be at risk from predators. A range of different strategies to reduce predation risk has been developed. These typically involve: (1) modifying the nestbox itself by, for example, adding a metal plate around the entrance hole to stop predators enlarging the hole or changing construction materials; (2) modifying the immediate surroundings of the nestbox, for example, by using barriers to prevent predator access; or (3) modifying nestbox placement. A common assumption is that such interventions provide a net benefit. However, this is not necessarily true as predator-proofing avian nestboxes often has hidden costs, such as changing nest temperature or humidity or making it harder for adult birds to feed their chicks. This review considers intervention effectiveness and the potential for hidden costs to make recommendations for practice.

Abstract: Nestboxes are commonly used to increase the number and quality of nest sites available to birds that usually use tree cavities and are considered an important conservation intervention. Although usually safer than natural cavities, birds nesting in simple, unmodified wooden nestboxes remain at risk of depredation. Accordingly, numerous design and placement modifications have been developed to 'predator-proof' nestboxes. These include: (1) adding metal plates around entrance holes to prevent enlargement; (2) affixing wire mesh to side panels; (3) deepening boxes to increase distance to nest cup; (4) creating external entrance 'tunnels' or internal wooden ledges; (5) using more robust construction materials; (6) developing photosensitive shutters to exclude nocturnal predators; (7) using baffles to block climbing mammals; and (8) regular replacement and relocation. However, the benefits and costs of these modifications are not always well understood. In this global review, we collate information on predator-proofing avian nestboxes designed for tree cavity-nesting birds to assess the efficacy of techniques for different predators (mammalian, avian, and reptilian) in different contexts. We critique the potential for modifications to have unintended consequences—including increasing nest building effort, altering microclimate, reducing provisioning rate, and elevating ectoparasite and microbial loads—to identify hidden costs. We conclude by highlighting remaining gaps in knowledge and providing guidance on optimal modifications in different contexts.

Keywords: predation; nest box type; nest box design; cavity-nesting birds; woodcrete; trade-off

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1. Introduction

Nesting within a tree cavity is a common breeding strategy for birds [1,2]. Indeed, a recent global review by van der Hoek et al. [3] found that at least 1878 avian species (~20%) nest in tree cavities. Of the 1838 species with relatively well-characterised nesting behaviour, 481 species are primary cavity-nesters that excavate their own nest cavity. This guild is dominated by Woodpeckers (Picidae) and Barbets (Capitonidae, Semnornithidae, Megalaimidae and Lybiidae), which are obligate primary excavators. Some passerines, such as the Willow Tit (*Poecile montanus*) and Red-breasted Nuthatch (*Sitta canadensis*), are also included, but they are typically weaker and/or facultative primary excavators [4,5]. The remaining 1357 species in the tree cavity-nesting guild are secondary cavity-nesters that lack the ability to excavate their own cavity. These species utilise pre-existing cavities that either developed naturally via tree decay [6,7] or that were created initially by a primary cavity-nesting species [4,5].

Because of the inherent inability of secondary cavity-nesting species to excavate cavities, they fundamentally depend on the availability of suitable pre-existing nesting sites [4]. There is considerable evidence that a shortage of cavities can limit breeding density (e.g., [8–12]). This is especially true in urban environments, open landscapes such as wetlands, and within intensively managed woodlands. Across Europe, deforestation and rotational commercial silviculture often means that old, cavity-rich trees are becoming scarcer [13,14]. These young, even-aged, and cavity-poor stands are sub-optimal habitats and can become ecological traps [15]. Habitat fragmentation and resulting edge effects can also reduce the breeding success of non-excavating species by increasing competition for nest sites [16]. Indeed, of the 1611 cavity-nesting species studied by van der Hoek et al. [3] that have also been assessed by the International Union for the Conservation of Nature to determine extinction risk, 249 (15.5%) are currently listed as Vulnerable, Endangered, or Critically Endangered.

At this time of biodiversity crisis, developing effective conservation interventions that are rapid and cost-effective has never been more important. Population trends of woodland specialist birds, many of which are tree cavity-nesters, are showing a net decline of 18% across Europe [17] and >25% in specific countries such as the United Kingdom [18,19]. Although there are many drivers of decline, research indicates that improving breeding productivity can be a useful conservation strategy even when threats are largely external to breeding [20,21]. Many secondary cavity-nesting species will breed in artificial nestboxes if these are available and suitable. Accordingly, nestboxes are often added to cavity-poor environments, such as gardens, parkland and immature or plantation woodland [22,23]. Most nestboxes designed for secondary cavity-nesting species are rectangular wooden structures with a relatively small entrance hole providing access to the nesting chamber (Figure 1a). Such designs are often known as "tit boxes" but are used by many secondary cavity-nesting passerines other than Paridae, including (depending on location and hole diameter), Nuthatches (*Sitta* spp.), Flycatchers (*Ficedula* spp.), Bluebirds (*Sialia* spp.), European Starlings (*Sturnus vulgaris*), and Eurasian Tree Sparrows (*Passer montanus*) [24,25]. These tit boxes are typically placed in an elevated position attached to trees within woodlands, although in gardens and open habitats other supports such as posts, walls and fences are also used. These boxes are by far the most common and are thus the main focus of this review. There are other nestbox designs, such as wedge-shaped boxes (Figure 1b) that are designed specifically for Treecreepers (*Certhia* spp.), large tunnel boxes (Figure 1c) tied to the underside of tree branches for tree-nesting owls (e.g., Tawny Owl (*Strix aluco*)), and large open-fronted nestboxes (Figure 1d) designed for tree-nesting falcons, such as the European Kestrel (*Falco tinnunculus*).

In cavity-poor environments, use of nestboxes often results in population growth [8,9,26]. This can be due to an increase in the overall number of nest sites [27–29] or elevated numbers of high-quality nest sites [30–32]. Nestbox-induced population increases can also be accelerated by high productivity, as the number of young to fledge per brood is often higher in nestboxes than in natural cavities [33,34]. Higher productivity might be influenced by larger clutch sizes [35,36], but is predominantly due to increased hatching and fledging success. For example, for Tree Swallows (*Tachycineta bicolor*) in Canada, the mean number of young to hatch within nestboxes is substantially higher than for natural cavities (5.2 ± 1.1 nestlings versus 2.6 ± 2.0 nestlings, respectively) [37]. Nestbox-breeding birds were also over twice as successful at producing fledglings (93.4% of nestbox pairs fledged > 1 young versus 35.8% in natural cavities). Other studies have found similar patterns, for example, fledging in Common Treecreepers (*Certhia familiaris*) nesting in Finland and Lithuania was 69.9% for birds using nestboxes versus 36.2% for birds using natural cavities [38], while success of nestbox-breeding Western Bluebirds (*Sialia mexicana*) in the US was more than twice that of cavity-nesting conspecifics [33]. Fledging success is generally higher in nestboxes due to the combined effects of reduced chick exposure to extremes of weather and temperature [39] and reduced predation rates [33,40–43].

