Predator Proofing Avian Nest Boxes: Opportunities and Challenges, Costs and Benefits.

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Declaration

I declare that the work in this thesis was carried out in accordance with the regulations of the University of Gloucestershire and is original except where indicated by specific reference in the text. No part of the thesis has been submitted as part of any other academic award. The thesis has not been presented to any other education institution in the United Kingdom or overseas. Any views expressed in the thesis are those of the author and in no way represent those of the University.

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Abstract

The installation of nest boxes is a popular management strategy to increase nest site availability for secondary cavity-nesting birds. Standard-diameter wooden nest boxes are prone to predation, and various predator-prevention methods have therefore been developed with the intention of minimising nest box predation. However, nest box characteristics greatly affect the breeding behaviour of birds, and can therefore not only affect breeding success but are also a source of bias within the scientific literature. An initial literature review of nest box predator-prevention methods highlighted that relative to their widespread use, there is a considerable lack of research directly testing both their effectiveness and effects on breeding behaviour. A research project then showed how various life-history (e.g. brood size and nestling age) and environmental (e.g. habitat characteristics and meteorological conditions) variables affect the parental care patterns of four secondary cavity-nesting passerines (i.e., the European Pied Flycatcher (*Ficedula hypoleuca*), Eurasian Nuthatch (*Sitta europaea*), Great Tit (*Parus major*) and Blue Tit (*Cyanistes caeruleus*)) breeding in nest boxes at Nagshead Nature Reserve, a broadleaf woodland site in Gloucestershire, UK. A significant aspect of the project examined parent care behaviours in different types of nest boxes (i.e., standard, woodcrete, deep and guardian tube), aiming to test whether nest box type influences chick provisioning, a hypothesis initially proposed by Blunsden (2020). Results showed the prevalence of leaning behaviours (whereby parent birds feed nestlings by leaning into the nest chamber from the entrance hole, without having to enter fully) appeared to be an individual-specific behaviour and significantly reduced chick provisioning durations (i.e. the time taken for a bird to feed nestlings), thus having adaptive value. Although nest box type did not affect the prevalence of such behaviours, chick provisioning durations were significantly longer in woodcrete and deep nest boxes, showing these nest box types had adverse effects on a bird's ability to effectively enter and exit the nest box to feed nestlings. Overall, although predator-prevention methods are often assumed to have a net benefit to birds, preliminary research highlights potentially unintended negative consequences that are understudied. The severity of these adverse effects is uncertain and whether the provisioning of predator-proof nest boxes provides a net benefit remains unclear.

Contents

Chapter 1

Research Topic and Thesis Structure

Female Pied Flycatcher (*Ficedula hypoleuca*) caught for the BTO Ringing Scheme

(Image taken by Joseph Marcus)

1.1. Decline of Woodland Passerines

Across Europe, the rapid expansion of human populations and the resulting urbanisation has led to the drastic deterioration of many forest landscapes, inevitably reducing the availability and suitability of woodland habitats for arboreal birds (Geri *et al.*, 2010; Referowska-Chodak, 2019). The effect this environmental change has on natural populations greatly varies amongst species depending on their habitat requirements, where more specialised species are considered most vulnerable (Julliard *et al.*, 2004; Martin, 2015). At a European scale, population trends between 1980 to 2003 showed a net decline of 13% in 57 woodland bird species, and a net decline of 18% in 33 woodland specialists: although species such as the Blue Tit and Long-Tailed Tit (*Aegithalos caudatus*) have experienced moderate population increases, others such as the Willow Tit (*Poecile montanus*) and Common Nightingale (*Luscinia megarhynchos*) have undergone significant declines (Gregory *et al.*, 2007).

In the United Kingdom (UK), organisations such as the British Trust for Ornithology (BTO) and the Royal Society for the Protection of Birds (RSPB) run various monitoring programmes like the Breeding Bird Survey (BBS), which are often used to produce population trends for UK birds. Generally similar declines in woodland specialists have been found, where for example, the Repeat Woodland Bird Survey (RWBS) showed population declines greater than 25% in eight woodland specialists, such as the Spotted Flycatcher (*Muscicapa striata*) and Wood Warbler (*Phylloscopus sibilatrix*) (Hewson *et al.*, 2007). In 2021, the Department for Environment, Food and Rural Affairs (DEFRA) published the Wild Bird Populations in the UK indicator, which showed between 1970 and 2019, 37 woodland species experienced a net decline, with woodland specialists showing a significant 45% decline, and generalists showing a non-significant increase of 4% (Figure 1). Specifically, five woodland specialists declined by over 80% (Lesser Spotted Woodpecker (*Dendrocopos minor*), Lesser Redpoll (*Acanthis cabaret*), Spotted Flycatcher, Capercaillie (*Tetrao urogallus*) and Willow Tit), whereas numbers of Eurasian Nuthatch and Great Spotted Woodpecker (*Dendrocopos major*) have more than trebled (DEFRA, 2021). A review published by Fuller et al. (2005) highlighted seven possible causes of these UK population declines, including: (1) pressures on migrants during migration and/or winter; (2) the effects of climate change on breeding grounds; (3) reductions in invertebrate food supply; (4)

impacts of land use on woodland edges; (5) reduced management of woodland habitats; (6) increased grazing pressure from deer (Cervidae); and (7) intensified predation pressure from Grey Squirrels (*Sciurus carolinensis*), Great Spotted Woodpeckers and corvids.

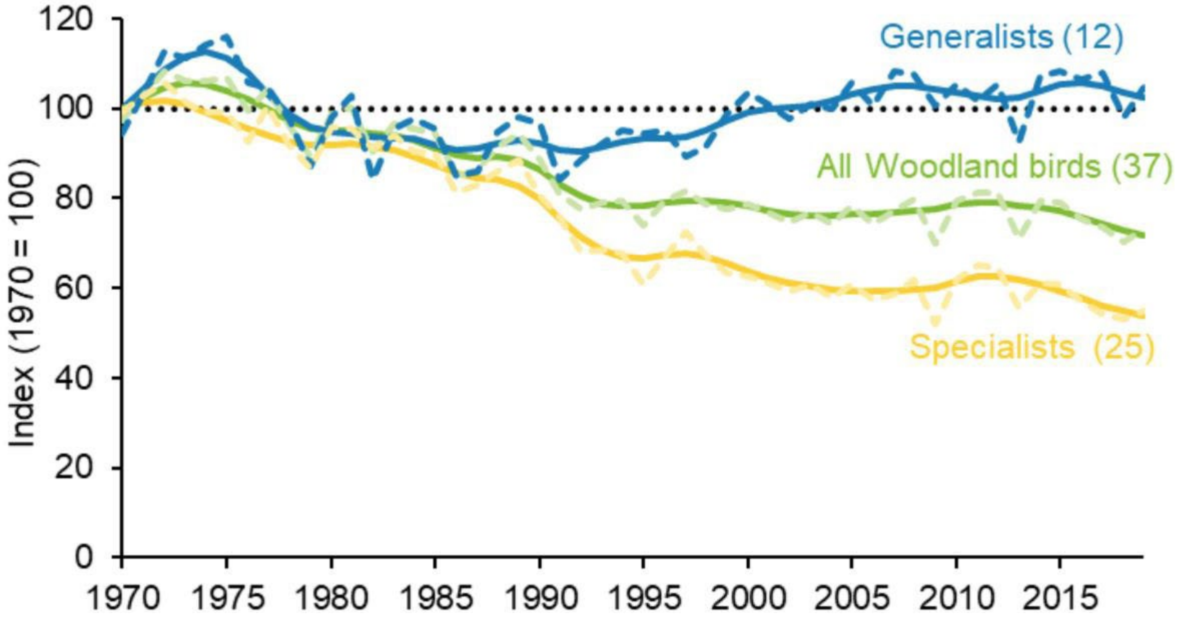


Figure 1. Population trends for breeding woodland birds in the United Kingdom, between 1970 and 2019. Illustration taken from DEFRA (2021).

1.2. Secondary Cavity-Nesting Birds and the Importance of Nest Box Schemes

Half of the avian orders use some form of cavity for roosting or nesting (Gill, 2007). In particular, cavity-nesting birds are an ecologically important component in woodland bird communities, usually accounting for around 25 to 30 % of the avifauna in a forest habitat (Scott *et al.*, 1980; Newton, 1994; Bai and Muhlenberg, 2008). Generally, cavity-nesters can be classified into two broad groups according to their method of hole acquisition. Primary cavity-nesters, which include most species of Woodpecker (Picidae), will excavate their own nest holes. Secondary cavity-nesters however, are incapable of excavation, and therefore breed in pre-existing cavities which have either developed through broken branches and decaying wood, or been previously formed by other primary cavity-nesting species. These non-excavating species therefore depend on the availability of suitable pre-existing nesting sites, and there is a plethora of circumstantial and empirical evidence supporting the theory that a shortage of tree cavities limits their breeding density (Newton, 1994; Cockle *et al.*, 2010). As a result, when selecting a breeding habitat many species such as Pied Flycatcher, Great Tit and Eurasian Nuthatch often show a preference for mature deciduous woodlands (Van Balen, 1973; Alatalo *et al.*, 1985; Lemel, 1989; Burkhardt *et al.*, 1998). Alongside other factors such as improved food availability, this preference is explained by the comparatively larger abundance of nest cavities naturally developing in this habitat type (Van Balen, 1973; Riddington and Gosler, 1995; Newton, 1998). However, across Europe inappropriate forest management has led to pinetization (i.e. the planting of pine forest on fertile soil) and Juvenalization (i.e. reduction of the mean tree age in forest stands), meaning old and decaying cavity-bearing trees are often felled as a standard practice (Referowska-Chodak, 2019). There is therefore an abundance of woodland with an insufficient amount of tree cavities, forcing cavity-nesting species to select and over-exploit these sub-optimal habitats, resulting in ecological traps (Mänd *et al.*, 2005). Habitat fragmentation and the resulting edge effects are also known to reduce the breeding success of non-excavating species by increasing competition for nest sites (Deng and Gao, 2005). In such situations, the erection of man-made nest boxes in a specific area (i.e. nest box schemes) is an extremely useful management strategy which can facilitate population growth by artificially increasing the availability of nesting locations (Mänd *et al.*, 2009; Robles *et al.*, 2012). Such nest box schemes are therefore an invaluable conservation tool for secondary cavity-nesting birds, especially declining migratory species such as the Pied Flycatcher and Common Redstart (*Phoenicurus phoenicurus*), both of which have an amber status on the BTO's Birds of Conservation Concern five (Lambrechts *et al.*, 2010; Stanbury *et al.*, 2021).

