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Negative effects of artificial nest boxes on birds: A review

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ABSTRACT

Artificial nest boxes are placed to attract birds to nest and breed in a specific location, and they are widely used in avian ecology research and in the attraction of insectivorous birds. There is evidence that artificial nest boxes can adversely affect breeding fitness but no great focus has been placed on this issue by researchers. Therefore, we retrieved 321 research papers regarding artificial nest boxes published from 2003 to 2022 and used the 'Biblioshiny' program to extract and integrate keywords; we then summarized the adverse effects of artificial nest boxes on avian breeding success. The studies highlighted many drawbacks and misuses in the designing and placement of nest boxes; furthermore, bird attraction was decreased by their inappropriate selection, thus reducing breeding success. Regarding nest box production, there were shortcomings in the construction material, color, smell, and structural design of the boxes used. Nest boxes were also placed at inappropriate densities, locations, orientations, heights, and managed incorrectly. Finally, we propose suggestions for more efficient and safer artificial nest boxes for future use in avian ecology research and bird conservation.

1. Introduction

Nest site selection and nesting environment are crucial to the success of avian breeding, population dynamics, and community composition (Robertson, 1995). The number of natural tree holes decreases sharply with human interference as large trees are removed and forests become composed of younger trees. This adversely affects the breeding of secondary cavity-nesting birds (Wang and Gao, 2002). Nest boxes have been gradually introduced since the 1920s. They are widely used in urban, rural, and wild areas to complement the nesting sites of secondary cavity nesting birds and are effective for scientific research (Cook, 1947; Wan et al., 2017). Nest boxes easily attract breeding birds, and are preferred by some (Li et al., 2008), which allows monitoring of the behavior of parents and nestlings, thus facilitating ecological studies. Nest boxes can also reduce burden of nest site lacking and allow the target bird population to increase gradually (Newton, 2007). Nest boxes can assist in research, including bird population dynamics, quantitative genetics, life history evolution, and edge effects (Evans et al., 2002; Cao, 2007); they can help protect endangered birds (Liu and Li, 2020), attract insectivorous birds to solve insect problems (Swinton et al., 2007; Tscharntke et al., 2012), and be used to measure the health of urban ecological environments (He et al., 2020). However, more experiments are revealing potential drawbacks of nest boxes. Inappropriate nest boxes may negatively impact threatened species and increase their extinction risk (Czeszczewik, 2004; Klein et al., 2007).

In this paper, we retrieved articles published from 2003 to 2022, regarding the adverse effects of nest boxes on birds, through Web of Science (http://www.webofscience.com) and China National Knowledge Infrastructure (CNKI; https://www.cnki.net). A total of 321 articles have been collected and analyzed using the 'Biblioshiny' program. By summarizing adverse effects of nest boxes we aimed to provide practical information for future research (Table 1).

2. Two-views of nest boxes for bird protection

Nest boxes play an important role in bird protection and theoretical research. For example, nest boxes have a direct ecological impact on nesting birds (Maziarz et al., 2017), increasing the nest site choice and

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Table 1
Keyword frequency ranking of research direction regarding the negative effects of artificial nest boxes.

Research area	Keywords [a]	Frequency	Percentage (%)
Nest box	Nest box; artificial nest box	137	33.9
Reproductive parameters	Reproductive success rate; reproduction; nesting; predation; strategy; nest predation; sleep; clutch size; nesting success rate; success rate; behavior; competition; intraspecific nest parasitism; sleep; reproductive effectiveness	91	22.5
Function	Conservation; habitat; habitat restoration; artificial habitat; biodiversity; reproductive ecology; urbanization; habitat loss; manual solicitation; avian resources; community structure; pest control	48	11.9
Research object	*Parus major*; *Aix sponsa*; avian; seabirds; *Athene cunicularia*; *Tyto alba*; secondary cavity-nesters; *Eudyptula minor*; *Sialia currucoides*; *Sialia sialis*; city birds; farmland birds; *Sialia mexicana*; *Athene cunicularia hypugaea*; *Falco sparverius*; *Ficedula hypoleuca*; *Sturnus sericeus*; *Sturnus vulgaris*; *Tachycineta bicolor*; *Ficedulaza thopygia*; *Strix uralensis*	82	20.3
Nest box parameters	Temperature; night artificial lighting; light pollution; artificial noise; humidity; entrance diameter	38	9.4
Negative effects	Ecological trap; trap	8	2.0

[a] Keywords with similar meanings and the research direction they represent have been merged.

not affecting the occupancy of natural nests (Zhao et al., 2011). This reduction of nesting burden should improve reproductive success (Teglhøj, 2018) and enhance comparisons of reproductive output between nest boxes and natural holes. The predation rate of some nest boxes is lower than that of natural holes, thus improving species survival rate. However, some studies show that nest boxes do not completely replicate natural holes (Lambrechts et al., 2010; Slevin et al., 2018).