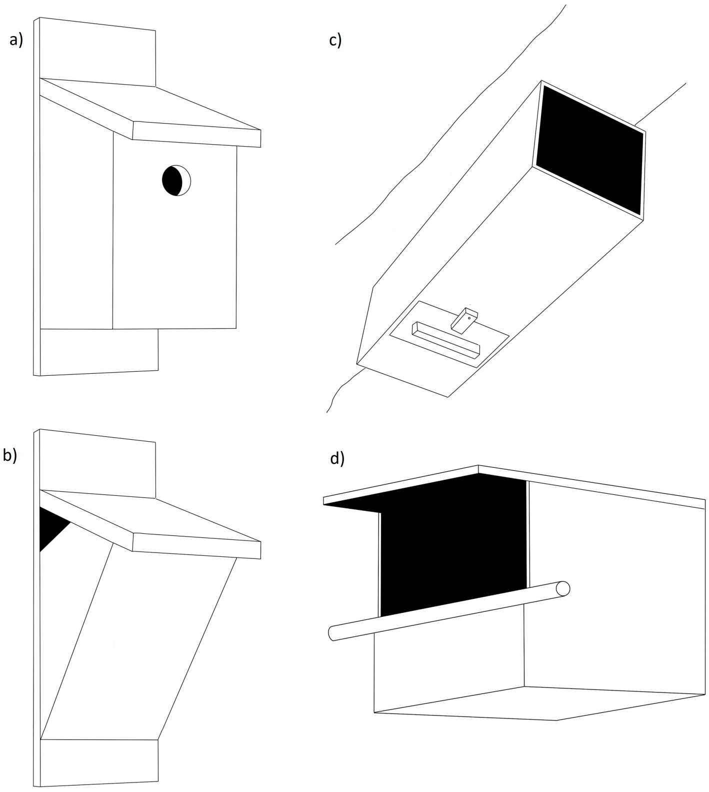

Figure 1. Common types of nestbox for secondary tree cavity-nesting birds: (**a**) standard wooden rectangular nestbox with a circular entrance hole suitable for numerous cavity-nesting species; (**b**) a wedge-shaped nestbox optimised for Treecreeper (*Certhia* spp.); (**c**) large tunnel boxes optimised for Tawny Owl (*Strix aluco*); and (**d**) large open-fronted nest boxes optimised for European Kestrel (*Falco tinnunculus*). Note that diagram elements c and d are not drawn to scale.

Use of nestboxes in scientific research has advanced understanding of avian ecology, behaviour, population dynamics, and evolution by allowing ornithologists to undertake studies that would otherwise be unpracticable [44,45]. Nestboxes, which often have hinged lids, allow researchers to monitor active nests, experimentally manipulate breeding parameters such as clutch size, control environmental factors such as cavity size, and repeatedly capture and identify parents and nestlings (e.g., [46–48]). The use of nestbox schemes can also greatly increase sample sizes as nesting site locations are known prior to the breeding season. As a result, secondary cavity-nesting passerines are extremely well studied [45].

Although this is not a "magic bullet" (e.g., [49]), erecting nestboxes is a quick, inexpensive, and, logistically, a relatively easy intervention that can support conservation and/or avian research. However, for such initiatives to be maximally effective, it is important to minimise nest predation, which can reach >50% in some situations [40,50,51], making it the largest cause of nest failure [33].

In this two-phase review, we first provide an overview of predation at nestboxes developed for, and utilised by, birds that nest in tree cavities. We highlight the magnitude of the threat, the main predator groups, and the different ways that predators access eggs and chicks (Section 3). In this section, we also explore the effects of predation on birds using nestboxes on parental perception of predation risk and breeding success. Then, in Section 4 and subsections therein, we review the main strategies used by ornithologists to modify nestboxes or their surroundings to reduce predation risk, and perception of predation risk, for nestbox-breeding birds. We assess the relative efficacy of each technique for decreasing predation risk in different contexts, before critiquing the potential for these modifications to have unintended consequences that are, or could be, to the disadvantage of the birds that use them. This includes increasing nest building effort, creating hotter or more humid nest microclimates, reducing provisioning rates, increasing ectoparasite loads, and changing the nest microbial load, especially for pathogenic species of bacteria and fungi. Throughout our review, we consider breeding attempts within a life-history context and focus on population-level (rather than individual-level) consequences wherever possible, although this approach is limited by literature being dominated by relatively short-term studies.

2. Methods

Literature was searched using Google Scholar and Scopus. Our eligibility criteria were that results should have been presented in a peer-reviewed output or (exceptionally) be from a formal ornithological organisation (e.g., BirdLife International). To ensure the widest possible scope, there were no geographical or date range criteria applied.

We first collated information on the magnitude of predation at nestboxes, predators involved, and predator detection of nestboxes, which was found using Boolean searching with wildcards (asterisks) applied. The key search terms used were "nestbox*" OR "nest box*" AND "pred*" to encompass any combination of nestbox, nestboxes, nest box, nest boxes, predation, predator, and predators. This general search was followed by the "pred*" element being replaced by major predator species highlighted by the initial search, using both vernacular and scientific names. Many of the articles found during this searching highlighted predation prevention modifications to nestboxes and these were recorded. We then collated information on nestbox modifications. For this part of the research, we used ""nestbox*" OR "nest box*" AND "[search term]*" where [search term] was either generic (e.g., "predation prevention") or the name of a specific modification with appropriate wildcards to allow for singular and plural contexts (e.g., "guardian tube*"). Finally, we also searched for each specific modification individually firstly with positive words added ("benefit" OR "effective*" OR "advantage*" OR "success") and then with negative words added ("cost" OR "problem" or "disadvantage") to ensure we had full information on advantages and disadvantages. We also took advantage of citation chaining to locate additional papers not found through our initial searches by checking the reference lists and citations in each paper we found.

In this way, we followed the fundamental precepts of PRISMA [52], but with increased flexibility and a wider scope. We considered this to be appropriate since our intention was to find all relevant information on this subject (to offer a comprehensive, critical, and constructive analysis of the existing literature, to identify current gaps in understanding, and provide recommendations to practitioners and researchers), rather than to undertake any form of meta-analysis, numerical presentation, or data analysis (e.g., of papers over time) where absolute objectivity is required to ensure consistency and repeatability.

3. Predation at Nestboxes

Despite the conservation and scientific value of nestbox schemes, predation can still be problematic. Although nestboxes are generally "safer" than natural cavities at an individual level, they are certainly not impenetrable. Indeed, predation rates can sometimes be considerable [53], reaching >50% in some situations [40,50,51], making it the largest cause of nest failure [33].

3.1. Possible Predators and Access Routes

Possible predators will depend on location, but some mammalian predators, such as wood mouse (*Apodemus sylvaticus*), European weasel (*Mustela nivalis*), and sugar glider (*Petaurus breviceps*), are small enough to enter nestboxes. This can also happen in the case of reptiles, including Montpellier snakes (*Malpolon monspessulanus*), ladder snakes (*Zamenis scalaris*), and black rat snakes (*Pantherophis obsoletus*). Larger mammalian predators, such as stoat (*Mustela erminea*), pine marten (*Martes martes*), stone marten (*Martes foina*), polecat (*Mustela putorius*), racoon (*Procyon lotor*), red squirrel (*Sciurus vulgaris*), grey squirrel (*Sciurus carolinensis*), wolverine (*Gulo gulo*), and brushtail possum (*Trichosurus vulpecula*) are too big to enter a nestbox completely but can sometimes reach through the entrance to reach the nest, especially if they are able to enlarge the entrance hole [50,54]. It is also sometimes possible for primary cavity-nesting bird species, such as woodpeckers, to penetrate the sides of wooden boxes to access eggs and chicks [55,56] and also, more rarely, enlarge entrance holes.

3.2. Predation Risk

Nestboxes affixed to trees are more conspicuous and are thus easier for predators to detect relative to natural internal cavities within trees [56,57]. Predators can also sometimes change their learned behaviour to exploit nestboxes as a reliable food source by using spatial memory to learn locations of nestboxes they depredate [53,58–62]. This might be inadvertently facilitated by the propensity of ecologists to arrange nestboxes in grid formations, meaning that predators could potentially use spatial prediction to find new nestboxes when searching for further feeding opportunities. Nestbox schemes can elevate avian nest density, which can have a concomitant effect on predator density. This scenario occurred at Wytham Woods, UK, where a long-term project involving ~1000 nestboxes artificially elevated the local population density of the predatory European Weasel [50,51].