The use of nest box schemes in scientific research has also considerably improved our understanding of the breeding biology of cavity-nesting birds, allowing ornithologists to formulate experimental designs that would otherwise be impractical or impossible (Lambrechts *et al.*, 2010). Nest boxes allow researchers to monitor active nests, experimentally manipulate breeding parameters (e.g. clutch size), control environmental factors (e.g. cavity size), and repeatedly capture and identify parents and nestlings (e.g. Winkler and Allen, 1995; García-Navas and Sanz, 2010; Fokkema *et al.*, 2018). The use of nest box schemes can also greatly increase sample sizes, not only because the locations of nesting sites are known prior to the breeding season, but because the local population size of cavity-nesting birds is often larger in nest box areas. As a result, secondary cavity-nesting passerines are one of the most studied groups of free-living birds in the world (Lambrechts *et al.*, 2010).

1.3. Nest Box Predation

Despite the conservation value of nest box schemes by artificially augmenting available nest cavities, predation can be higher in nest boxes relative to natural cavities (Miller, 2002). One potential reason for this is that predators learn to exploit nest boxes as a reliable food source: not only may nest boxes simply be more conspicuous and easier for predators to spot (Evans *et al.*, 2002; Skwarska *et al.*, 2009), but predators can also use long-term spatial memory to learn the locations of previously depredated boxes (Sonerud, 1985; Sonerud and Fjeld, 1987; Nilsson *et al.*, 1991; Miller, 2002; Pelech *et al.*, 2010). Furthermore, nest boxes are often laid out on grids for ease of revisiting by researchers, who may not have as good spatial memories as these predators. This means predators can perhaps use spatial prediction to find other nest boxes when searching for further feeding opportunities. Nest box schemes can also make the breeding density of birds abnormally high, which can therefore result in more predation (Dunn, 1977).

Conventional, standard nest boxes are typically a wooden rectangular structure with an entrance hole providing access to the internal chamber (Figure 2a). Such boxes will be used by most secondary cavity-nesting passerines, including Blue Tits, Great Tits, Eurasian Nuthatches, Pied Flycatchers, Common Redstarts and House Sparrows (*Passer domesticus*), although forms can vary to mimic the natural cavities used by a species, such as the wedge-shaped Eurasian Treecreeper (*Certhia familiaris*) box shown in Figure 2b. These standard wooden boxes are prone to predation from a variety of species such as Great Spotted Woodpeckers (*Dendrocopos major*), which will excavate and drill holes in the wooden panels (Mainwaring and Hartley, 2008; Skwarska *et al.*, 2009), and Pine Martens (*Martes martes*), which will reach through the entrance hole and grab nestlings/eggs (Kalinski *et al.*, 2014).

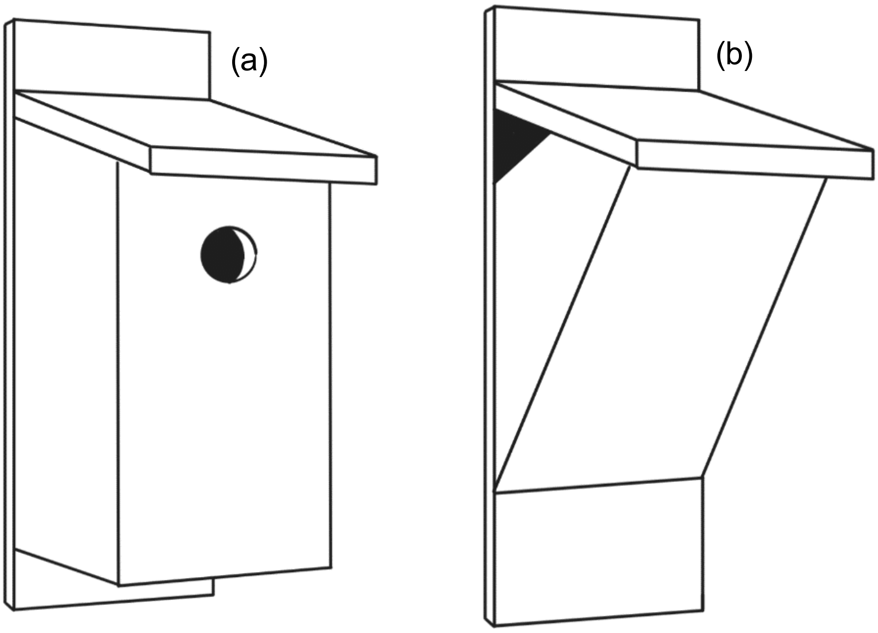


Figure 2. Different nest box designs. (a) Standard wooden rectangular nest box with a circular entrance hole, suitable for most cavity-nesting passerines. (b) A wedge-shaped wooden nest boxes suitable for Eurasian Treecreepers. Illustrations made by Joseph Marcus

Various predator guards and predator-proof nest box designs have therefore been developed with the intention of preventing predators from depredating nest boxes (Bailey and Bonter, 2017). However, the design and characteristics of a nest box can directly and indirectly affect the breeding behaviour of birds by influencing biotic and abiotic factors within the nest chamber, and can therefore not only affect breeding success but is a source of bias within scientific literature (Lambrechts *et al.*, 2010; Møller *et al.*, 2014). It is often assumed predation-prevention strategies provide net benefit to birds, but, some adverse effects of predator-proof nest boxes have been identified (e.g. Bueno-Enciso *et al.*, 2016; Blunsden and Goodenough, 2023). It is also worth noting the ethical implications of erecting ill-conceived nest boxes which may have potentially negative effects on predation pressure and breeding behaviour. The installation of nest boxes is therefore not only a conservation tool but also a responsibility, and it is paramount that their use is based on sound scientific reasoning.

In order for the installation of these modified nest box types to produce the desired outcome (minimise nest predation and thus increase breeding success), especially when used as a conservation tool for threatened species, it is important to understand all aspects of avian behaviour and physiology in relation to these different nest box designs. Chapter 2 of this thesis therefore aims to provide a review of predator-prevention methods employed to protect nest boxes from predation: detailing the current understanding of their efficacy, identifying any unintended negative consequences of their use, and highlighting gaps in the literature where further research is required. Chapter 3 then aims to contribute towards further understanding the effects of different predator-proof nest box designs, examining chick food provisioning across four types of nest box at RSPB Nagshead Nature Reserve, Gloucestershire, UK.

Chapter 2

Predator-Proofing Avian Nest Boxes: A Review of Intervention Types and Relative Success in Reducing Predation

Blue Tit fledging from a predator-proof ‘woodcrete’ nest box

(Image taken by Joseph Marcus)

2.1. Introduction

The simplicity of nest boxes has resulted in their wide use by both conservationists and landowners: in the UK alone, there are at least 4.7 million privately-owned nest boxes (Davies *et al.*, 2009). As detailed in sections 1.2 and 1.3, predation is still a primary source of nest failure in standard wooden nest boxes, and numerous predator guards and predator-proof designs are currently used to minimise predation. However, differences in nest box design can affect the breeding biology and nesting success of the birds that inhabit them, which also creates a source of bias in the scientific literature (Lambrechts *et al.*, 2010; Møller *et al.*, 2014). This review therefore collates the current scientific literature on the topic, aiming to assess the predation pressure in relation to each predator-prevention method, as well as identify any effects they may have on the behaviour and physiology of breeding birds. It is worth noting that throughout the review, breeding attempts are not always considered within a life-history context (e.g. how breeding performance differs in relation to factors such as avian age and experience). This is in part to maintain focus on the direct effects of each predator-prevention method, and partly due to limitations in the current literature, which is dominated by short-term studies. Table 2, located at the end of the review, provides a summary of the advantages and disadvantages of each predator-prevention method discussed throughout the chapter.

2.2. Deep Nest Boxes

When using natural cavities, many species like the Great Tit and Marsh Tit (*Parus palustris*) have been shown to select deeper over shallow cavities with a sizable distance between the nest cup and entrance hole, termed the ‘danger distance’. Perceived predation risk is an important selective pressure on the choice of a nest site, and this is therefore likely to be an anti-predator adaptation which prevents larger predators such as Pine Martens from accessing a cavity and reaching eggs/nestlings (Figure 3) (Wesołowski, 2002; Maziarz *et al.*, 2016). This natural preference for deeper nest cavities has been shown to be applicable to artificial nest sites too, where field studies show a variety of species, including the Planalto Woodcreeper (*Dendrocolaptes platyrostris*), Common Starling (*Sturnus vulgaris*) and various species of Paridae, will actively select taller nest boxes (Van Balen, 1984; Löhrl, 1986; Summers and Taylor, 1996; Mazgajski, 2003; Cockle and Bodrati, 2009). Although exceptions to this have been observed, there is the possibility that this preference is species-dependent. For example, House Wrens (*Troglodytes aedon*) typically build heavier nests due to a stick foundation and observed preferences for small nest boxes may therefore be an adaptation to counteract the species' increased costs of nest building (Vergara, 2007). A study examining relationships between nest height, cavity depth, and species-dependent nest characteristics could provide more insight into this hypothesis. Blue Tits have also been shown to have a higher occupation of shallower nest boxes, but this likely resulted from interspecific competition as coexisting Great Tits may have outcompeted them for deeper nest boxes (Kalinski *et al.*, 2014). This might be partly due to their larger nest size requiring more space for both a sufficient danger distance and adequate nest height for insulation (Kalinski *et al.*, 2014).

Figure 3. Pine Marten attempting to depredate a nest box by reaching through the entrance hole, a characteristic hunting behaviour for this species. Camera trap image from Fokkema, Ubels and Tinbergen (2018).

Both deep nest boxes and deep natural cavities have been shown to have reduced predation (Kalinski *et al.*, 2014; Maziarz *et al.*, 2016), although this benefit may be reduced if birds simply add additional nest material to build nests higher than normal, thereby reducing or eliminating the theoretical benefit of the increased danger distance.