Regarding population density, providing nest boxes can increase the number of Great Tits (*Parus major*) (Mänd et al., 2009), but a high density of nest boxes can lead to higher predation rate and lower fledging rate (Mainwaring et al., 2014; Fuentes et al., 2019). Regarding research on behavior in nest boxes, the begging behavior of nestlings and reproductive input of parent birds can be more easily observed (Hofstetter and Ritchison, 1998). Regarding the effects of nest materials and ectoparasites on site selection of birds, experiments by Breistøl et al. (2015) on the Pied Flycatcher (*Ficedula hyoleuca*) show that birds prefer to nest in clean nest boxes without external parasites.

Ecological processes can be changed in nest box research owing to both design and manufacture of nest boxes, and pressure from humans and environmental changes that interfere with the nest sites (Burhans and Thompson, 2006). Therefore, nest boxes can have a negative effect on birds and form ecological traps, i.e., birds choose their habitat based on certain factors or preferences. However, the results after selection cannot be predicted (Gates and Gysel, 1978; Robertson and Hutto, 2006). Ecological traps are becoming a burden on the reproduction of species (Hale and Swearer, 2016). However, as human interference is a common cause of ecological traps, the negative effects may be predictable in some cases (Robertson et al., 2013). Conservation should aim to reduce or eliminate the negative effects of traps through prediction.

Currently, nest boxes are used to study species that adapt to using them (Lambrechts et al., 2010). However, owing to errors caused by a lack of expertise, birds may be misled when choosing nest sites. A combination of nest predation, competition, parasite infestation, parental behavior, microenvironment, and study species preference should be considered when choosing nest box appearance, material, and structure (e.g., entrance size, internal volume, height below entrance, nest box material thickness), to avoid the negative effects of nesting boxes on birds (Goldingay and Stevens, 2009).

It is also necessary to adjust nest boxes according to their geographical location, population characteristics, height, and nest opening orientation. Unreasonable mass customization of nest boxes and random placement leads to incorrect guidance for birds. Therefore, results obtained in the nest box may not accurately reflect research conducted in natural cavities (Lambrechts et al., 2010). In areas with rich nest site resources, the addition of nest boxes may become a new interference (Goldingay and Stevens, 2009). The adaptability of birds to nest boxes varies according to various aspects: bird species preference, geographical differences, and environmental conditions (von Brömssen and Jansson, 1980; Orell and Ojanen, 1983).

3. Nest predation

Nest predation affects the reproductive rate of birds, and the design, placement, and management of nest boxes can affect predation risk.

Box design, including the structure, color and odor may affect the rate of predation. Birds may also be affected by the design of the nest box entrance. Generally, entrances are designed as a round hole to prevent wind, rain, and predator exposure, which provides better protection (Leroux et al., 2018). The breeding success of birds in nest boxes with a slot-type entrance is lower than for those with a round entrance, owing to exposure and predation (Leroux et al., 2018). Nest boxes with wedge-shaped entrances are easier to assemble, but they allow more sunlight entry and nest predation. Consequently, these nest boxes are less frequently selected (Browne, 2006). Some antipredation nest boxes can avoid the further enlargement of the nest box entrance, reduce the nest predation rate, and improve nestling survival. Such nest box designs can affect bird population dynamics and produce large-scale changes in life history characteristics (McCleery et al., 1996; Julliard et al., 1997). Furthermore, the size of a nest box is also related to predation risk (Chen et al., 2019). A deeper nest box can help birds avoid predators (Moeed and Dawson, 1979); however, if a box is too wide, predators can easily enter and exit (Ding et al., 1999).

Nest predation is related to nest box color. Different colors can change the characteristics of nest boxes, through concealment, temperature, and parasite infection; thus, birds have color preferences (Browne, 2006; Zhang et al., 2012).

Concealment of a nest box can reduce nest predation and potential reproductive failure (Martin, 1993a). Artificial boxes are sometimes easier to find than natural cavity nests, leading to a higher risk of predation (Martin, 1987; Sloan et al., 1998; Skwarska et al., 2009). Green or brown coloring, with better camouflage, are now preferred (Wei, 2014; Griffiths et al., 2017). Some studies show that attraction rate to cavity-nesting birds, based on nest box color from low to high, was: untreated primary color nest box, black and white, brown or green or blue, and red had the highest attraction rate (Chen, 1989; Browne, 2006; Zhang et al., 2012).

Despite multiple studies on the effect of nest box color, there is no consensus. The breeding success of birds is restricted by biotic and abiotic factors in the local ecosystem, so it is necessary to evaluate when nest boxes of different colors are actually being used. Furthermore, during nest box assembly, it is usually painted to integrate it into its surroundings and reduce weathering damage (Goldingay, 2015) by treatment with preservatives (Lambrechts et al., 2010). However, such treatment leaves an odor, and it remains controversial whether this affects birds and predators (Zanette, 2002; Ekner and Tryjanowski, 2008). Some scholars believe that the olfactory sense of birds is degraded and that the odor left after treatment has no effect (Ding et al., 1999), whereas others believe that birds have an excellent olfactory sense (Amo et al., 2008); for example, it is known that songbirds can avoid predators through odor recognition (Steiger et al., 2008). Thus, chemical odors left on the nest boxes may directly or indirectly affect breeding (Browne, 2006); for example, mammalian predators can track human residual odor to prey on eggs and nestlings in nest boxes. Alternately, predators may also avoid nest boxes because of human odor (Zanette, 2002).