3.3. Effects of Predation

Predation axiomatically causes direct impacts on survival of individuals and their offspring, with potential for population-level impacts. However, what is less well understood is that predation risk, and avian perception of this risk, has indirect effects on life-history. Behavioural plasticity has been observed in cases where parent birds reduce their reproductive investment in eggs or nestlings as perception of predation risk increases [63,64]. Predation risk is assessed using a range of cues [65], including alarm calls from conspecifics [66], direct experience [67], and pheromones left by predators [68]. Behavioural changes can have indirect productivity consequences. For example, Fokkema et al. [48] hypothesised that increased clutch size and hatching success in Blue Tits (*Cyanistes caeruleus*) at safer nesting sites was driven by predation perception, especially as this relationship occurred irrespective of local predation pressure. The authors concluded that parent birds inhabiting nest sites perceived as being at greater risk of predation were likely to have reduced investment in their reproductive attempt. A potential evolutionary rationale for this behaviour is that the breeding success of any second brood partly depends on the amount of parental care already provided to the initial brood. Moreover, as time is limited in a breeding season, individuals can save time by laying a smaller clutch, increasing the potential for a second brood if the first is depredated [69,70]. Similarly, there are known costs of parental investment on the survival of adults [71] and reproductive success in subsequent breeding seasons [72]. Such behaviours align with the bet-hedging hypothesis [73]. It should also be noted that there can be carry-over effects of predation during the breeding season on selection of winter roost sites. Ekner and Tryjanowski [74] found that passerines avoided roosting in nestboxes to which predator scent had been experimentally added, while Dhondt et al. [75] highlight that birds that do use nestboxes as winter roosting sites remain at risk of predation.

4. Nestbox Predation Prevention Strategies

To ensure that nestboxes and nestbox schemes are maximally effective, by reducing actual predation risk and avian perception of predation risk, several modifications to nestbox design and placement have been developed. These are summarised in Table 1. Effectiveness and adverse unintended consequences are critiqued throughout the remainder of Section 4 (Sections 4.1–4.8 inclusive).

Table 1. Overview of predation prevention interventions for nestboxes and their placement.

Modification Category	Specific Modification	Details
Changes to wooden nestboxes	Metal plate around entrance	A thin metal plate is affixed to a wooden nestbox around the entrance hole to prevent mammalian predators using their teeth to enlarge the hole.
	Wire mesh enclosing nestbox	Panels of a wooden nestbox are covered in galvanised wire mesh to reduce predation from predators penetrating the sides of a box.
	Deep nestbox	Design is very similar to a typical wooden nestbox but vertically elongated, increasing the distance between the entrance hole and nest cup; reduces risk of a predator reaching through the entrance to access eggs or chicks.
	Guardian, hole extender, Noel guard	A plastic, wooden, or wire structure attached to the outside of the nestbox to create an entrance tunnel, thereby increasing the distance from entrance to nest cup.
	Internal ledges below entrance	An internal modification of a small ledge inside the nestbox below the entrance hole to make it harder for mammalian predators to reach nestbox contents.
Changes to nestbox materials	Woodcrete nestboxes	A mixture of cement and sawdust (“woodcrete”) that is easily moulded to produce nestboxes of various shapes and sizes—these tough nestboxes are much less likely to be penetrated or suffer hole enlargement by predators.
Technological solutions	Photosensitive shutters	A novel anti-predator strategy to prevent nocturnal predators entering nestboxes via a shutter over the entrance hole that closes in low light conditions.
Changes to nestbox positioning or replacement schedule	Baffles	Passive barriers placed below a nestbox to prevent climbing predators from reaching the nestbox; baffles are usually a stovepipe or a cone design.
	Regular replacement of nestboxes	Wooden nestboxes decay over time and become more susceptible to penetration or hole enlargement as they age. Regular replacement can reduce this risk.
	Regular movement of nestboxes	Predators can use spatial memory to locate nestboxes that they have successfully depredated previously. Periodic movement of nestboxes can reduce this risk.

4.1. Advantages and Disadvantages of Metal Plates around Entrance or Wire Mesh Panels

Predators can break into nestboxes to gain access to eggs or chicks either by enlarging the original entrance hole (usually mammals such as Grey Squirrels) or by penetrating the sides of nestboxes (usually primary cavity-nesting birds such as Woodpeckers) [55,56,76]. A common method of combating the former is to affix a thin metal plate around the entrance hole, which can either be added to new nestboxes or retrofitted to those already in-situ [24,45,77] (Figure 2a). Preventing new holes from being created is more complex because this can involve penetration of any of the nestbox panels. Mainwaring and Hartley [55] tested a novel method of preventing predation by Great Spotted woodpeckers (*Dendrocopos major*) by covering nestboxes in galvanised wire mesh sheets affixed directly to the outside of the box (Figure 2b). These approaches can be used in tandem if required.

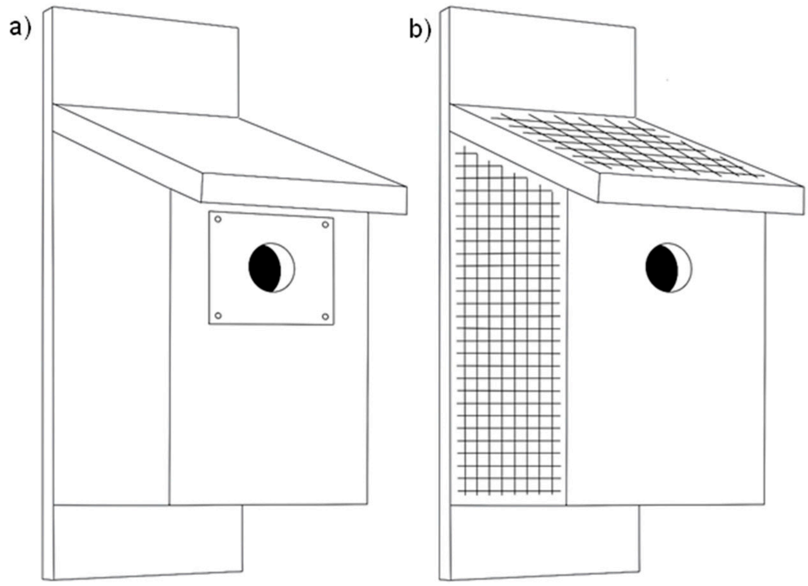

Figure 2. Nestboxes modified using (**a**) a metal plate affixed to the front of the nestbox around the entrance to prevent hole enlargement; and (**b**) wire mesh added to the sides and top of a nestbox.

Although the use of metal plates around entrance holes is common, the practice seems to have developed from ad-hoc evidence of hole enlargement on unmodified nestboxes rather than being empirically tested as a predation prevention measure. However, the method is cheap, easy, and straightforward and is also likely to extend the life of nestboxes, which has financial and logistical benefits. Multiple studies have also shown additional inadvertent avian benefits by preventing larger (often competitively superior) birds from enlarging entrance holes to allow them to use nestboxes with small holes designed for smaller (often competitively inferior) species. For example, this was successful in protecting Red-cockaded Woodpecker (*Picoides borealis*) nests by preventing larger cavity-nesting species from usurping the nestbox after enlargement of the entrance hole [77,78]; this strategy could be useful in other contexts, for example, to prevent enlargement of entrance holes of nestboxes designed for small passerines by competitively dominant Syrian Woodpeckers (*Dendrocopos syriacus*) [79]. These incidental benefits have been taken further through deliberate use of a metal plate as a restrictor mechanism, which can be especially helpful for reducing impacts of invasive non-native species [12]. For example, metal hole restrictors have been used proactively to prevent enlargement of entrance holes of nestboxes by Rose-ringed Parakeets (*Psittacula krameri*) [80].

The wire mesh method is much less common but shares the advantage of being relatively cheap and simple, as well as having the potential for easy retrofitting to nestboxes that have already been deployed. The method greatly reduced predation of Blue Tit nestboxes by Great Spotted Woodpeckers [55], although the authors suggested mesh < 13 mm would further improve efficacy.