Fokkema, Ubels and Tinbergen (2018) quantified how both the actual and perceived predation risk from predators including Pine Martens, as well as the overall breeding success of Blue Tits, is affected by nest box depth. The authors conducted both a free-choice experiment, where nest box depth was established before nest building started, and a forced-choice experiment, where nest box depth was altered after the onset of egg laying by adding wooden blocks underneath the nest. This experimental framework aimed to control intraspecific competition for nest sites, thus accounting for the potential association between nest box depth and parental quality (Sergio *et al.*, 2009; Fokkema, Ubels and Tinbergen, 2018). Generally, the study found a clear positive relationship between nest box depth and breeding success, where deeper boxes had small but positive effects on clutch size and hatching success, and large positive effects on fledging success. The authors suggested that the latter relationship was driven by reduced predation in deeper nest boxes, despite the statistical analysis showing no significant effect of nest box depth on predation. This is because fledging success only increased with nest box depth in study sites with higher predation. Predation was also the cause of most cases of breeding attempt failure, especially of the entire brood. Furthermore, when the authors excluded instances of complete brood failure from analysis, the relationship between nest box depth and fledging success was no longer significant, suggesting that total nest predation was the main driver behind the positive relationship seen in the full model. Fokkema, Ubels and Tinbergen (2018) suggested flaws in their predator detection methods likely resulted in their dataset under-estimating the extent of actual predation. It was likely Pine Martens were able to depredate some, but not all, nestlings without leaving any signs of their presence, a situation that would not have been recorded as a predation event during routine nest box checks. It was also suggested that the motion sensors on the camera traps were not sufficiently sensitive to be triggered by small predators such as weasels (*Mustela nivalis*). These issues are common amongst these methods of quantifying predation (Major, 1991; Rowcliffe *et al.*, 2011). This could have caused a source of bias, being a potential explanation as to why no effect of nest box depth on predation was found.

Predation can also indirectly affect the life-history traits of prey by eliciting behavioural changes in reproductive strategy as a result of the prey’s perceived risk of predation. This behavioural plasticity has been demonstrated in ornithological research, where parent birds will reduce their reproductive investment in eggs/nestlings as perception of predation risk increases (Fontaine and Martin, 2006a; Hua *et al.*, 2014). Similar changes in breeding parameters were observed by Fokkema, Ubels and Tinbergen (2018), who therefore suggested this was the main driver behind the observed positive effects of nest box depth on clutch size and hatching success, especially as this relationship occurred irrespective of local predation pressure. It was likely parent birds inhabiting shallower nest boxes reduced investment in their clutch in response to a perceived lower predation risk in this box type. A potential evolutionary rationale for this behaviour is the breeding success of a second clutch depends on the amount of parental care already provided to the initial brood. Time is limited in a breeding season, so in areas where nest failure is high, individuals can save time by laying a smaller clutch, increasing the chances of survival for a second brood by re-nesting sooner (Slagsvold, 1984; Farnsworth and Simons, 2001). Therefore, to compensate for a potentially higher predation risk in shallower boxes, birds may alter their reproductive strategy; distributing their parental investment across multiple nesting attempts which could effectively ‘safeguard’ their annual fecundity. Such behaviours would align the bet-hedging hypothesis (Olofsson *et al.*, 2009).

Generally, birds can assess predation risk from a variety of cues (Lima, 2009) including referential communication (Suzuki, 2015), direct experiences (Chalfoun and Martin, 2010b) and olfactory scents left by predators (Amo *et al.*, 2008). It is therefore likely that the internal dimensions of a nest cavity imply aspects of its quality, where birds might respond to cavity depth due to awareness of the heightened predation risk associated with a lower danger distance. Empirical evidence tangentially supports this hypothesis, showing birds will reduce the height of their nests in shallower cavities, likely in an attempt to increase the danger distance and thus minimise predation (Mazgajski and Rykowska, 2008; Kalinski *et al.*, 2014). This behaviour is only seen during nest building, and cavity-nesting bird species will not alter the height of their nest after it is initially completed (Fokkema *et al.*, 2018). However, building thinner nests may also have consequences: a larger volume of nest material may be required for better thermal insulation and water absorption and thus be important in preventing chick hypothermia and nest-soaking (Wesołowski *et al.*, 2002; Heenan, 2013). Larger nests are also more sanitary, having a larger storage capacity for waste materials such as non-hatched eggs, food remains and deceased chicks (Alabrundzinska *et al.*, 2003). Therefore, birds nesting in shallow cavities likely face a trade-off between the protection of the brood/clutch, and maintaining an appropriate nesting environment

(Mazgajski and Rykowska, 2008; Kalinski *et al.*, 2014). Such trade-offs between predation prevention and microclimate have been studied in the Piping Plover (*Charadrius melodus*) and Hoopoe Lark (*Alaemon alaudipes*), both of which are ground-nesting species (Tieleman *et al.*, 2008; Mayer *et al.*, 2009), but there are seemingly no studies dedicated to testing these trade-offs in secondary cavity-nesting species. In deep nest boxes, nest mass is comparatively less restricted by danger distance, enabling birds to build sufficiently large nests for thermoregulation etc., whilst still maintaining a safe distance from the entrance hole to minimise predation risk. This could therefore be contributing to the higher breeding success seen in deeper nest cavities (Mazgajski and Rykowska, 2008; Fokkema *et al.*, 2018).

2.2.1. Nest illumination and ventilation

Despite studies observing higher breeding success in deep nest boxes, there can be important trade-offs and negative consequences. For example, in the study by Kalinski *et al.* (2014), predation in deep nest boxes was entirely avoided, except when nests were built higher than 6 cm, thus negating the safety benefits of this nest box type. Increased nest height in deeper nest boxes could be an adaptive behaviour to maximise the amount of light reaching a nest, driven by the significant decline in nest illumination with cavity depth (Wesołowski and Maziarz, 2012; Podkowa and Surmacki, 2017). Light exposure can have multiple positive effects on avian physiology, including the photo-acceleration of embryonic development (Cooper *et al.*, 2011; Austin *et al.*, 2014) and facilitating better use of colour vision (Wesołowski and Maziarz, 2012). Birds have therefore been shown to have a preference for cavities with elevated illumination, and will build significantly higher nests in darker nest boxes, a behaviour which likely aims to increase ambient light levels (Podkowa and Surmacki, 2017). This highlights a potential trade-off that may be intensified in deeper nest boxes. Similarly, deep cavities could also have reduced ventilation, so birds may nest closer to the entrance to avoid hypoxia, although this idea remains speculative. A study similar to that of Howe and Kilgore (1987) could compare the ventilation between nest boxes of varying depths/dimensions, where empty nest boxes could be flushed with a low O_2, high CO_2 mixture, and the resulting time taken for O_2 and CO_2 levels to return to free atmospheric levels recorded.

2.2.2. Sexual display hypothesis

A bird’s nest building behaviour and the resulting structure of the finished nest can reflect that bird’s fitness and willingness to invest in reproduction, acting as a sexually selective trait for the non-building individual (Tomas *et al.*, 2006; Mainwaring *et al.*, 2008). Therefore, differences in nest characteristics may be related to variations in the age and proficiency of the breeding birds, and these are therefore important considerations when explaining variations in nest height. A study could be conducted where adult birds breeding in nest boxes of varying depths are also captured and aged, in order to determine whether age and experience are related nest height, alongside cavity depth.

2.2.3. Parasite loads

Ectoparasite load can be significantly higher in nest boxes with more nest material, likely due to factors such as microclimate, increased food availability and more refuge space (Gold and Dahlsten, 1989; Rendell and Verbeek, 1996). An increased ectoparasite load can negatively affect both nestling and adult body condition, significantly reducing reproductive success (e.g. Weddle, 2000; Puchala, 2004; Tomas *et al.*, 2007). Blunsden (2020) studied the effects of nest box type on parasite abundance in the nests of Blue Tits, Great Tits, Pied Flycatchers and Eurasian Nuthatches. Compared to standard nest boxes, deep nest boxes contained significantly more Hen Fleas (*Ceratophyllus gallinae*) and Blowfly Pupae (Protocalliphora), likely due to the increased nest volume in this nest box type (Blunsden, 2020; Blunsden and Goodenough, 2023). Nevertheless, this had no significant effect on the breeding success of the four passerine species, suggesting the consequences of an increased parasite load does not always reduce fitness. Numerous hypotheses could explain this, such as increasing parental feeding frequency to compensate for reductions in nestling condition, potentially driven by changes in their begging behaviour. Low virulence could also be a factor, arising largely due to selective pressure on the parasites to avoid killing their hosts, which would reduce their transmission success. Density-dependant factors could also still be limiting parasite abundance to a level that although higher in deep boxes, is still insufficient in significantly affecting nestling body condition (Thomas and Shutler, 2001).

2.2.4. Nest-building effort

Finally, nest construction alone can be both time and energy intensive, also causing trade-offs between the costs of construction and the benefits of a larger nest volume (Hilton *et al.*, 2004). It requires more energy investment to build a larger nest, which birds may be forced to do in deeper boxes. Otherwise they may sacrifice other benefits such as increased nest illumination. The severity of such trade-offs may also vary between species according to whether one bird or both birds in a social pair contribute towards nest building. The energetic costs of nest building (per individual) may be heightened in species where the male or female alone builds the nest, compared to species where both sexes contribute. There are no current studies investigating these potential relationships, and future research could therefore test these hypotheses.

Overall, despite limited literature, breeding success appears to increase in deeper nest boxes, likely due to the positive effects of reduced actual and perceived predation risk. It would therefore be unwarranted to advise against using this nest box type, as negative consequences are potentially outweighed by protection from predators, especially as predation is a large cause of nest failure. However, the few studies directed towards testing the efficacy of deep nest boxes highlight many potential trade-offs that could negatively affect avian physiology, despite increasing fledging success. Many of these hypotheses are untested, and future research is suggested in order to unveil their severity. It is also worth mentioning such projects focus on species of Paridae, namely Blue Tits and Great Tits, and the costs and benefits of deeper nest boxes may not directly translate to other species such as wrens (*Troglodytes*) and Nuthatches (*Sitta*).

2.3. Guardian Tubes and Hole Extenders

Similarly to deep nest boxes, guardian tubes aim to increase the distance from the nest boxes entrance to the nest cup to prevent larger predator species (which are restricted by their limbs' flexibility and length (Kalinski *et al.*, 2014)) from reaching the eggs/chicks. However, rather than creating this additional distance by increasing the depth of the cavity, these designs involve building out from the entrance hole, outside the box structure. Guardian designs typically involve an elongated tube fixed around the entrance hole, typically made out of plastic piping, usually Polyvinyl Chloride (PVC) (Figure 4a). Commercial designs often include a perch at the base of the entrance, presumably to aid access by the nesting adult. Despite this, it has been hypothesised that guardian tubes may negatively decrease the speed at which adult birds can provision chicks (Blunsden, 2020). Once chicks are older, parent birds can land on the edge of the entrance hole and lean into the box to feed the chicks without having to enter the nest box completely. However, guardian tubes render this natural behaviour impossible such that adult birds have to enter the nest box completely, potentially reducing chick feeding frequency and increasing their own energy expenditure.