Concealment of nest boxes also affects nest predation and this varies depending on placement. Nest predation rates in some urban areas are even higher than in the wild (Huhta, 2000) as domestic and stray cats will prey on wild birds (Evans et al., 2011). Artificial nest boxes are easier to find in cities (Wilcove, 1985; Huhta, 2000) and may attract predators more easily than natural nest boxes (Willebrand and Marcström, 1988). In wildlife reserves, resources can be abundant, and the number of natural predators of birds is increasing, especially snakes (Zhang et al., 2014). Some researchers believe that predators may lack experience with nest boxes; alternately, after some experimentation, predators can identify nest boxes as food sources (Slevin et al., 2018) and predation rates in areas with a high density of nest boxes rises rapidly (Petit and Petit, 1996; Slevin et al., 2018). The predation rate of ground nests remains low (Martin, 1993b), but that of artificial nests placed on the ground and in bushes is higher than that of natural nests (Burke et al., 2004).

Predation pressure affects the nest site selection of birds (Eggers et al., 2006) and optimal height varies depending on species. More elevated nest boxes have low accessibility and can prevent nest predation (Carstens et al., 2019), whereas those placed in relatively low positions can help parent birds escape quickly under dangerous conditions to hide in nearby shrubs (Kaluthota and Rendall, 2017). Without predation pressure, small birds choose their preferred habitat to build nests, but they will move to a more secure and higher nest site if predation pressure develops (Latif et al., 2012). It is worth mentioning that human damage to nests is a major factor in breeding failure of birds (Zhang et al., 2008b); therefore, the correct placement of nest boxes reduces the risk of human damage to artificial nests.

Nest box management also affects nest predation. An examination of old nest boxes found that the accumulation of nesting materials in an old nest will reduce box depth and shorten the distance between the entrance and the eggs or nestlings (Mazgajski, 2007a). An increase in this “dangerous distance” will increase predation risk (Wesołowski, 2002). At the same time, a heavy parasite burden may cause nestlings to call louder, thus attracting predators (Møller and Moller, 1989). Furthermore, some predators may recheck old nest boxes on which they have previously preyed, suggesting that predation risk on old nest boxes is higher than that of new ones (Sorace et al., 2004). However, there remain different views on whether predators randomly check old nests or repeatedly check nest boxes; further research is needed.

4. Competition

An excessive number of nest boxes have been shown to increase bird population densities (Taylor, 1976; Stamps and Krishnan, 1990), thus intensifying both intra- and interspecies competition. Intraspecific competition caused by nest boxes consists of nest parasitism, mating, and competing for various resources including nest sites. Providing nest boxes can alleviate the nest parasitism of Red-billed Starlings (*Sturnus sericeus*) (Jiang et al., 2012) to some extent, but the nest parasitism of Chinese Merganser (*Mergus squamatus*) may be aggravated (Liu and Li, 2020). In addition, impacts on extra-pair matings (Kempenaers et al., 1992), and the allocation of parent birds to becoming territorial guards may also occur. If the number of birds attracted exceeds the carrying capacity of the local resources (Mänd et al., 2005; Kilgas et al., 2007), or too many nest boxes are placed in areas where resources are scarce, birds will increasingly compete for the limited local resources (Dhondt, 2012), with negative effects (Wesołowski, 2011). The impacts of interspecific competition include endocrine fluctuations in female parent birds (Mazuc et al., 2003), a decrease in clutch size (Nicolaus et al., 2009), a change in food resources caused by overlapping foraging sites (Custer et al., 2003), an interference of fledging rate (Fuentes et al., 2019), and a change in species aggressiveness (Bhardwaj et al., 2015).

Over-dense nest box placement can cause a reduction in reproductive success (Mainwaring, 2017). An inappropriate number of nest boxes will also lead to competition between migratory species and resident species for territory and food (Leveau, 2018) as the migrants will also use local resources (Mac Arthur, 1959; Hurlbert and Haskell, 2003). However, when the number of local species increases dramatically, the resources available to migrants will be greatly reduced. Additionally, directly increasing the number of nest boxes produces a potential feast for predators which also has negative consequences for birds (Skwarska et al., 2009), thus indirectly affecting their distribution (Mainwaring et al., 2014); ultimately, this will determine the recruitment of nest boxes in the area.

The distribution and population structure of birds attracted and protected through the use of nesting boxes is affected by the density of nest box placement, including their centralized distribution and increased density (Zhai, 2007). This indirectly affects environmental carrying capacity (Liu, 2005), changes the diversity and evenness of communities, and ultimately changes the stability of ecosystems (Zuo, 2005; Wu, 2011; Li, 2015). Limiting the nest entrance size is an effective way to exclude non-target birds and reduce interspecific competition, in addition to adjusting the overall number of nest boxes.