4.2. Advantages and Disadvantages of Deep Nestboxes

When using natural cavities, many species, including the Great Tit (*Parus major*) and Marsh Tit (*Poecile palustris*), select deeper cavities over shallow ones when these are available [81,82]. Deeper cavities allow for a greater gap between nest cup and entrance hole, which decreases predation risk by increasing the 'danger distance'. Perceived predation risk is an important selection pressure on nest site choice, and this preference is likely an anti-predator adaptation to prevent larger mammalian predators from accessing eggs or chicks via the nest entrance. This preference for deep nest cavities translates to artificial nest sites as well; for example Planalto Woodcreeper (*Dendrocolaptes platyrostris*), European Starling, and many Paridae actively select deeper nestboxes [83–87] (Figure 3). Where exceptions are seen, they often relate to interspecific competition. For example, higher occupation of shallow nestboxes by Blue Tits in a study in Poland may have occurred because they were excluded from their preferred deeper nestboxes by competitively dominant Great Tits [54].

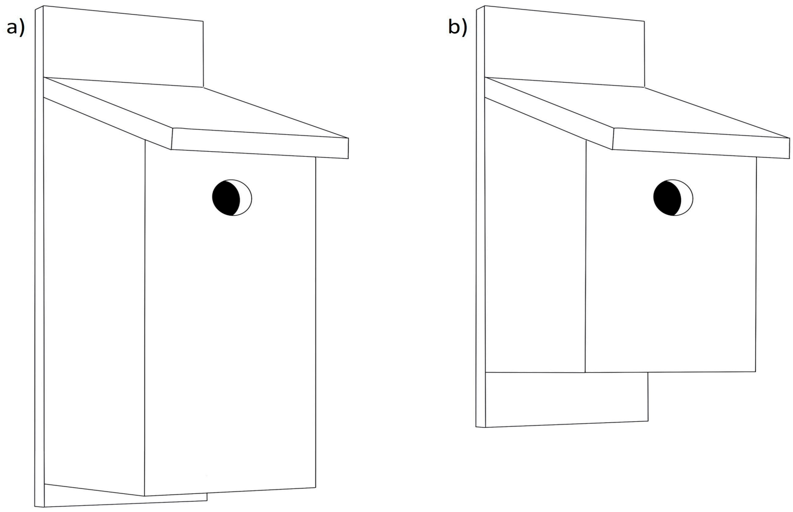

Figure 3. (**a**) Deep wooden nestbox versus (**b**) wooden nestbox of typical proportions.

Nesting in deep nestboxes and natural cavities has been shown to reduce predation in Blue Tits [54] and Great Tits [54,82]. To better understand this, Fokkema et al. [48] quantified actual and perceived predation risk, as well as overall breeding success of Blue Tits, in relation to nestbox depth. The authors conducted a free-choice experiment, where depth was established before nest building, and a forced-choice experiment, where depth was altered after the onset of egg laying. This experimental framework aimed to control for intraspecific competition to account for the potential association between nestbox depth and parental quality [48,88]. Deeper boxes were associated with small but significant increases in clutch size and hatching success, augmented by substantial and significant increases in fledging success. The authors suggested that, as predation was the most common cause of total nest failure, the latter relationship was driven by reduced predation in deeper nestboxes. When cases of complete brood failure were excluded from analysis, the relationship between depth and fledging success was no longer significant, suggesting that total nest predation was the main driver behind the initial positive relationship. The authors also suggested that predator detection was likely underestimated, especially for partial predation or events involving small predators such as European weasels, which were less likely to trigger motion sensors on camera traps. These issues are common when quantifying avian nest predation [89–91].

Deep nestboxes are often associated with larger nests [92,93], which can provide thermal benefits and reduce the risk of water saturating the nest material [48,94–96]. Larger nests can also be more sanitary as they have a larger capacity for waste materials, such as non-hatched eggs, food remains, and dead chicks [97]. However, nest construction is time and energy intensive, and there are inevitable trade-offs between the costs inherent in constructing larger nests and the benefits such nests confer [98,99]. The magnitude of such trade-offs is likely to be higher for species where only one parent builds the nest, such as the Pied Flycatcher (*Ficedula hypoleuca*), compared to those with biparental nest construction, as seen, for example, in Swallow-tailed Cotingas (*Phibalura flavirostris*). For species where nest construction is energetically costly, deep nestboxes might be disadvantageous.

Ectoparasite load can be significantly higher in nestboxes with more nest material, including deep nestboxes used as an anti-predator strategy. This pattern is likely due to a more favourable microclimate, increased food availability, and more refuge space [100,101]. Higher ectoparasite loads can negatively affect both nestling and adult body condition, significantly reducing reproductive success (e.g., [102–105]). Blunsden and Goodenough [93] studied the effects of nestbox type on parasite abundance in the nests of Blue Tits, Great Tits, Pied Flycatchers, and Eurasian Nuthatches (*Sitta europaea*). Compared to standard nestboxes, deep nestboxes contained significantly more hen fleas (*Ceratophyllus gallinae*) and haematophagous blowfly (*Protocalliphora* spp.), likely due to the increased nest volume. The effects of parasitism can manifest either during the nesting period as anaemia and slow growth for chicks and weight loss for adults [106–109], or afterwards via carry-over effects [110,111]. The positive relationship between nest volume and ectoparasite load in deep boxes might be offset to an extent by the larger distance between nest cup and entrance hole, as this decreases parasitism by blowfly since the nest is harder for free-living adults to detect [92].

Other potential negative consequence of deep nestboxes relate to light and oxygen levels. There is a significant decrease in nest illumination with cavity depth [112,113]. Light exposure can have multiple positive effects on avian physiology, including photo-acceleration of embryonic development [114,115], and by facilitating better use of colour vision [112]. Deep cavities could also reduce ventilation and lead to a build-up of carbon dioxide and a reduction in oxygen, although this idea remains speculative. To test this, empty nestboxes of different depths could be flushed with a low O_2/high CO_2 mixture, with the time taken for gaseous composition to normalise being measured [116].

The effect of birds adding additional nesting material to deep nestboxes, potentially driven by selection to increase nest light levels and nest ventilation, can be problematic. Indeed, this process could reduce or eliminate the entire *raison d'être* of deep nestboxes as a predation prevention strategy by decreasing the distance to the nest hole so eggs and chicks are within reach of predators once again. For example, in a study of Blue Tits and Great Tits by Kaliński et al. [54], predation in deep nestboxes was entirely avoided, except when nests were built higher than 6 cm, which negated the safety benefits of this nestbox type. Raising the nest structure to be closer to the hole can also increase detection by ectoparasites that have a free-living adult stage by making the nest easier to locate [92].

4.3. Advantages and Disadvantages of Guardian Tubes, Noel Guards, Hole Extenders, and Internal Ledges

Based on the same principle as deep nestboxes, guardian tubes, Noel guards, and hole extenders are used to increase the distance from the nestbox entrance to the nest cup to prevent larger mammalian predators from reaching eggs and chicks [54]. Rather than the additional distance being created by increasing cavity depth, these designs all involve building outside the nestbox structure to create an entrance 'tunnel'. Nestbox guardians typically involve an elongated tube made from Polyvinyl Chloride (PVC) that is affixed to the nestbox around the entrance hole (Figure 4a). A variation on this is a Noel guard. Popular in the USA, Noel guards use essentially the same premise but are made from wire rather than plastic (Figure 4b). A third variation is the addition of a thick wooden block with a central opening over the entrance hole to create a hole extender [117] (Figure 4c). All three of these external modifications also reduce the ability of predators to increase the size of a cavity's entrance hole, effectively functioning similarly to a metal plate around the entrance but with additional benefits. Yamaguchi et al. [118] also tested a unique variant of this concept: a small wooden block fixed on the inside of the box's front panel, 25 mm below the entrance hole, to create an internal ledge below nestbox entrance (Figure 4d).