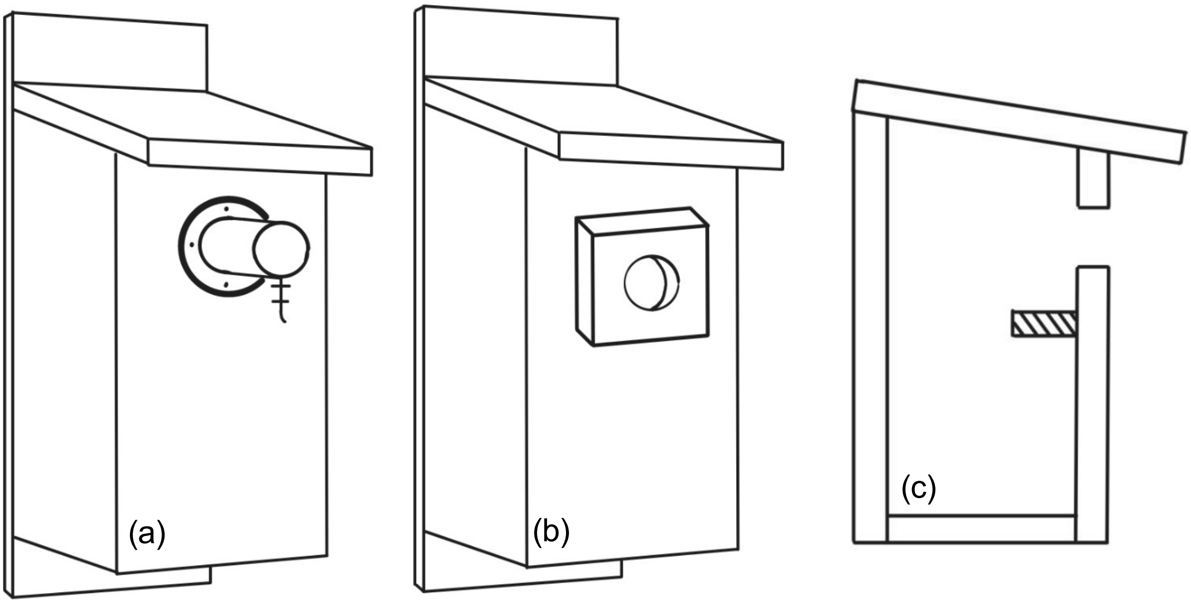


Figure 4. Illustrations of nest boxes with three different variations of nest box guardians installed: (a) plastic entrance tubes, (b) wooden hole extenders and (c) Internal wooden protection plates. Illustrations made by Joseph Marcus.

It is worth noting that materials and designs other than plastic piping can be used. For example, thick wooden blocks with a central opening can be placed over the entrance hole; these are referred to as hole extenders by Bailey and Bonter (2017) (Figure 4b). Although not their intended purpose, these designs could also deter predators such as Grey Squirrels increasing the size of a cavity's entrance hole, similar to the metal protection plates discussed in section 2.4. Yamaguchi *et al*. (2005) also tested a unique variation on this design comprising a small 14 mm thick wooden block fixed on the inside of the box's front panel, 25 mm below the entrance hole, effectively creating an internal shelf below the hole on the nest box (Figure 4c). This did not affect the occupation of nest boxes and successfully lowered Pine Marten predation from 22.4% to 5.9%. It is also likely this did not disturb fledging behaviour, as the nestling stage was not extended.

Kalinski *et al*. (2014) utilised the installation of PVC nest box guardians between breeding seasons to compare the nest heights of Great Tits and Blue Tits with and without the resulting reduction in Pine Marten predation. Not only were less nests depredated after tubes were installed, there was also no difference in the usage of nest boxes, suggesting the devices did not affect nest site choice within the population. However, datasets from the nest box scheme at RSPB Nagshead Nature Reserve show a low uptake of nest boxes with plastic guardian tubes attached (Blunsden, 2020), suggesting potential avoidance behaviour. This lack of congruence could arise from nest site selection being a complicated process, where a plethora of factors that may vary across spatial scales will likely cause inconsistency in results between different sites. The data gathered by Kalinski *et al*. (2014) also showed that birds inhabiting boxes with tubes installed significantly increased the height of their nests. This behaviour persisted over multiple years, thus excluding the possibility that the differences occurred due to annual variation. This nest building behaviour is similar to that observed in deep boxes, and explanations for such behaviours in both nest box types are comparable, where reductions in both perceived predation risk and light intensity are likely to be driving factors. It is therefore possible that guardian tubes and deep boxes have analogous costs and benefits, allowing for a balance between nesting environment and predation risk, but having potential trade-offs with light intensity and ectoparasite load. However, compared to deep nest boxes, it could be reasonable to hypothesise that the effects of reduced light intensity are more profound in boxes with guardian tubes attached. In comparison to standard entrance holes, nest box guardians could reduce the angle at which light is able to directly enter the box, without being reflected along the inside of the tunnel. The attenuation of light levels upon entering a standard tree-mounted next box can be 1,000 times or more (Reynolds *et al*., 2009) and the installation of a guardian tube could further increase this, having more substantial effects on avian physiology. Similarly, an elongated entrance hole could affect airflow, altering a cavity’s microclimate and risking hypoxia. Research measuring light and humidity levels in boxes with guardian tubes installed is therefore recommended to assess the severity of these effects on nestling body condition and fledging success.

2.4. Metal Protection Plates and Wire Mesh

Many large predatory species will break into nest boxes to gain access to the internal chamber and depredate eggs/nestlings. Grey Squirrels for example will gnaw at and enlarge the entrance hole of nest boxes (Broughton, 2020). A common method of preventing such damage is to retrofit thin metal plates around the entrance hole, as shown in Figure 5b (Carter *et al.*, 1989; Lambrechts *et al.*, 2010). Generally, these devices are commonly used by both landowners and researchers as a simple method of reducing predation and prolonging the lifetime of nest box. However, seemingly, scientific research directly testing their efficacy and the potential effects on breeding behaviour (e.g. nest box choice) is minimal. Some studies have shown the method to be successful in protecting Red-cockaded Woodpecker (*Picoides borealis*) nests by both deterring other cavity-nesting species from usurping the nest and preventing predators enlarging the cavities entrance (Carter *et al.*, 1989; Blanc and Walters, 2008).

Figure 5. (a) A depredated Blue Tit nest box, where a Great Spotted Woodpecker has pecked a hole through the side panel to gain access. (b) The sides of a nest box covered in wire mesh to prevent Great Spotted Woodpecker predation, and a metal protection plate fixed around the entrance hole. Images taken from Mainwaring and Hartley (2008).

Whilst metal protection plates can prevent damage to a nest box's opening, avian predators such as the Great Spotted Woodpecker will frequently depredate nests by drilling new holes in wooden boxes, usually by pecking and expanding the gaps between the wooden panels (Figure 5a) (Mainwaring and Hartley, 2008; Skwarska *et al.*, 2009). Mainwaring and Hartley (2008) tested a novel method of preventing Great Spotted Woodpecker predation by covering nest boxes in galvanised wire mesh sheets (13 × 13 mm square mesh), as shown in Figure 5b, and demonstrated how the technique greatly reduced predation. However, the authors did suggest the use of a finer scale mesh to further improve the method's efficacy.

2.5. Relocating and Replacing Old Nest Boxes

Wild birds may alter their nest site fidelity in response to predation risk, an adaptive behaviour corresponding to the *Win-Stay, Lose-Shift* hypothesis (Fontaine and Martin, 2006b). Based on a bird's own reproductive success, or that of neighbouring conspecifics, individuals will remain at (or return to) safe nesting sites, but will abandon high-risk locations and re-locate (Hoover, 2003; Schmidt *et al.*, 2006; Chalfoun and Martin, 2010a; Karell *et al.*, 2020). Novel research suggests that the *Win-Stay* behaviour may be temporally restricted: the longer the time that had elapsed since a successful nesting attempt, the more likely Boreal Owls (*Aegolius funereus*) were to abandon the site (Sonerud, 2021). This was likely due to the positive relationship between predation events and nest box age. One reason predation may be higher at old nest boxes, relative to new boxes, is because the wooden walls will rot and soften over time, becoming more susceptible to damage from predators such as the Great Spotted Woodpecker. Natural cavities in rotten wood are depredated more frequently, and species such as Marsh Tits will therefore avoid nesting in dead wood (Wesołowski, 1996; 2002). Therefore, both nest predation could decrease, and nest box occupation could increase, when old and rotten boxes are replaced with reconditioned or new ones.

Empirical evidence also shows various nest predators will return to nest sites they have previously depredated, with predation thereby being partly determined by a positive feedback loop as predators use prior experience and spatial memory to learn nest site locations (Sonerud, 1985; Sonerud and Fjeld, 1987; Pelech *et al.*, 2010; Weidinger and Kocvara, 2010). These natural mechanisms could be circumvented by the periodic relocation of nest boxes as a useful strategy in reducing predation levels. Although there is limited research testing the efficacy of this method, the relocation of nest boxes after depredation has been shown to reduce predation of Boreal Owl (*Aegolius funereus*) and Paridae nests (Sonerud, 1989; Sonerud, 1993; Sorace *et al.*, 2004). Spatial scale also influences the effectiveness of this method: relocation of nest boxes should be greater than 800 m to ensure successful reductions in predation

(Sorace *et al.*, 2004). However, due to limited space, or constraints from long-term breeding studies, the relocation of nest boxes is not always possible, and this reduced practicality is a potential reason behind the lack of research, and will likely restrict the method's future use. Furthermore, relocating nest boxes may adversely affect breeding populations of highly sedentary species such as Eurasian Nuthatches, who often return to specific nesting sites which they have previously bred successfully.