Extremely low nest sites (nest site resource shortage) will also lead to fierce interspecific competition. Nest boxes can protect endangered birds or attract specific birds, while other birds and species will compete for nest site resources (Stojanovic et al., 2021). For example, when Great Tits breed, Spotted Flycatchers (*Muscicapa striata*) migrate to the breeding place, which creates a scarcity of nest site resources. Spotted Flycatchers may compete with Great Tits for nest boxes (Mainwaring, 2017) with a low probability of success (Slagsvold, 1975), and sometimes the Spotted Flycatcher dies (Slagsvold, 1975). The Great Tits will be replaced only when Spotted Flycatchers are dominant in number (Tompa, 1967). Additionally, other creatures, such as Wasps (*Hymenoptera*) (Broughton et al., 2015), Bats (*Chiroptera* spp.) (Goldingay and Stevens, 2009), and Squirrels (*Sciurus vulgaris*) (Wang et al., 2014) also occupy nest boxes, causing further competition.

Quality of the breeding habitat should be assessed comprehensively before placing nest boxes. The premise for setting nest boxes to attract birds to breed is that the habitat can both meet various needs and avoid damages for the attracted birds (Demeyrier et al., 2016). Special attentions should be paid on adequacy of food resources and avoiding human interference. Tree species, tree age, and vegetation coverage can also affect birds' breeding output by increasing competing on limited resources (Mänd et al., 2005). Providing abundant nest sites in a habitat with plenty of food or insect outbreak (Barbaro and Battisti, 2011; Liang, 2018) seems suitable, but the hidden negative effects are always ignored (Krams et al., 2021). In some research cases, sufficient nest boxes and outbreaking insects of the Tenthredinidae family provided plenty food and thus attracted birds to breed (Zhao et al., 2011; Martínez-Abraín and Jiménez, 2019), but Tenthredinidae insects had also damaged the trees and reduced other insects which relied on these tree leaves. Decrease in abundance of other insects negatively influenced the birds by potential competition among these birds that mainly forage on there insects. Limited foods can then lead to malnutrition and an increase in nestling mortality rate during the brooding period (Robinson and Holmes, 1982; Holmes and Schultz, 1988; Rytkönen and Orell, 2001; Rytkönen and Krams, 2003; Krams et al., 2021). What's more, some insects and their larvae also have a negative impact on avian breeding and the health of nestlings, leading to a decline in bird density in the region (Enemar et al., 2004; Barbaro and Battisti, 2011; Krams et al., 2021). Some birds prefer to breed in large-sized nest boxes and the amount of breeding investment is significant in cities. However, urbanization leads to the fledging rate of nestlings being lower (Solonen, 2001; Chamberlain et al., 2009; Demeyrier et al., 2016), which needs to be investigated in future.

Old nest boxes can alleviate the shortage of nest sites during the breeding season. In early research and experiments, old nest boxes were generally considered to have a negative impact on breeding, and old nesting materials were generally cleared for new experimental periods. However, with further study of nest boxes, the potential value of older boxes is gradually emerging. This may explain why birds sometimes prefer old nests (Fehérvári et al., 2015), especially in environments with intense interspecific competition and tight nest site resources. Reusing nest boxes can reduce the time and energy spent on nesting preparation (Reid et al., 2000; Wang, 2011) in the process of finding suitable nesting sites, and relieve competitive pressures and nest predation risks that may exist in the nesting process (Eggers et al., 2006). On this basis, breeding behavior may be completed in a shorter period of time. Furthermore, the nest material accumulated in old nest boxes may provide clues to the reproductive success of birds and predation risk assessment (Zhang et al., 2009; Wang, 2011; Mingju et al., 2019).

5. Parental behavior

The structure and placement of nest boxes will indirectly affect the relationship between parents and offspring, and also affect their health.

Nest box size influences breeding success (Norris et al., 2018) and the reproductive investments of birds (Demeyrier et al., 2016). Studies show that clutch size in nest boxes is larger than that in natural cavity nests (You, 2007; Zhang et al., 2008a, 2009), but the reason remains unclear. It is necessary to evaluate whether the number of eggs in the nest is affected by the area of the nest box (Karlsson and Nilsson, 1977) or whether high-quality parent birds with good fertility occupy the nest boxes. Clutch size in some nests increases slightly if a larger nest box is unsuitably selected, potentially increasing the burden of breeding input of parent birds, causing the chicks to grow more slowly owing to insufficient food supply (Zhang et al., 2008a).

Additionally, not only does an ill-fitting nest box impact reproduction, its internal size and depth also affect the temperature of the nest box (Stanback et al., 2013). The heat dissipation area of nest boxes is positively related to the floor area. Birds need to consume more energy to maintain the temperature in a larger nest box, whereas small nest boxes can lead to the death of young birds because of overcrowding and overheating (Karlsson and Nilsson, 1977; Meyrom et al., 2009).

The nest box entrance also affects parent bird behavior and should be designed for different target species. For example, the common secondary cavity-nesting birds, the Great Tit and the Varied Tit (*Sittiparus varius*), prefer nest boxes with an entrance diameter of 4.0–5.0 cm. In contrast, the Marsh Tit (*Poecile palustris*) prefers a nest box with an entrance diameter of about 3.0 cm (Choi et al., 2007; Wan et al., 2017). Nest box entrance diameters should be slightly larger than the cross-section diameter of the carina on the chest of the target species. The feeding behaviors of the birds entering and exiting the box and their parent bird-feeding behaviors are affected if the entrance is too narrow (Clark et al., 2020).