The effectiveness of these interventions has rarely been tested, but Kaliński et al. [54] installed PVC nestbox guardians between breeding seasons on nestboxes used by Blue and Great Tits at a site where pine marten predation was common. Not only did fewer nests become depredated after tubes were installed, but there was also no difference in nestbox uptake, thereby suggesting the devices did not negatively affect nest site choice within these populations. At a continental-scale, data from 24,114 nestboxes in the USA submitted to NestWatch citizen-science program (nestwatch.org) found that average daily survival probability of nests with predation proofing rose from 0.78 to 0.84 across all species [117]. Although estimates were not provided specifically for Noel guards and hole extenders versus boxes with no protection, extenders were the most effective intervention tested. Finally, although this was not their intended purpose, plastic guardians, wire Noel guards, and wooden hole extenders (Figure 4a–c) can all greatly reduce rain ingress [119]. Moreover, internal ledges, either below the entrance or affixed to other panels, could assist parents in feeding their chicks without contact with the nest structure.

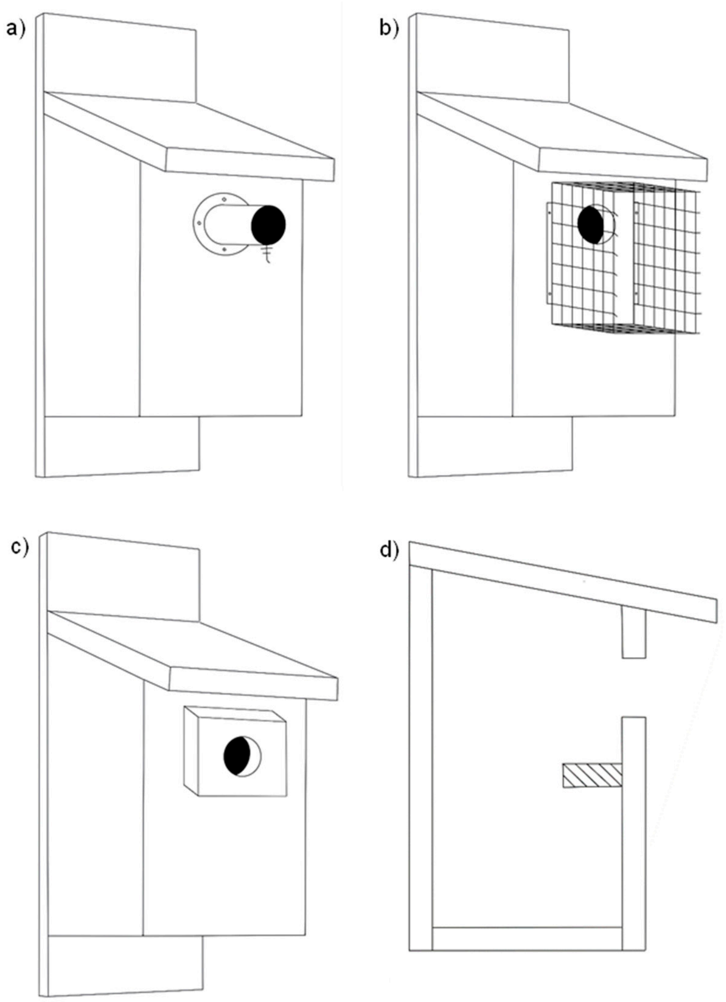

Figure 4. Modifications to wooden nestboxes: (**a**) nestbox guardian plastic entrance tube; (**b**) wire mesh Noel guard; (**c**) wooden hole extender; and (**d**) internal wooden ledges immediately below the entrance hole.

There are also some possible disadvantages of entrance extensions. Ad-hoc observations by Blunsden and Goodenough [93] indicated that guardian tubes may decrease provisioning rates since adults always need to enter the nest chamber rather than feeding older chicks from the entrance. Moreover, Kaliński et al. [54] found that Blue and Great Tits using boxes with guardians used significantly more nest material relative to nests constructed in the same nestboxes before guardians were added. This behaviour, which was similar to that observed by birds using deep nestboxes, persisted over multiple years. Explanations for this behaviour in both types of modified nestbox are likely similar, with reductions in light intensity or ventilation being probable drivers. It is therefore possible that guardian tubes and deep boxes have analogous benefits and costs, reducing predation risk but having potential trade-offs with light intensity, nest microclimate, nest building costs, and ectoparasite loads. The attenuation of light levels upon entering a standard tree-mounted next box can be 1000 times or more [120] and the installation of a guardian tube would exacerbate this by reducing the angle at which direct light is able to enter the box. Similarly, an elongated entrance hole could affect airflow, altering a cavity's microclimate and potentially lowering oxygen or elevating carbon dioxide levels. Research that measures light and airflow in boxes with guardian tubes installed, and any effects on provisioning rates, is therefore recommended to better understand the full impact of these modifications on nestling body condition and fledging success.

4.4. Advantages and Disadvantages of Woodcrete Nestboxes

Although nestboxes for secondary cavity-nesting species are typically made from wood, other materials can reduce the risk predators accessing the nest contents via panel penetration or hole enlargement. Woodcrete (also known as sawdust-concrete) is a mixture of cement and sawdust that does not need chemical treatment with preservatives and is tougher and more durable than wood [45,121]. Although usually considerably more expensive than wooden boxes, and with much less opportunity for home-made construction, the longevity of woodcrete nestboxes means that they do not need to be replaced as frequently. Such boxes can be affixed to a tree in a similar way to a wooden nestbox (Figure 5a) or suspended by wire from a branch or from the truck using a bracket (Figure 5b).

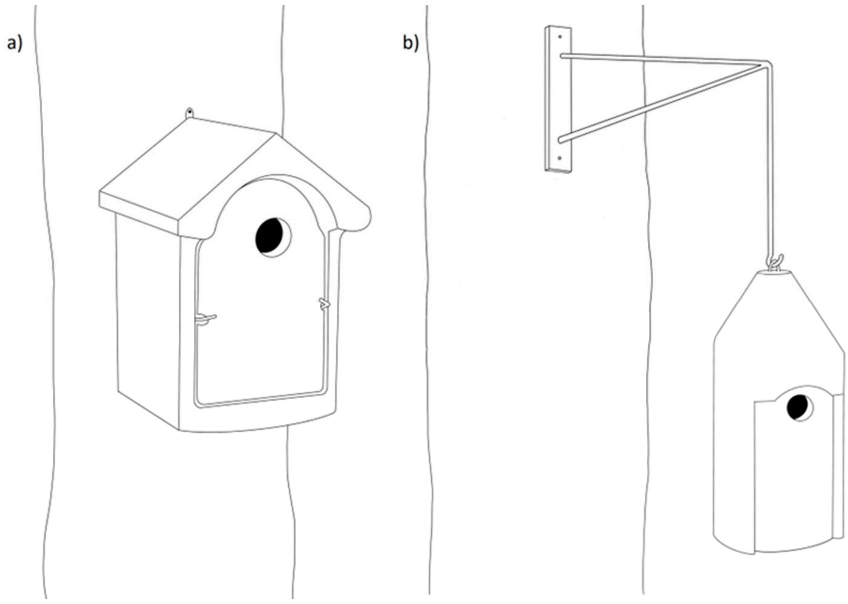

Figure 5. Two types of woodcrete nestboxes: (**a**) affixed to the trunk of a tree; and (**b**) suspended from a branch or a trunk-mounted bracket.