2.6. Woodcrete Nest Boxes

A mixture of cement and sawdust ("woodcrete") can be easily moulded to produce woodcrete nest boxes of various shapes and sizes. This rugged material does not necessitate frequent chemical treatment with preservatives, and produces a more durable and long-lasting design compared to wood (Browne, 2006; Lambrechts *et al.*, 2010). Woodcrete nest boxes therefore act as an alternative to traditional wooden designs which, as mentioned in section 2.5, become increasingly susceptible to damage from predators as the material softens and becomes rotten over time. The durable nature of woodcrete nest boxes means they do not need to be replaced as frequently and provide added protection against predators, reducing damage caused by species such as Woodpeckers. However, there are limited studies showing a reduction in the number of predation events (e.g. McCleery *et al.*, 1996), and in some locations increased predation has been observed. For example, in central Spain, Ladder Snakes (*Rhinechis scalaris*) have been shown to predate the eggs/nestlings inside woodcrete nest boxes more often than wooden boxes. This was likely due to stronger olfactory cues, where the reduced ventilation in this box type causes the smell of the nest and brood to accumulate (Bueno-Enciso *et al.*, 2016).

A series of four studies has examined the differences between woodcrete and wooden boxes in nesting Tree Sparrows (*Passer montanus*), Blue Tits and Great Tits (Browne, 2006; García-Navas *et al.*, 2008; García-Navas *et al.*, 2010; Bueno-Enciso *et al.*, 2016). All woodcrete boxes were cylindrical, and were narrower and deeper than the quadrangular wooden boxes with smaller internal volumes (either 188cm^3 or 334cm^3 smaller). One overarching finding across these papers was the significantly higher uptake of woodcrete nest boxes compared to standard nest boxes, suggesting a preference for this nest box type. In Browne (2006), Paridae also showed a preference for free-hanging woodcrete designs, rather than boxes that were fixed to tree trunks.

For each of these studies, the experimental design controlled for various environmental factors that are known to influence breeding success and nest box choice. For example, nest boxes were of a similar height and orientation, with entrance holes being a standardized diameter of 32 mm. Nest box types were either paired together on the same tree trunk (García-Navas *et al.*, 2008; García-Navas *et al.*, 2010; Bueno-Enciso *et al.*, 2016), or arranged in close proximity ensuring the distance between them was less than the size of the species' natural territory (Browne, 2006). Reduced internal volume and darkness, improved insulating properties, and perceived protection against predation were all suggested as factors affecting the comparatively higher uptake of woodcrete boxes (Browne, 2006; García-Navas *et al.*, 2008). An important consideration was that the woodcrete boxes in all four studies were deeper than the wooden counterparts, which could have affected nest site selection. As discussed earlier, nest cavity depth, and the resultant increased danger distance, can reduce an adult bird's perception of predation risk, potentially making a nest site more attractive (Mazgajski and Rykowska, 2008; Kalinski *et al.*, 2014; Fokkema *et al.*, 2018). Future research could use woodcrete and wooden boxes of the same depth, in order to determine if the observed preference for woodcrete boxes in these studies is mainly driven by their depth, not material composition. It is also important to consider potential biases that are difficult to control *in situ*. Interspecific competition for nest cavities could result in one species making more use of a nest box type, forcing another species to inhabit a different box type as choice of a restricted resource is not independent (Browne, 2006). For example, it is likely that the deeper internal dimensions of woodcrete boxes combined with the Great Tits larger and heavier morphology (relative to that of Blue Tits), allows them to build more nest material for comfort whilst still maintaining a safe distance from the entrance hole (Bueno-Enciso *et al.*, 2016). This could explain the only exception in the preference for woodcrete boxes observed by Browne (2006), where there was a relatively low uptake of tree-attached woodcrete boxes by Blue Tits.

These four papers also revealed a difference in the microclimate of the woodcrete nest boxes, likely resulting from the material's increased insulation and thermal conductivity. Compared to wooden boxes, significantly higher mean, maximum and minimum temperatures have been detected with data loggers (García-Navas *et al.*, 2008; García-Navas *et al.*, 2010). However, using similar equipment, Bueno-Enciso *et* *al*. (2016) took more frequent recordings every 10 minutes and saw no effect on mean temperature, but instead detected significant differences in the daily temperature pattern, with higher maximum and lower minimum readings. Temperature has various effects on the breeding biology of birds, especially by influencing an individual's energy expenditure during incubation (Ardia *et al.*, 2006a; Bueno-Enciso *et al.*, 2016; Bleu *et al.*, 2017). Hyperthermia is also a significant cause of nestling mortality, where their underdeveloped plumage results in poor thermoregulatory capabilities (Greno *et al.*, 2008). Overall, heightened ambient temperature is described as the overarching negative consequence of woodcrete boxes and the likely cause for many of the observed differences in breeding parameters, which are detailed in Table 1 (García-Navas *et al.*, 2008; García-Navas *et al.*, 2010; Bueno-Enciso *et al.*, 2016).

An important consideration regarding the effects of temperature, is the plasticity exhibited by breeding birds in response to ambient temperatures. Prior to clutch initiation and 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 (Deeming, 2011; Deeming *et al.*, 2012). 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/health (Cunningham *et al.*, 2013). Although broods in woodcrete boxes are more frequently exposed to higher temperatures, temperature recordings seldom exceed critical thresholds. It has therefore been suggested that the effects of overheating are not sufficiently detrimental to offset the alternative advantages of woodcrete boxes (García-Navas *et al.*, 2010). However, these four studies were conducted at temperate latitudes, so this issue may be magnified in warmer equatorial climates, although, birds will also vary their nest construction in relation to spatial variations in temperature (Mainwaring *et al.*, 2012). Alongside variation in temperature, the enclosed design of woodcrete nest boxes and less porous material also results in a more humid environment (Bueno-Enciso *et al.*, 2016).

Table 1. Summary of four recent scientific studies testing the effects woodcrete nest boxes have on various breeding parameters of nesting birds. N/A means a breeding parameter was not studied.

Breeding Parameters Prior to Hatching						Breeding Parameters Post-Hatching				Breeding Success	Citation
Laying Date	Clutch Size	Egg Volume	Hatching Success	Egg Cooling	Incubation	Tarsus Length	Wing Length	Body Mass	Haematocrit		
N/A	No effect	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	No effect	Browne, 2006
Earlier	No effect	N/A	No effect	N/A	Shorter On-bouts	No effect	No effect	No effect	N/A	Higher	Garcia-Navas *et al*., 2008
N/A	Larger	N/A	No effect	N/A	No effect	No effect	No effect	Lighter	No effect	No effect	Garcia-Navas, Arroyo and Sanz, 2010
Earlier	No effect	Smaller	No effect	Reduced	Various effects	No effect	Shorter	No effect	N/A	Reduced	Bueno-Enciso *et al*., 2016

Overall, Table 1 demonstrates that woodcrete nest boxes can affect aspects of breeding biology and breeding success, but, effects are highly variable and can be conflicting, meaning definitive conclusions cannot be drawn. Biological effects of woodcrete boxes may be slight, and therefore vary between projects and study sites as a result of variation in factors such as food availability, parental fitness and predator abundance. For example, older, more experienced pairs of birds may select for woodcrete boxes, demoting competitively inferior pairs to wooden boxes and thus creating a source of bias. In this regard, the study conducted by Bueno-Enciso *et al.*, (2016) may be most reliable as adult birds were captured and subsequently measured and weighed. Plumage characteristics were also examined to differentiate between yearlings and adults greater than one year old, thus examining effects in relation to avian age and experience. They found no difference in morphology or parental age between the two nest box types, suggesting there was minimal effect of parental fitness. A large-scale and long-term project could be utilised to compare the breeding success across a wide spatial and temporal range, with substantial sample sizes and robust statistics. A nest recording citizen science project could potentially be utilised to perform this at a national or international scale. These four studies also had a broad aim, testing the general efficacy of woodcrete boxes and identifying life-history traits that are affected. Targeted research with experimental designs dedicated to testing specific breeding parameters may be required to verify the effects of nesting in woodcrete boxes. These effects are important to understand as the provisioning of woodcrete boxes could act as an ecological trap, being actively chosen by birds despite having potential negative impacts on nestling development and survival.

2.7. Photosensitive Triggered Doors

A novel design for excluding small nocturnal predators, such as the introduced Sugar Glider (*Petaurus breviceps*) on Tasmania, Australia was field tested by Stojanovic *et al.*, (2019). Photosensitive triggered doors, termed “Possum-Keeper-Outterers” (PKO), can be retrofitted to exiting boxes and were designed to open or close when ambient light exceeds or drops below 20 lumens, respectively. This effectively closes the nest box’s entrance hole at night, and repeatedly prevented nocturnal predators from entering the box, improving the nest success of Tree Martins (*Petrochelidon nigricans*) by 56%. A significant issue with PKOs are the ethical implications and the high risk of mortality if devices fail and birds are trapped. In Stojanovic *et al*., (2019) only one of the tested PKOs failed due to shading of the solar panels. The authors suggested that frequent maintenance checks, the installation of back-up batteries and the use of multiple solar panels in shaded habitats to ensure proper operation of the mechanism. The authors observed no obvious actions symptomatic of distress in the Tree Martins, but behavioural changes were not explicitly tested for, so further research is warranted. In order to reduce neophobia the authors suggested installing decoy units on all nest boxes prior to the breeding season, before changing them to operational PKOs when nest boxes are selected by breeding birds. Finally, PKOs are relatively expensive, costing approximately $340 USD per unit (Stojanovic *et al*., 2019), and therefore are impractical for large nest box schemes.

2.8. Baffles

Passive barriers placed on a nest's support structure can be used as a cheap and simple method of directly blocking tree-climbing predators, such as Stoats (*Mustela erminea*) and Grey Squirrels from reaching a nest. These barriers, often termed "baffles", typically assume a conical or stovepipe/collar design, where cheap and accessible materials such as plastic or metal sheeting is often used in a makeshift manner (Figure 6). Data from the citizen science project *NestWatch*, showed stovepipe baffles are one of the most used forms of predator guards for standard nest boxes (Bailey and Bonter, 2017).