Nest boxes are often placed in cities to attract insectivorous birds, such as Passeriformes (Reynolds et al., 2016; Duckworth et al., 2017; Lambrechts et al., 2017) with the intention of biological control and assessment of the relationship between the environment and biodiversity (Rytkönen and Krams, 2003; Marzluff, 2017). Locality of nest box is closely related to the effectiveness of bird attraction and health. The impact of urbanization on ecosystems is global (Marzluff et al., 2001) and hazards, such as noise and light pollution caused by human activities (Leveau, 2018), pose similar risks to predation (Curtin, 2002). Urban noise can be harmful to birds (Rheindt, 2003; Kurucz et al., 2021), especially for those nesting near busy roads (Xie et al., 2021). Even though nest boxes are placed in gardens and greenbelts far away from urban noise, the birds using them will inevitably be negatively impacted by urban buildings and roads (Chen et al., 2002). Noise pollution has a more obvious negative impact on birds with low frequency songs (Rheindt, 2003; Halfwerk et al., 2011a). Furthermore, nest sites that are closer to a noise source are more seriously affected. Birds exposed to noise are more likely to display hormone imbalance (Mulholland et al., 2018), cognitive impairment, and over vigilance (Quinn et al., 2006), all of which will affect their foraging status (Ware et al., 2015). Songbirds (Patricelli and Blickley, 2006) will also sing more energetically (Lohr et al., 2003) or change their pronunciation modes near urbanized areas (Pijanowski et al., 2011). Male birds are more exposed to predation in open sites which are more likely to broadcast their songs in noisy environment (Møller et al., 2006; Halfwerk et al., 2012). Noise interference can also affect interspecific communication (Swaddle and Page, 2007), delay the singing response of females to males (Halfwerk et al., 2011a), affect the quality of female mate selection, clutch size, and the physiological health of birds (Blickley et al., 2012). Additionally, communication between parents and nestlings can be affected badly (Schroe et al., 2012; Lucass et al., 2016), reducing breeding success (Halfwerk et al., 2011b; Schroe et al., 2012). Noise may also influence birds' attention, affecting their cognitive ability (Chan et al., 2010) and making them over-alert and thus affecting their foraging behavior (Quinn et al., 2006). It is therefore recommended that environmental background noise at the target location is fully considered before placing nest boxes (Xie et al., 2021).

Long-term artificial light can affect avian breeding (Malek and Haim, 2019); the longer the exposure, the more serious this becomes. Insects may be attracted by artificial light at night, providing food for insectivorous birds (Wang et al., 2021), but the light exposure can affect the sleep status of birds (Raap et al., 2015, 2016c) and change their photoperiodic behavior (Farner, 1964). Abnormal hormonal secretions, including melatonin (Dominoni et al., 2013) can lead to disordered rhythms (Jones et al., 2015), a reduction in immunity, and an increase in disease incidence (Ouyang et al., 2017). Therefore, nest boxes should avoid strong light source sensor lights that may encourage long-term vigilance (Yorzinski et al., 2015).

The effect of light is not obvious during early brooding (Raap et al., 2016a), but becomes obvious in the mid-brooding or in secondary reproduction (Wang et al., 2021). Some parent birds, such as the Great Tit and the Blue Tit (*Cyanistes caeruleus*), will try to observe the nestlings and eggs with the help of light and will reduce the thickness of the nest with the increased of light intensity (Holveck et al., 2010; Gomez et al., 2014). However, it's not clear what is potential negative effect on nestlings if the nest became thiner.

6. Parasite infestation

Birds choose to breed in nests where parasites are almost absent (Breistøl et al., 2015), and the multiplication of nest parasites can be affected by box design and management. The depth of the nest box can interfere with parasite detection as, the deeper the box, the lower the range of sunlight (Podkowa et al., 2019). A sudden decrease in light makes birds vulnerable to fleas when entering a dark environment from a bright one (Du Feu, 1992). However, nestlings in shallow nests are exposed to intense sunlight for too long, which increases the intensity of feeding from parent birds (Wang et al., 2021), thus reducing their rest time (Ouyang et al., 2017) and increasing the brooding burden (Verhulst, 1998).

The suspension height of nest boxes will affect the nest selection preference of birds, because light not only creates the right temperature but also affects parasite load. The illumination range is related to controllable nest height (Holveck et al., 2019); birds tend to nest in places with more illumination, which usually means a higher nest box. Such warm environments are suitable for nestling growth, and the ultraviolet rays kill ectoparasites (Beard, 1972). This may also explain why parent birds build shallow nests during the late breeding period (Gwinner and Scheuerlein, 1998).