Several studies have concluded that woodcrete nestboxes are preferred relative to wooden nestboxes by nesting birds, including Eurasian Tree Sparrows, Blue Tits, and Great Tits [47,121–123]. In these studies, woodcrete and wooden nestboxes were paired either as a dyad on the same tree [47,122,123], or on separate trees but within minimum territory size [121]. Browne [121] further showed that Paridae exhibited a preference for hanging woodcrete nestboxes rather than those affixed to tree trunks. Better thermal insulation and perceived predation risk were suggested as the main factors driving higher uptake of woodcrete boxes [121,122]. However, in all four studies, the woodcrete boxes had a smaller internal volume and were deeper than paired wooden nestboxes, which could have affected choice (e.g., [48,54,96]). Moreover, a preference for woodcrete nestbox does not hold universally. In a study of ectoparasites in different nestbox types at Nagshead Nature Reserve, UK, Blunsden and Goodenough [93] were unable to consider any of the 100 woodcrete boxes offered in dyads with similarly sized wooden nestboxes to Blue Tit, Great Tit, European Nuthatch and Pied Flycatcher because uptake of woodcrete boxes almost zero (this compared with ~70% occupancy of wooden nestboxes). Future research on choice using woodcrete and wooden nestboxes of the same depth is needed to determine if the observed preference for woodcrete boxes in most studies is partly driven by depth rather than material composition.

Woodcrete nestboxes can be highly effective at reducing predation risk in some circumstances. For example, replacing trunk-mounted wooden nestboxes with suspended woodcrete nestboxes at the nestbox scheme at Wytham Woods, UK, decreased predation by Weasels from ~50% to almost 0% and increased the number of fledglings entering the local population by 60% [52,71]. However, a reduction in predation risk is not axiomatic; indeed, sometimes it can increase. For example, in central Spain, ladder snakes depredate eggs and chicks inside woodcrete nestboxes more often than in wooden boxes at the same site [123]. The authors hypothesised that this was due to stronger olfactory cues due to reduced ventilation in woodcrete nestboxes attracting reptilian predators that could still reach the entrance hole despite nestboxes being suspended by wire.

However, although woodcrete nestboxes are (usually) effective at decreasing predation, there are several potential disadvantages, some of which are species- and location specific. This means that their effects on breeding success is mixed, and thus suitability within conservation contexts can be questionable. For Blue and Great tits nesting in woodcrete boxes in mixed habitats in the UK [121], and for Eurasian Tree Sparrows using woodcrete boxes in woodland and parkland in Spain [47], there was no overall change in nesting success. This was despite opposing trends at different nest stages, with a significant increase in clutch size possibly offsetting the counter trend of a significant decrease in nestling weight for broods raised in woodcrete versus wooden boxes [47]. The increase in clutch size was interpreted as being a reflection on parental quality, with fitter or more experienced birds using the safer option. The decrease in nestling weight was thought to be due to chicks overheating in woodcrete boxes, with resultant dehydration, which was partly supported by significantly higher temperatures recorded by within-nest dataloggers. Hyperthermia-induced dehydration, slow nestling growth, and lower nestling weights, have all been recorded in other species, including Cliff Swallows (*Petrochelidon pyrrhonota*) nesting in natural nests built on heat-retaining man-made structures [124], Great Tits exposed to naturally hot conditions within wooden nestboxes [125], and Blue Tits where nest temperatures were artificially raised [126]. Higher temperatures can also be associated with higher abundance of avian ectoparasites [127,128], although this is not always the case; recent studies suggest these linkages are both species- and location-specific [129–131].

Interestingly, two studies of Eurasian Tree Sparrows nesting in woodcrete nestboxes in central Spain studied by García-Navas et al. [47,122] gave conflicting results in the effects of elevated temperatures on nesting success. Higher internal temperatures were recorded in woodcrete nestboxes compared to wooden nestboxes in both studies (average 1.5 °C increase) [47,122]. In the 2008 study, however, breeding success was statistically higher for broods raised in woodcrete nestboxes relative to wooden boxes, and a negative effect on nestling weight was recorded, such that the temperature increase was deemed insignificant (indeed, potential benefits to maternal energy expenditure during incubation were hypothesised as incubation intervals were shorter) [122]. This contrasted with the 2010 study where negative impacts were recorded, such that the temperature increase was deemed significant [47]. The difference was that the 2008 study considered only first broods, when ambient temperature and solar gain were comparatively low, whereas the 2010 study included second and third broods when ambient temperature and solar gain were considerably higher. It thus appears that the benefits derived from thermal properties of woodcrete nestboxes early in the season, which might influence nestbox choice [122], may become disadvantages as the season advances [47,132]: a classic example of an ecological trap.

In some cases, woodcrete boxes can be associated with net negative outcomes. Bueno-Enciso et al. [123] found that nesting success was lower for Blue and Great Tits using woodcrete boxes than those nesting in wooden nestboxes. Although this was partly due to increased predation by snakes, it was also notable that nestlings were smaller than those raised in wooden nestboxes the same year, suggesting slower growth rates for chicks in [hotter] woodcrete nestboxes. Humidity was also suggested as a casual factor alongside temperature, which has previously been suggested as a driver of high nest microbial load and negative consequences for chicks of this species [133].

An important consideration when considering the effects of nestbox microclimate temperature is the plasticity exhibited by breeding birds in response to ambient temperatures. During nest construction, birds will adjust the mass of their nest in response to the ambient temperature at that time, adding more nest material for improved insulation in cooler temperatures, and vice versa [134,135]. Whether this behaviour is sufficient to control the extreme temperatures recorded in woodcrete boxes is unknown, and future studies could therefore examine potential relationships between nest mass and woodcrete boxes. There are also critical temperature thresholds, beyond which effects on breeding parameters start to significantly affect nestling survival and health [136]. Although broods in woodcrete boxes are more frequently exposed to hot conditions, temperatures seldom exceed critical thresholds, and thus the effects of overheating might not be sufficiently detrimental to offset the predation reduction advantages of woodcrete boxes, at least at temperate latitudes [47,137].

Finally, it should be noted that bats (Chiroptera), which can compete with birds for the use of bird nestboxes, have been found to be more likely to use woodcrete bird nestboxes than standard wooden bird nestboxes [138], such that switching nestbox materials could alter the competition dynamics at some sites.

4.5. Advantages and Disadvantages of Photosensitive Shutters

A novel design for excluding small nocturnal predators from nestboxes occupied by Tree Martins (*Petrochelidon nigricans*) in Tasmania, Australia, was developed and tested by Stojanovic and colleagues [139]. In this case, the main predation threat came from a non-native—and nocturnal—possum species, the sugar glider. Photosensitive shutters, colloquially termed "Possum-Keeper-Outterers" (PKO), were retrofitted to nestboxes that would only open when ambient light exceeded 20 lumens. This covered the entrance hole at night, when adult birds would be in the nestbox, thereby preventing nocturnal predators from entering the nestbox and improving nest success by 56% (Figure 6). However, a significant issue was the high mortality risk as device failure could entrap birds, a situation that did occur during field testing [139]. This could be mitigated by frequent maintenance checks, installation of back-up batteries and the use of multiple solar panels in shaded habitats to ensure proper operation of the mechanism. There was no obvious neophobia or distress in Tree Martins, but behavioural changes were not explicitly examined. It should be noted that PKOs are expensive, costing approximately $340 USD per unit [139] and rendering them impractical for large nestbox schemes; they are also unsuitable for protecting against diurnal predators.