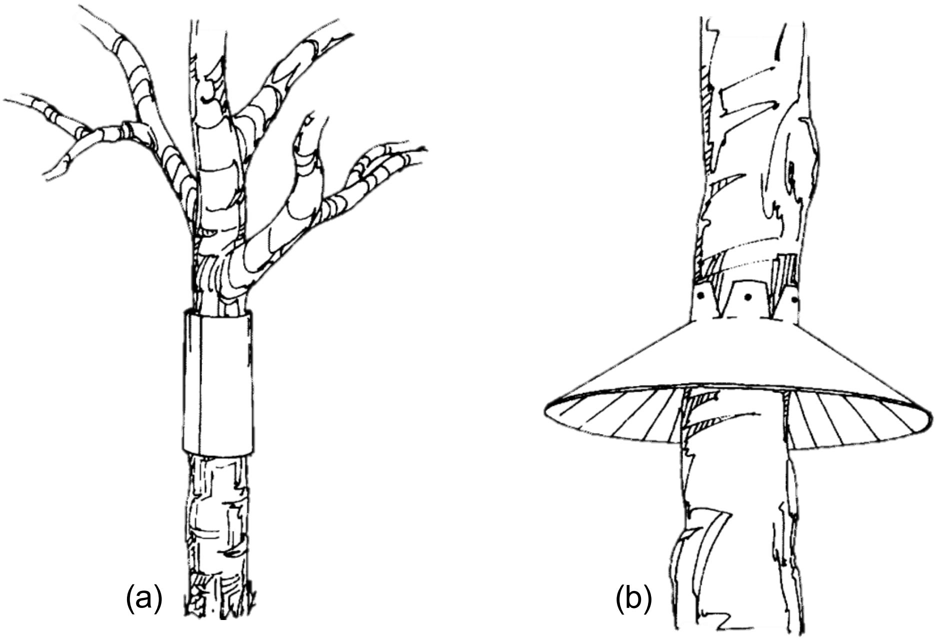


Figure 6. Illustrations of a (a) stovepipe baffle and (b) collar baffle. Image taken from Cates and Allen (2002)

Many predators, such as Stoats, are able to jump to nest boxes from surrounding objects (Greene and Jones, 2003), and baffles in dense woodland habitats may therefore be less effective due to predators accessing the nest box from nearby flora or crossing trees from the canopy. Garnett, Pedler and Crowley (1999) counteracted this by pruning surrounding trees, although this may not always be feasible. Social pair birds may also use such foliage as sentinel and singing posts to maintain contact with the other bird in the pair, especially when they are incubating and brooding.

Many studies use baffles to protect cavity-nesting waterfowl species, such as Black-bellied Tree Ducks (*Dendrocygna autumnalis*) and Wood Ducks (*Aix sponsa*), where nest boxes are often isolated in open wetlands and their support structures (e.g. tree trunk or pole) are the only way of accessing nest boxes for ground mammals like American Mink (*Neovison vison*). These studies have shown an improved nesting success when using both stovepipe and conical baffles, with the latter having no effect on nest box choice by the breeding birds (Bolen, 1967; Lacki *et al.*, 1987; Laubergs and Viksne, 2004). Keo, Collar and Sutherland (2009) demonstrated how US$5 hard plastic baffles, in a stovepipe design, increased the fledging success of a critically endangered Giant Ibis (*Thaumatibis gigantea*) population by 50%. The authors also implied this technique may be useful for preventing predation by snakes (Serpentes), a taxonomic group that is challenging to deter due to ease in climbing, hanging and entering tight structures like tubes. Navalpotro, Mazzoni and Senar (2021) tested the effectiveness of the method employed in preventing nest box predation by Montpellier snakes (*Malpolon monspessulanus*) and ladder snakes (*Zamenis scalaris*). Statistical analysis showed a significant increase in fledging success between protected and control nest boxes without the plastic baffles. The only instance where a protected box was invaded was likely due to a snake crossing to the box from a nearby tree, a behaviour that had been previously observed. The authors suggested putting the same plastic baffles around surrounding trees (Navalpotro *et al.*, 2021).

Studies testing the use of baffles to protect passerine nest boxes in woodland habitats are relatively limited in number, with papers generally using the guards as an aspect of a wider study. Baffles used to protect nest boxes in woodlands have not been effective in improving the nesting success of both House Wrens (*Troglodytes aedon*) and Riflemen (*Acanthisitta chloris*) (Briskie *et al.*, 2014; Bowers *et al.*, 2016). Low predation levels at Prothonotary Warbler (*Protonotaria citrea*) boxes was assumed to be due to conical metal baffles in a hardwood forest in Mississippi, USA although this was not supported by statistical analysis (Mueller *et al.*, 2019). Eastern Bluebird (*Siala sialis*) nest boxes on suburban golf courses in Virginia, USA were more likely to fledge when predator baffles were installed, although predation was still the predominant cause of nest failure (Cornell *et al.*, 2011).

Table 2a. Summary of the advantages and disadvantages of nest box predator-prevention methods.

Deep Nest Boxes		Guardian Tube Nest Boxes		Metal Protection Plates		Wire Mesh	
Pros	Cons	Pros	Cons	Pros	Cons	Pros	Cons
Directly reduces predation by increasing the danger distance	Some predatory species like Woodpeckers can still predate nests by damaging and breaking into the nest box	Directly reduces predation by increasing the danger distance	Potentially decreases the frequency at which adult birds can provision chicks by hindering their ability to effectively enter the nest box	Can be retrofitted to existing nest boxes	Only protects the boxes entrance hole. Therefore does not prevent woodpecker predation	Can be retrofitted to existing nest boxes	Doesn't prevent species from reaching into and/or entering the nest box through the entrance hole
Nest mass is less restricted, enabling birds to build larger nests for nest sanitation and thermoregulation without compromising the danger distance	The benefits of an increased danger distance and reduced predation may become negligible if birds build larger nests	Increased danger distance enables birds to build larger nests	Reductions in Nest illumination and Ventilation. This can lead to birds building larger nests which can increase ectoparasites loads and nest building effort	Relatively inexpensive		Relatively inexpensive	
Reductions in the perceived predation risk can have positive effects on parental investment, improving clutch size and hatching success	Reductions in Nest illumination and Ventilation. This can lead to birds building larger nests which can increase ectoparasites loads and nest building effort	Doesn't always effect nest box choice	Some predatory species like Woodpeckers can still predate nests by damaging and breaking into the nest box	Prevents species such as Grey squirrels from enlarging a nest boxes entrance hole. This also increases the durability of the nest box		Prevents woodpecker species from pecking and expanding the gaps between the wooden panels, thus reducing predation	
Many passerine species select for deeper boxes, likely due to an decreased perceived predation risk	Increased ectoparasite loads have been observed in deeper nest boxes with more nest material	Can be retrofitted to existing nest boxes					

Table 2b. Summary of the advantages and disadvantages of various nest box predator-prevention methods

Replacing Old Nest Boxes		Relocating Old Nest Boxes		Woodcrete Nest Boxes		Photosensitive Triggered Doors		Baffles	
Pros	Cons	Pros	Cons	Pros	Cons	Pros	Cons	Pros	Cons
Prevents nest boxes softening over time as they become rotten. This reduces predation by species which will damage and break into nest boxes	Expensive and time-consuming for large nest box schemes	Reduces predation by stopping predators using prior experience and spatial memory to learn nest site locations	May impact highly sedentary species that return to the same nest box each breeding season	Improved insulative properties can lead to heightened ambient temperatures, which can have both positive and negative effects on breeding parameters		Can be retrofitted to existing nest boxes	Ethical implications associated with preventing nesting birds from exiting the nest boxes at night	Can be retrofitted to existing nest boxes	Less effective in dense habitats due to predators accessing the nest box from nearby flora or crossing trees from the canopy
May reduce the chances of highly sedentary species abandoning a regularly used nest site due to the nest box becoming rotten and prone to predation			Due to limited space, or constraints from long-term breeding studies, the relocation of nest boxes is not always possible	Provides added protection against predatory species that damage nest boxes in order to access the nest chamber	Increased predation by snakes, likely due to a reduction in ventilation causing the smell of the nest to accumulate.	Reduces predation from nocturnal predators that enter nest boxes trough the entrance hole	High risk of mortality in nesting birds if devices fail	Relatively inexpensive and widely available. Can also be home-made	
			Time-consuming and impractical for large nest box schemes	Some passerine species prefer and select for woodcrete nest boxes	Relatively more expensive compared to wooden nest boxes		Expensive	Prevents predators from climbing a nest boxes support structure and can therefore reduce predation	
				Rugged material with a durable design that does not need frequent chemical treatment with preservatives					

Chapter 3

Impact of Breeding Parameters and Predator-Proof Nest Box Designs on Chick Provisioning Frequency

RSPB Nagshead Nature Reserve in June 2022

(Image taken by Joseph Marcus)

3.1. Research Introduction and Study Aims

Based on a variety of factors, such as nestling growth rate and parental care patterns, ornithologists generally categorise avian species over an altricial to precocial spectrum. At one extreme, precocial nestlings (e.g. Waterfowl [*Anseriformes*]) hatch with their eyes open, are covered in down, and are generally capable of regulating their body temperature and feeding themselves. At the other extreme, altricial nestlings (e.g. song-birds [*Passeriformes*]) are helpless, hatching naked, blind, and are solely reliant on parental care for feeding and thermoregulation (Starck and Ricklefs, 1998).

The nestlings of woodland secondary cavity-nesting passerines are altricial and nidicolous, remaining in the nest for some time before fledging, usually for 12 to 30 days (Brooke and Birkhead, 1991). During this period, nestlings have high food requirements and their growth and survival greatly relies on the parent bird's ability to provide them with food (Boag, 1987; Searcy *et al.*, 2004). Chick food provisioning is one of the most time and energy consuming forms of parental care, and the time allocated for such behaviours has to be balanced with other activities such as nest defence, territory guarding, brooding, nest sanitation and self-feeding (Ydenberg and Houston, 1986; Martin, 1987; Moreno and Hillstrom, 1992; Martins and Wright, 1993; Whittingham, 1993; Markman *et al.*, 1995; Grieco, 2002a). The efficiency of chick provisioning is therefore crucial, and factors such as food availability and weather conditions can have significant effects on nestling and parent survival (Naef-Daenzer and Keller, 1999; Radford *et al.*, 2001; Oberg *et al.*, 2015). Identifying potential factors that influence chick provisioning is therefore imperative for conservation, and this was the predominant focus of the current research project.