The method of nest box maintenance will affect their reuse by birds. Whether old nest boxes can be continuously used is related to the extent of external damage and the internal conditions. Old nest materials and the ectoparasite load can affect the reuse rate of nest boxes, resulting in a low breeding success rate in old nest boxes (Mazgajski, 2007b). Feces, nest materials, and even dead nestling carcasses left in the nest will breed bacteria, affect bird health (Zabotni et al., 2020), and change the microclimate (Schwartz et al., 2020); however, easy-to-clean nest boxes under good management can avoid this problem. In addition to providing a warm environment for birds, old nest materials provide conditions for parasites to breed, develop, and survive during the winter (Rendell and Verbeek, 1996; Puchala, 2004). Previous studies show that using old nest materials to build new nests may increase the infection rate of parasites and pathogens (Soltész et al., 2018). The recurrence of parasites increases the energy consumption and begging behavior of nestlings (Becker et al., 2020), and forces parent birds to increase their investment in rearing (Raap et al., 2016a, 2016b). This may lead to a significant reduction in breeding success in old nest boxes and an increase in the mortality rate of nestlings (Malek and Haim, 2019). After heavy parasite infestations, nestlings may fledge early or die. Although birds may avoid nest boxes with too many parasites (Breistøl et al., 2015), they may be forced to use such boxes where resources are limited. Birds may also remove parasites (Cade, 1973; Moyer and Wagenbach, 1995; Bush and Clayton, 2018), remove old nest materials (Pacejka et al., 1996), and desert nest boxes (Christe et al., 1996); they may use water baths, sand baths, and practice feather tanning; such behavioral responses can increase the reproductive investment of parent birds.

Fortunately, nesting boxes are easy to clean. As some birds may prefer the contents of used nests and need to rely on them to judge the suitability of the nest site, it is suggested that nest boxes be cleaned once or twice a year (Soltész et al., 2018; Jaworski et al., 2022). Microwaves and other methods for cleaning nest materials that do not produce odor may be more suitable than directly removing the entire nest contents.

Evaluating the management of reusable nest boxes is necessary during research studies. The service life should be extended for as long as possible, and regular inspection (better in the nonbreeding season) is needed to confirm nest box integrity (McNabb and Greenwood, 2011) and sanitation. Clean nest boxes, particularly deep ones, can attract birds, reduce parasite infection, and prevent nest hunting.

If the same type of nest box is placed in the same area for a long time, birds may also be affected if the nest box is replaced with a different type (Sonerud, 1989; Sorace et al., 2004). In addition, when researchers open a nest box for inspection, it may change its chemical environment, such as the concentration of CO_2, which affects the attractiveness for insects (Tomás et al., 2008). Cleaning and disinfection of nest boxes will also change the original microenvironment and should be done carefully (Mazgajski, 2007b).

7. Microenvironments and nest boxes

In addition to the above biological factors, abiotic factors and the microenvironment can negatively affect avian reproduction in nest boxes. Together these constitute a complex ecological environment in the nest box.

The construction materials of nest boxes affect their performance. In the 1990s, Song (1994) summarized the main types, advantages, and disadvantages of nest boxes. For example, wooden nest boxes are prone to warping, cracking, deformation (Song, 1994; Shi and Liu, 2018), decay, and damage (Wei, 2014) after long-term use. However, they are more natural than other nest boxes and therefore more likely to attract birds (Wan et al., 2017). They also have the advantages of camouflage, convenient fixation, and easy cleaning (Song, 1994). Nest box construction is constantly changing, based on bird ecology in different areas (Tryjanowski et al., 2006). Standard nest boxes are made of bamboo (Shi and Liu, 2018), glass (Lei et al., 2014), linoleum paper (Song, 1994), metal (Lesiński, 2000), pottery (Zhu et al., 2016), wood plywood (Zhang et al., 2017), cement, and sawdust (Wan et al., 2017). But not all birds are able to live in synthetic nest boxes. Too much heat will accumulate in the enclosed environment of metal nest boxes (Wei, 2014), especially during hot summers or uncovered locations (Ellis, 2016) and nestlings or parent birds may suffocate owing to high temperatures and poor ventilation. The high reflectivity of glass nest box weakens the ultraviolet rays and affects birds' perception and/or discrimination to the environment. In such cases, birds spend more energy regulating their body temperature, which affects their daily behavior (Lei et al., 2014; Wei, 2014).

Currently, wooden nest boxes are the most widely used; however, the problems associated with them are listed below.

(1) Thermal insulation of nest box (Goldingay and Stevens, 2009). Nest boxes are most commonly placed to attract Passeriformes species; their optimal temperature for embryo hatching is between 36 °C and 40 °C (DuRant et al., 2013). If the temperature exceeds this range for a long time, embryos will develop abnormally or die (Webb, 1987; Dawson et al., 2005; Pérez et al., 2008; Ardia et al., 2010; DuRant et al., 2013). Parent birds have to spend more time incubating under low temperatures, this reduces foraging time, and nestlings require more energy (Krijgsveld et al., 2003). Dawson et al. (2005) accelerated the growth of the Tree Swallow (*Tachycineta bicolor*) by optimally heating a nest box; meanwhile Murphy (1985) showed that although warm boxes attract birds to build nests, excessive temperature or long-term exposure to direct sunlight causes heat stress to nestlings. Microclimates in natural cavity nests are not completely simulated by wooden nest boxes (Schwartz et al., 2020; Lan et al., 2021), with poor heat insulation performance and a weak ability to buffer extreme climates (Isaac et al., 2008). This could negatively affect species that are sensitive to climate fluctuations (Robertson, 1995; Zhang et al., 2014). In cases of extremely high temperatures, the average temperature in the nest box is notably higher than outside (Grüebler et al., 2014). Excessive direct sunlight leads to high temperatures in thin wooden plywood nest boxes and to the dehydration of nestlings, which seriously impacts hatching and brooding (Salaberria et al., 2014). Additionally, the improved anti-predation nest box made of cement and sawdust is fully airtight (McCleery et al., 1996). Thus, under extremely high temperatures, the breeding success of birds in a nest box may be decreased (García-Navas et al., 2008).