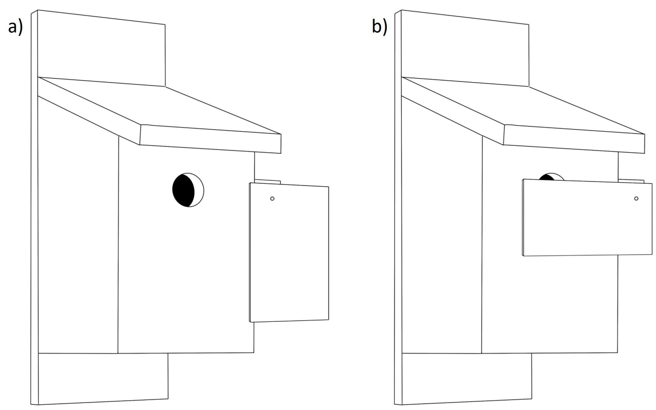

Figure 6. Photosensitive shutter fitted to a nestbox. This pivots between: (**a**) diurnal configuration whereby the entrance hole is unobscured; and (**b**) nocturnal configuration to cover the entrance hole during low-light conditions to exclude nocturnal predators.

4.6. Advantages and Disadvantages of Baffles

Rather than modifying nestboxes themselves, a different option is to modify the support to which a nestbox is affixed. Passive barriers placed below a nestbox can be a cheap and simple method of directly blocking tree-climbing predators, including mammals such as stoats and reptiles such as snakes, from reaching nests. These barriers, often termed "baffles", typically have a conical or stovepipe design [117,140] (Figure 7). Baffles are usually constructed from cheap and readily available materials, such as plastic or metal sheeting.

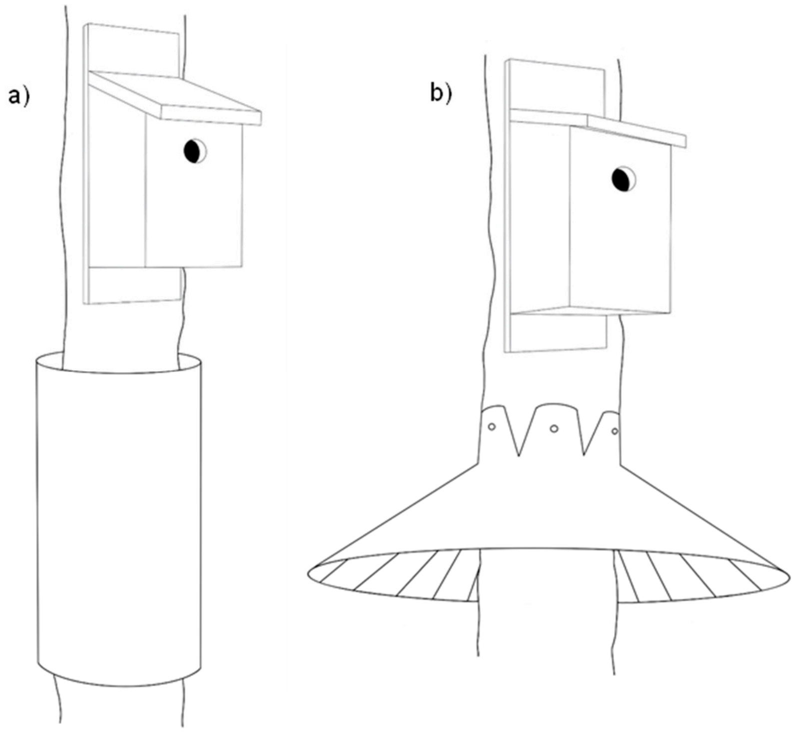

Figure 7. Baffles used to protect nestboxes: (**a**) stovepipe design and (**b**) collar design.

Data from 24,114 nestboxes monitored via the US citizen science project NestWatch, showed that baffles, especially stovepipe baffles, are one of the most common anti-predator interventions [117]. They are effective when used for tree- or post-mounted nestboxes located in open habitats. This includes nestboxes located within open wetlands on single support structures used by cavity-nesting ducks, including Black-bellied Whistling Ducks (*Dendrocygna autumnalis*) and Wood Ducks (*Aix sponsa*) [141,142], as well as waterfowl that are usually considered to be open-nesting species but will use nestboxes when provided, including Mallards (*Anas platyrhynchos*) [143]. In all these studies, the support structure for the nestbox was the sole access route for ground mammals, such as American mink (*Neovison vison*), and nesting success improved when supports were fitted with stovepipe or conical baffles due to decreased predation rates [141–143]. Other wetland species can also benefit from such interventions. For example, Keo et al. [144] demonstrated that cheap plastic stovepipe baffles can increase fledging success of the critically endangered Giant Ibis (*Thaumatibis gigantea*) by 50%. The technique can also be suitable for passerines within open environments. For example, Eastern Bluebird (*Sialia sialis*) nests in boxes on suburban golf courses in Virginia, USA, were more likely to fledge when predator baffles were installed [145], although predation was still the predominant cause of nest failure.

Studies testing the effectiveness of baffles in protecting passerine nestboxes in woodland habitats are relatively limited as they are generally used as one aspect of a wider study. The intervention was not effective in improving breeding success of Riflemen (*Acanthisitta chloris*) in New Zealand [146] or Prothonotary Warblers (*Protonotaria citrea*) in a hardwood forest in Mississippi, USA [147]. In these cases, it is likely that predators circumvented baffles by accessing nestboxes from surrounding trees rather than by climbing directly from the ground [148], which meant that the use of baffles in dense woodland habitat was ineffective. Although it is theoretically possible to eliminate this potential by pruning vegetation (e.g., [149]), such a high level of intensive management is unlikely to be regularly feasible on a large scale. Moreover, in some locations, pruning could have deleterious impacts on arboreal species such as hazel dormice (*Muscardinus avellanarius*), for whom structural complexity and above-ground connectivity is vital [150]. However, despite these limitations, baffles can be effective for some woodland predators. For example, there was a significant increase in fledging success in Paridae nests in Mediterranean woodlands where baffles had been used to prevent depredation by Montpellier and ladder snakes compared to control nestboxes [151]. The only instance where a protected box was invaded was due to a snake crossing to the box from a nearby tree. This prompted the suggestion that use of baffles on trees surrounding the focal nestbox tree could be useful when arboreal connectivity is high [151].

4.7. Advantages and Disadvantages of Regular Replacement and/or Relocation of Nestboxes

Birds frequently alter their nest site fidelity in response to perceived predation risk, an adaptive behaviour summarised by the *Win-Stay*, *Lose-Shift* hypothesis [152]. Based on individual reproductive success, or reproductive success of neighbouring conspecifics, birds remain at (or return to) safe nesting sites but abandon high-risk locations and relocate [153–156]. Recent research suggests that the *Win-Stay* behaviour may be temporally restricted. For Boreal (Tengmalm's) Owls (*Aegolius funereus*), elapsed time since successful nesting was positively correlated with abandonment of nest sites [157]. This was likely due to the positive relationship between predation events and nestbox age. One reason that predation may be higher at old nestboxes relative to new nestboxes is that wooden walls rot and soften over time, becoming more susceptible to damage from predators. Natural cavities in rotten wood are depredated more frequently, and species such as Marsh Tit will therefore avoid nesting in dead wood [81,158]. This suggests that nest predation could decrease, and nestbox occupation increase, when old boxes are replaced with new ones. However, the benefit of this could be offset given that non-target species, such as social Hymenoptera, which can occupy nestboxes and thereby exclude birds, prefer new nestboxes to old nestboxes [159]

Empirical evidence also shows that some nest predators will return to nest sites they have previously depredated, with predation risk thus being partly determined by a positive feedback loop as predators use prior experience and spatial memory to learn nest locations [58,60,62,160]. This could be circumvented by the periodic relocation of nestboxes. Although there is limited research testing the efficacy of this method, relocation of boxes has been shown to reduce predation of Boreal Owl and Paridae nests [59,161,162]. Spatial scale affects intervention effectiveness: relocation should be greater than 800 m for successful predation reduction [162]. However, due to limited space, relocation of nestboxes is not always possible, and this likely links to the lack of research into, and use of, this intervention. Furthermore, relocating nestboxes may adversely affect breeding populations of highly sedentary species such as Eurasian Nuthatch, which often return to previous nesting sites [163,164].