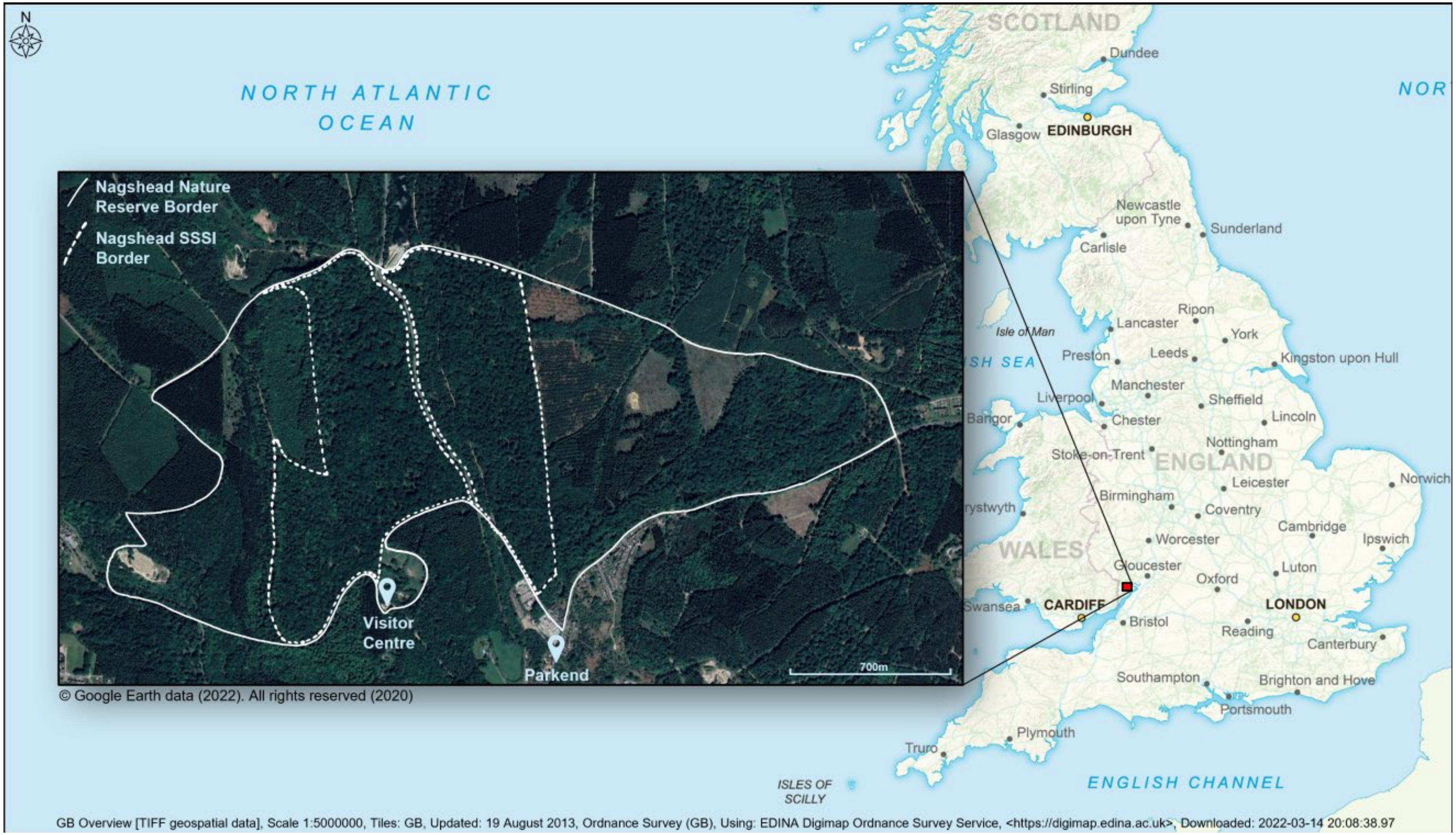
The study was exploratory and examined the potential effects of a variety of life-history (e.g. brood size and nestling age) and environmental (e.g. habitat and rainfall) factors on chick food provisioning, thus identifying areas for future research. This was done by quantifying the parental nest visitations and chick provisioning of four secondary cavity-nesting passerines, nesting in man-made nest boxes at a semi-natural broadleaf woodland site in the Forest of Dean, Gloucestershire, UK.

A significant aspect of the project examined chick food provisioning across different types of predator-proof nest boxes. This focus aimed to test the hypothesis proposed by Blunsden (2020), who suggested nest box type may be a factor that influences chick provisioning: the author hypothesised that deep nest boxes and nest boxes fitted with guardian tubes may reduce a bird’s ability to feed nestlings. This is because once nestlings are older, parent birds will land on the edge of a nest box’s entrance hole and lean into the nest chamber to feed chicks (without having to enter completely). However, these predator-proof nest box designs may prevent this ‘leaning’ behaviour, meaning birds have to enter the box completely, thus slowing down food delivery and potentially impacting provisioning frequency to a level that might be reflected in lower breeding success, especially in years where prey abundance is low (which is an increasing problem due to climate change (e.g. Leech and Crick, 2007; Cole *et al.*, 2015)). The study therefore aimed to be the first to examine this potential unintended negative consequence of predator-proof nest boxes on chick provisioning.

3.2. Methodology

3.2.1. Study Site Overview

The study took place in 2022-23 at Nagshead Nature Reserve (2°34’0”W, 51°47’0”N), a 305 hectare broadleaf woodland site adjoining the post-industrial village of Parkend, Gloucestershire, England (Figure 7). The reserve is situated on the east-facing slopes of the Cannop Valley, where the bedrock predominantly consists of the pennant sandstone typically found within the coal measures throughout the Forest of Dean (Campbell, 1968). The majority of the site has anthropogenic origins, dominated by the Napoleonic oaks (*Quercus spp.*) that were planted in the early 19th century for the ship-building industry. However, with the plantation never being felled, 126 hectares now forms the largest continuous patch of pre-1850 oak woodland in Southwest England (Proctor and Pollard, 2000; Goodenough, 2007). Alongside these oak plantations is a mosaic of additional habitat types, including coniferous plantations and smaller areas of semi-improved grassland and acidic shrubland (Tickner and Evans, 1990).



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GB Overview [TIFF geospatial data], Scale 1:5000000, Tiles: GB, Updated: 19 August 2013, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, <https://digimap.edina.ac.uk>, Downloaded: 2022-03-14 20:08:38.97

Figure 7. The national geographic location of RSPB Nagshead Nature Reserve; where the inset features the reserve border and the Nagshead SSSI border.

Nagshead supports breeding populations of many British woodland species listed on the BTO's Birds of Conservation Concern List Five (BoCC), including Pied Flycatcher, Spotted Flycatcher, Wood Warbler (*Phylloscopus sibilatrix*), Common Redstart, Lesser Spotted Woodpecker and the occasional nesting Hawfinch (*Coccothraustes coccothraustes*) (Stanbury *et al.*, 2021; Natural England, 2022b; RSPB, 2023). Therefore, due to the site's ornithological importance, Nagshead was designated as an RSPB reserve in 1974, and is now managed by the organisation in partnership with the Forestry Commission (Goodenough, 2007). An onsite visitor centre located at 51°46'24.67"N 2°34'16.13"W is managed by the RSPB and maintained and run by both volunteers and the site's wardens.

In 1972, 130 hectares of the site was notified as a Site of Special Scientific Interest (SSSI), which was re-notified in 1985 under the Wildlife and Countryside Act 1981. During Natural England's most recent assessment in late 2021, the SSSI's formal condition assessment classification was revised from being 'favourable' to 'unfavourable'. This was due to the lack of oak regeneration, alongside the habitat disturbance and grazing pressure from deer and Wild Boar (*Sus scrofa*) (Natural England, 2022a; 2022b). Wild Boar have been widespread across the Forest of Dean after their unofficial reintroduction from farm stock in 1999. The absence of natural predators has caused rapid growth in their population, and the species' rooting behaviour can negatively impact woodland vegetation (Massei and Genov, 2004; Barrios-Garcia and Ballari, 2012). In 2013 it was estimated that there were approximately seven Wild Boar per km^2 in Oatenhill, a woodland site less than 2 km south-east of Nagshead (Massei *et al.*, 2018). A survey conducted by the Forestry Commission in 2015 found that Fallow Deer (*Dama dama*) were the most abundant deer species in the Forest of Dean, with smaller numbers of Muntjac (*Muntiacus reevesi*) and Roe (*Capreolus capreolus*) (Gill and Ferryman, 2015). Grazing pressure from deer can considerably reduce the density of foliage in woodland habitats, and can therefore indirectly affect the species composition of avian populations (Fuller, 2001; Kirby, 2001).

3.2.2. History of Nagshead Nest box Scheme

Prior to the breeding season in 1942, 84 standard-diameter wooden nest boxes (dimensions listed in section 3.2.3.1) were erected at Nagshead. The primary objective was to encourage insectivorous species that would act as a biological control for the frequent population booms of Lepidoptera, especially Oak Roller Moth (*Tortrix viridana*) (Taylor, 1944). As intended, the boxes were predominantly populated by Great Tits and Blue Tits, but unexpectedly, 15 boxes were inhabited by European Pied Flycatchers, signifying the species' first confirmed breeding record in the Forest of Dean (Brown, 1943; Campbell, 1968). This breeding population of Pied Flycatchers increased over the following years and was a driving factor in developing and expanding the nest box scheme.

By 2018 the Nagshead nest box scheme comprised of 409 standard-diameter nest boxes. However, in 2019 the reserve collaborated with Gloucestershire Wildlife Trust and the University of Gloucestershire to trial three different predator-proof nest box designs: woodcrete, deep and standard boxes with guardian tubes (dimensions listed in section 3.2.3.1). As part of this project, nest box dyads were set up across the reserve, whereby 302 of the pre-existing standard nest boxes were paired with one of the three predator-proofed nest boxes on the same tree. The presence of two nest box types per tree allowed for direct comparisons into the uptake of each nest box type without availability biasing results. A large driver for this project was the Forest of Dean and Wyre Valley Pine Marten reintroduction scheme, managed by the Gloucestershire Wildlife Trust, the Forestry Commission and the Vincent Wildlife Trust. Therefore, the installation of predator-proof nest boxes also aimed to assess predation in each nest box type, alongside the reintroduction of this predatory species. Following a feasibility study, 35 individual Pine Martens were reintroduced into the Forest of Dean between 2019 and 2021. During the time of my study in 2022, the population in the Forest of Dean was estimated to be 40 individuals (Stringer *et al.*, 2018; Gloucestershire Wildlife Trust, 2022).

From 1948, the inhabitants of the nest boxes and their resulting breeding success have been recorded each year, resulting in what is now the longest running nest box scheme in Britain (Campbell, 1968). However, differing field methods and changing management resulted in these data being considered inconsistent up until 1974, when the RSPB took over management of the reserve and started coordinating weekly nest checks every breeding season (Goodenough, 2007).