(2) Humidity in the nest box (Wiebe, 2001; Harper et al., 2005). Suitable humidity is crucial to the development of embryos and nestlings and parasite load (Hebda et al., 2017). Nest boxes with a dry microclimate and poor buffering will have a negative impact on nestling health (Schwartz et al., 2020). Compared with the thin wall of nest boxes, natural cavity nests have better climate regulation (McComb and Noble, 1981), and even on sunny days, the interior can still be damp (McComb and Noble, 1981; Wesolowski et al., 2002; Radford and Du Plessis, 2003; Rhodes et al., 2009), which will supplement the water consumed by the embryo owing to the rising temperature (Rahn et al., 1977). It is challenging to maintain high humidity in nest boxes (Wesolowski et al., 2002), and parent birds are forced by this difference in microclimate to increase reproductive input (Schwartz et al., 2020). In addition, better wintering and breeding environments for fleas and other parasites are provided by the warm and dry environmental conditions of nest boxes and accumulated nest materials (Rendell and Verbeek, 1996). Survival of some ectoparasites, such as fleas, and entomopathogens, may be inhibited by high humidity in natural cavity nests (Wesołowski, 2011), reducing the harm of parasites to nestlings (Heeb et al., 2000; Hebda and Wesołowski, 2012).

(3) Decomposition of nest materials (Heeb et al., 2000). Proper humidity in natural cavity nests can promote the decay and decomposition of nest materials (Hebda et al., 2017; Maziarz et al., 2017). Researchers have attempted to create cavity nests by hollowing out a section of a natural tree trunk and fixing it on to a tree, or directly creating a tree hole to attract birds; these have achieved better attraction results (Griffiths et al., 2020) and are favored by some researchers. The woodcraft box has been used for

some time worldwide; it successfully attracts breeding birds and can reduce the risk of predation. The material of the nest box is different from that of the standard wooden nest box, which heats up faster and can store more heat. The entry of large finches may be restricted by the entrance design, which also offers more protection (Browne, 2006; García-Navas et al., 2008). However, there is no literature on the use of woodcraft boxes in China, so further studies are needed in this regard.

The color of the nest box affects its internal temperature (Goldingay, 2015). Differences in the reflectivity of colors lead to different heat energy absorption effects of nest boxes (Griffiths et al., 2017); these affect breeding by changing the microclimate in the nest (Kerth et al., 2001; Lourenço and Palmeirim, 2004; Lambrechts et al., 2010; Griffiths et al., 2017). Dark colors have lower reflectivity and good heat absorption, resulting in higher internal temperatures than lighter colors and more significant differences in diurnal temperatures (Nussear et al., 2000; Lourenço and Palmeirim, 2004). Painting is a relatively simple and economical way to control nest box temperature (Brittingham and Williams, 2000). The reflectivity of brown is similar to that of green in various shades of sunlight, and it is easy to camouflage nest boxes with these colors. The internal temperature of nest boxes of these colors is higher than that of white nest boxes (Goldingay, 2015; Griffiths et al., 2017); dark green and black boxes show similar results. In such boxes, fragile individuals are more likely to reduce energy consumption and maintain body temperature to survive the cold winter (Griffiths et al., 2017). This also means that in non-extreme cases, an overheated environment in dark green nest boxes creates more physiological pressure than in light green nest boxes (Griffiths et al., 2017).

Internal temperature and other micro habitats may be affected by nest box thickness (Goldingay, 2015; Strain et al., 2021), and this should be a consideration in different geographical locations. Nest boxes with thick nest walls have better heat preservation capacity for buffering against unsuitable temperatures (Strain et al., 2021). Therefore, it is better to use such boxes in cold areas (Lambrechts et al., 2010) where they can mitigate the impact of temperature change (Strain et al., 2021). Compared with thin-walled plywood nest boxes, thick-walled pine nest boxes show superior thermal insulation performance (Isaac et al., 2008). A natural cavity nest with a slightly thick nest wall may be a perfect buffer zone when the ambient temperature is extreme (Strain et al., 2021). However, nest boxes cannot perfectly simulate the buffering capacity of natural cavity nests (Goldingay, 2015).