4.8. Summary of the Advantages and Disadvantages of Nestbox Predation Prevention Strategies: Weighing up the Evidence

Although avian nestboxes are not helpful for all species-at-risk [49], they are undoubtedly an important conservation strategy. This is especially true if they can be optimised by reducing predation risk whilst also ensuring that any unintended consequences from anti-predator modifications are minimised. Modification options depend on the types of predators involved, as outlined in Figure 8, but ultimately, the decision whether, and how, to predator-proof avian nestboxes depends on several factors. These include: (1) the level of predation risk; (2) the type(s) of predators involved and the main way(s) they access nests; (3) how effective interventions will be in reducing actual and perceived predation risk; (4) whether the benefits of reducing predation outweigh potential costs that the predation-prevention modification imposes; and (5) any logistical limitations or constraints in cost, time and labour.

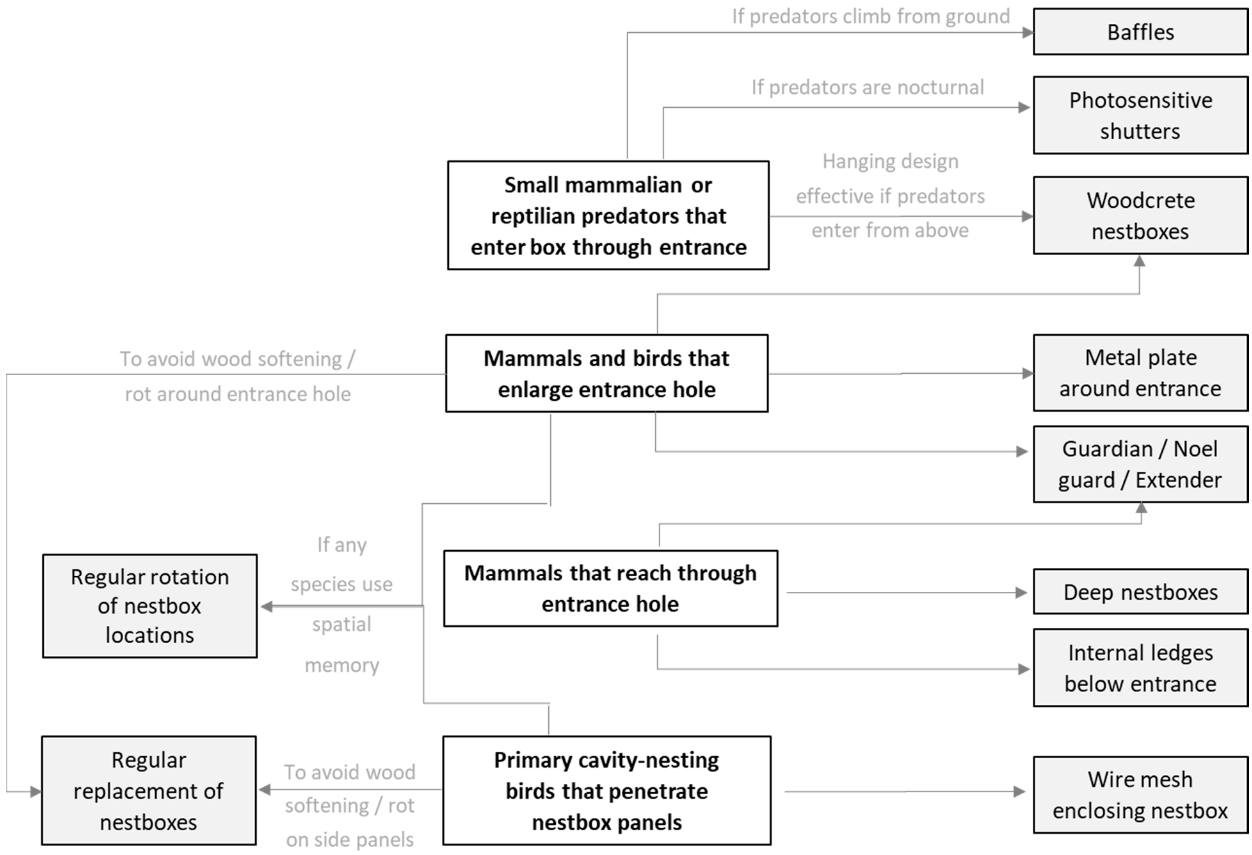

Figure 8. Selecting a suitable predator-proof intervention based on predator, size and access route.

In some cases, the risks associated with predator-proofing avian nestboxes are largely those relating to possible ineffectiveness and financial costs (e.g., metal plates around entrance holes, wire mesh enclosing nestboxes, and photosensitive shutters). However, for other predator-proofing interventions, there is potential for important unintended consequences (e.g., guardian tubes, Noel guards and hole extenders, deep nestboxes, and woodcrete nestboxes). These are not always obvious, especially when costs and benefits are multifaceted or interact with one another in complex ways (see Table 2).

Table 2. Summary of key hidden costs of interventions to reduce predation of avian nestboxes and unanswered questions, either in relation to specific costs or in general.

Intervention	Hidden Costs		Unanswered Questions
Guardians, Noel guards, hole extenders	Potential decreases in provisioning rates as adults always need to enter the nest chamber rather than feeding older chicks from the entrance.	→	Based on ad-hoc observations, so extent and significance of this is unclear.
	Changes in the ventilation and light within the nest cavity.	→	Seemingly not investigated.

Table 2. *Cont.*

Intervention	Hidden Costs		Unanswered Questions
Deep nestboxes	Additional material being added to nestbox, with possible implications on nest building costs and first egg date. Also, relationships between nest volume and ectoparasite load.	→	Cost of extra material largely speculative and needs empirical quantification. Optimal box depth for ensuring that any extra nesting material will not decrease the (theoretically larger) distance between nest cup and entrance required.
	Changes in the ventilation and light within the nest cavity.	→	Seemingly not investigated.
Woodcrete nestboxes	Increase in nestbox internal temperature can have negative impacts on chick growth, especially when ambient temperatures are high or nestbox is exposed to sunlight for extended periods (including in gardens or open habitats).	→	Trade-offs between predation prevention and microclimate studied in ground-nesting species such as Piping Plover (*Charadrius melodus*) and Hoopoe Lark (*Alaemon alaudipes*) [165,166], but not in secondary cavity-nesting species. Critical temperature thresholds are thus unclear, as is the magnitude of benefits and costs.
	Increase in humidity with possible implications for nest microbial load.	→	Seemingly not investigated, despite links between nestbox temperature, pathogenic microbial loads, and chick health in wooden nestboxes (e.g., [133]).
	Potentially more intense smell could increase predation from species that can enter cavity directly.	→	Investigated for snake predation of Blue and Great Tit nests in central Spain [123]; unclear if risk was site- or predator-specific or indicative of widespread issue.

5. Conclusions and Future Directions

Although nestboxes developed for, and utilised by, secondary cavity-nesting species that use tree cavities are generally "safer" than natural cavities, predation is still the largest cause of nest failure [33] and reaches >50% in some situations [40,50,51]. However, the assumption that reducing predation by modifying nestboxes to reduce predation risk will axiomatically confer a net benefit to birds is incorrect. Developing and applying interventions to reduce nestbox predation will necessarily be context-specific and might sometimes (and potentially very frequently) need to be made in the absence of full information, especially in relation to unintended consequences. However, the more that strategies for reducing predation are empirically tested, and the more that potential trade-offs are explicitly considered, the more informed ecological practitioners, conservationists, researchers, and the millions of people who try to "do their bit" for garden birds will be. Ultimately, therefore, further studies of the costs and benefits of approaches, and the nuance involved (including local variation and acknowledging species differences), should make interventions even more effective.

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