Additionally, the microclimate and ventilation in the nest are affected by the airtightness and shape of the nest box. Highly airtight nest boxes can reduce the negative impact of rain on nestlings (Wesołowski, 2011); however, nest boxes without waterproof treatment leak (García-Navas et al., 2008; Lambrechts et al., 2010), resulting in a loss of heat or even nestling death owing to wet feathers (Anctil et al., 2014). Therefore, it is important to apply waterproof treatments and appropriately extend the box cover and eaves (Zhu et al., 1998; Chen et al., 2019).

Microclimate varies depending on the type of nest box. Compared with natural nests with uniform heat and light and a constant internal temperature (McComb and Noble, 1981), nest boxes, which are commonly rectangular or cylindrical, can be unevenly heated (Maziarz et al., 2017). Different box shapes have different contact areas with trees. Cuboid boxes are made by splicing multiple surfaces, leading to uneven solar radiation. Standard cylindrical nest boxes are mostly made of wood concrete or a section of thick natural tree trunks that resemble a natural cavity to obtain uniform heating and provide a stable thermal environment with higher thermal insulation (García-Navas et al., 2008; Chen et al., 2019). The water vapor naturally flowing out of eggs during incubation depends on the airflow and volatilization into the atmosphere (Rahn et al., 1977). Oxygen levels in nest boxes also require a maintenance of airflow (Yom-Tov and Ar, 1993; Wiebe, 2007), and must be well-ventilated. However, few nest boxes have been designed with this problem in mind (Chen et al., 2019), and further exploration is needed.

Attention should be paid to the design of unique structures inside nest boxes. For example, the nest wall can be designed as a double layer to improve insulation (Ellis and Rhind, 2021). In contrast, nests made of hexagonal-density fiberboard boxes with two nest entrances have poorer thermal insulation than ordinary wooden nests with one entrance (Moore et al., 2010). At the same time, we need to pay close attention to whether these structures have a negative impact on birds (Lambrechts et al., 2010).

Different bird species in different regions have varying preferences for nest box orientation, as orientation can affect microclimate (Schwartz et al., 2020). A nest box suspended towards the sun can absorb higher levels of radiation (Zhou et al., 2009). Setting the entrance of the nest box towards the sun in cold areas can reduce incubation costs and facilitate early reproduction (Kaluthota and Rendall, 2017). Accordingly, in warm regions, dehydration caused by extremely high temperatures in nest boxes can increase nestling mortality (Catry et al., 2011). Temperature differences between sun-exposed nest boxes and non-sun-exposed nest boxes are pronounced in the morning and tend to be the same in the afternoon (Ardia et al., 2006). Nest boxes in different areas should be placed with consideration to local geographical location. Nest boxes in the northern hemisphere would favor a northwest-northeast orientation. Those nest boxes placed in the middle latitudes should face east. In the southern hemisphere, boxes should face southwest-southeast to reduce maximum temperature and temperature fluctuation (Burton, 2007; Schwartz et al., 2020), while those in the cold regions should face towards the sun.

The placement and orientation should be set according to the experimental site conditions to meet the nesting preferences of birds. At the same time, extreme temperatures, rain, and wind should be avoided as these variables can negatively affect nesting boxes and lead to breeding failure.

8. Conclusion and prospects

The impact of artificial nest boxes on birds has received relatively little attention, and more in-depth research is still needed. From the perspective of bird species, the current literature mainly focuses on small Passeriformes birds, especially the tits and flycatchers. Based on this summary of negative effects of nest boxes, we suggest that more focus should be placed on disadvantages of nest boxes from following aspects.

First, it is necessary to evaluate the construction of artificial cavities in trees to attract birds. Nest boxes are short-lived when hung and need to be repaired and maintained. Natural cavities not only have a less negative impact on birds but are also more conducive to long-term research and bird protection at a low cost.

Second, research on nest boxes in urban environments should increase appropriately. Most nest box research is conducted in the field; their use in cities has received little attention. However, with the progress of urbanization, more birds choose to settle and breed in cities. Because of a lack of nesting sites, owing to the limited coverage of artificial vegetation and the young age of trees in cities, it is important to conduct and present relevant research to – among others – city planners to help better protect urban birds.

Finally, it remains to be explored whether various odors in nest boxes impact birds. Research on the olfactory sense of birds is mainly focused on foraging, avoiding natural enemies, and nesting. Few scholars have addressed the influence of odors in nest boxes on bird breeding. Odors can be caused by using chemicals when handling nest boxes, or the human odor left when conducting research. Whether these odors will affect bird choice of a nest box or lead to nest predation needs to be evaluated in the future.

In summary, artificial nest boxes can attract beneficial birds, promote biological control, and significantly contribute to bird breeding ecology, diversity protection, population genetics, and population dynamics. With the development of citizen science, we can also promote scientific research related to the protection of birds with nest boxes. Negative impact of nest boxes on birds should be summarized and eliminated timely, which will be conducive to protecting birds and biodiversity, and maintaining the balance of the ecosystem.

Authors' contributions

ZL collected and analyzed the data and wrote the first draft; MX analyzed the data and revised the drafts; CZ, WC, LZ and LX revised the manuscript; XX conceived, wrote, and revised the manuscript. All authors read and approved the final manuscript.

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Ethics statement

Not applicable.

Declaration of competing interest

The authors declare that they have no competing interest.

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