3.2.3. Nest Box Configuration

At the time of this study in 2022-23, the Nagshead nest box scheme covered approximately 50 hectares of the site, primarily within the Napoleonic *Quercus* plantation. The nest box area is shown in Figure 8, and contained 107 individual standard nest boxes, and 302 nest box dyads (as described above (3.2.2)), giving a total of 409 nest box trees, but 711 nest boxes. All nest boxes were installed on species of oak trees, at heights unreachable without a ladder to prevent interference from the public. Whilst some boxes were visible from the public access paths throughout the reserve, most were situated at a sufficient distance to avoid regular disturbance. Before the breeding season in 2022, a Garmin eTrex® 62 GPS unit (Southampton, UK) was used to record the GPS location of all 409 nest box trees. These GPS locations were spatially plotted using QGIS (version: 3.22.4) and shown in Figure 8, alongside which nest box trees supported dyads. Figure 8 also shows how the boxes were split into 12 groups/routes to aid the volunteers who conducted weekly nest box checks (3.2.6.1). Aside from the 28 nest boxes that comprised route 9, all other boxes were located within the SSSI. The density of nest boxes was approximately 9.5 boxes per hectare, calculated in QGIS. All boxes were situated on the east side of the B4234 road which bisects the overall reserve.

Satellite Image: © Google Earth data (2022). All rights reserved (2020)

Base Map: OS MasterMap® Topography Layer [TIFF geospatial data], Scale 1:1000, Tiles: so5908_clipped,so5909_clipped,so6008_clipped,so6009_clipped,so6108_clipped,so6109_clipped, Updated: 18 May 2017, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, <https://digimap.edina.ac.uk>, Downloaded: 2022-04-23 13:05:02.57

Figure 8. The nest box area at Nagshead Nature reserve, with GPS coordinates marking the location of each nest box tree and its corresponding route. Circles show trees with nest box dyads installed, and diamonds show trees with a single nest box installed. The old fence is also highlighted, where the north side was historically grazed by sheep (*Ovis aries*).

3.2.3.1. Nest Box Types

As detailed in chapter 2, the design of nest boxes can vary, which can greatly affect physiology and breeding success of birds. It is therefore important to detail the design and dimensions of each of the nest boxes included in the study (Lambrechts *et al.*, 2010). The four nest box types that were in reserve are described below, and their corresponding dimensions are listed in Table 3.

Table 3. The approximate dimensions of the four nest box types installed at Nagshead Nature Reserve.

Nest Box Type	Internal Measurements (cm)			Chamber Volume (cm^2)	Entrance Hole Diameter (cm)
	Width	Length	Centre Point Height		
Standard (S)	11	15	25	4,125	3.2
Woodcrete (W)	12	12	23	N/A	3.2
Deep (D)	11	15	32	5,280	3.2
Guardian (G)	11	15	25	4,125	4.0

Standard Boxes (S):

These were traditional, rectangular, wooden nest boxes, with a downward sloping roof, where a latch could be unhooked to lift back the top panel and gain access. Due to their periodic instalment and handmade design, the dimensions of the standard boxes were slightly variable. As shown in Figure 9a, thin metal protection plates were affixed to the majority of standard boxes, preventing predators such as Grey Squirrels from increasing the size of the entrance hole, thereby reducing predation and prolonging longevity.

Alongside the installation of nest box dyads in 2019, 100 brand new standard boxes were fitted. However, 50 of these boxes were used to mount guardian tubes, and therefore only 50 were left as standard boxes.

Woodcrete Boxes (W):

The woodcrete nest boxes on the reserve were WoodStone® nest boxes made by *Vivara*, constructed from a blend of concrete and wood fibres. The front panel completely separates from the box and is held on by two latches, which can be rotated through 180 degrees to free the plate and gain access. Although the woodcrete boxes appear to have a rectangular design, the back wall is curved and the roof is arched (Figure 9b). Internal volume was therefore not calculated. It is important to note the entrance hole protrudes by approximately 1 cm.

Deep Boxes (D):

These were wooden nest boxes designed to have the same length and width (and thus have the same basal area) as the standard boxes, but a greater depth.

Guardian Tubes (G):

Commercial guardian tubes, made from a rigid plastic polymer, affixed to the entrance hole of standard nest boxes. The length of each tube was 6 cm, with a 4 cm diameter, although it is worth noting that the original 3.2 cm entrance hole in the nest boxes themselves was still present.

When installing nest box dyads, 100 new standard nest boxes were paired with pre-existing standard boxes, and these dyads were used for the installation of the guardian tubes. Because birds can show preferences for nest boxes according to the nest box's age (Ekner-Grzyb *et al.*, 2014), it was important to avoid such preferences causing bias when studying the choice of boxes with or without a guardian tube. Therefore, the tubes were affixed to each new box in 50 of these dyads, and affixed to the old boxes in the other 50 dyads.

Figure 9. The four types of nest boxes installed at Nagshead Nature Reserve: (a) Standard. (b) Woodcrete. (c) Deep. (d) Guardian Tube. Images taken at Nagshead Nature Reserve by Joseph Marcus.

3.2.4. Habitat of Nest Box Area

The nest box area was in the 19th century, semi-ancient, Pedunculate Oak (*Quercus robur*) plantation. This habitat was therefore dominated by Pedunculate Oak which had a uniform distribution throughout the site, suggestive of the reserve's planted origins. Other species such as Beech (*Fagus sylvatica*), Sweet Chestnut (*Castanea sativa*) and Sycamore (*Acer pseudoplatanus*) were also located throughout the nest box area, but had a more sparse and patchy distribution. Occasional groups of young coniferous trees, such as Scots Pine (*Pinus sylvestris*), were naturally found where the oak plantation borders neighbouring coniferous stands. The occurrence of Ivy (*Hedera helix*) was common on many of the mature oak tree trunks. There was little oak regeneration occurring in the nest box area which was one of the reasons for the Nagshead SSSI classification being classified as being 'unfavourable' in 2021 (Natural England, 2022a).

Understory vegetation varied across the nest box area due to historic sheep-grazing. Figure 8 shows the location of an old fence line, where the north side historically contained sheep, thus separating the habitat into grazed and un-grazed areas. In 2001, these livestock were culled due to outbreaks of foot and mouth disease, and the habitat was left to develop in the absence of sheep. However, at the time of my study, the effects of the historic sheep grazing were still prominent, and there were clear differences in the shrub layer on either side of the old fence line. Although there was overlap in the presence of certain species, the un-grazed area had a much more dense understory, predominantly containing species such as Holly (*Ilex aquifolium*), Rowan (Sorbus spp.), and Bramble (*Rubus fruticosus*). The sheep-grazed section however had a more open environment with fewer shrubs and tree saplings and was dominated by Common BlueBell (*Hyacinthoides non-scripta*) and Bracken (*Pteridium aquilinum*) (Natural England, 2022b).

Deadwood was abundant across the whole site (Natural England, 2022a), an important characteristic that provides habitat for forest-dwelling birds, mammals, invertebrates, fungi and lichens (Radu, 2006). Figure 8 shows the four main ponds located in the nest box area, one of which was adjacent to the visitor centre, and the others were adjoining the public bird hides on the reserve. The nest box area is on an east facing slope, where the elevation declines from 183 m to 54 m above sea level (asl). The B4234 road was located to the East of the nest box area, and can be seen from the eastern nest boxes in routes 8a and 8b (see Figure 8).

3.2.5. Study Species

The nest boxes in the reserve were predominantly inhabited by Blue Tits, Great Tits, European Pied Flycatchers and Eurasian Nuthatches, all of which are secondary cavity nesters that produce altricial young. These species were therefore included in the current project. One nest box was occupied by Common Redstarts, but was ignored due to the small sample size.

3.2.5.1. Pied Flycatcher

The Pied Flycatcher (PF) (Figure 10) is a long-distance Afro-Palearctic migratory species, spending spring and summer months breeding in Europe before migrating to Western Africa (Holden and Gregory, 2021). The global population of Pied Flycatchers is classified as ‘least concern’ by the International Union for Conservation of Nature (IUCN) Red List and Birdlife International. The estimated global population is approximately 33 to 52 million mature individuals, and although population trends show a steady decline, they do not approach the thresholds required to categorise a species as ‘vulnerable’ (BirdLife International, 2018a; 2023). Compared to other parts of its range, the UK population is in significant decline. The BTO’s Breeding Bird Survey (BBS) recorded a sudden and sharp decline in the British population from 1995 to present (Woodward *et al.*, 2020b). This prompted the species to the moved to an amber status and then red status in the 2009 and 2015 BoCC reports, respectively. Within the 2021 BoCC report, the species was moved back to an amber status, with a population decline of -43.4%. However, it is important to note this was due to small variations in population trends, and the species is still close to the -50% red-list threshold (Stanbury *et al.*, 2021). In 2016, the British population contained an estimate of 22,000 to 25,000 breeding pairs (Woodward *et al.*, 2020a).

In the UK, Pied flycatchers prefer mature upland woodland, where they frequently hunt from a perch, darting off to catch flying insects, however, unlike the Spotted Flycatcher they rarely return to the same perch. Their diet mainly consists of arthropods, including spiders (Araneae), insects (Insecta) and caterpillars (Lepidoptera), all of which are also fed to nestlings (Robinson, 2005; Holden and Gregory, 2021).

As shown in Figure 10, breeding adults have distinct sexual dimorphism, where males have a conspicuous black and white plumage compared to the female's more muted brown mantle and rump. Upon arrival on their breeding grounds, males will typically find a suitable nesting cavity and then advertise the site in order to attract a female. Pied Flycatchers can be either monogamous or polygamous, where the latter is common and adopts a system described as staggered simultaneous polygyny. In typical polygynous species, the male has a single territory, where each female occupies a section of this space (Von Haartman, 1969). However, male Pied Flycatchers are polyterritorial, where after mating with an initial (primary) female, the male will attempt to establish a new territory and attract and breed with another (secondary) female. Males can have multiple secondary females, but will typically abandon them, returning to the initial territory/female to provide parental care (Alatalo *et al.*, 1981). Polyterritoriality is likely an evolutionary adaptation to hide the fact the male is already paired, thus increasing the chances of secondary females mating with an already-mated male. This is referred to as the deception hypothesis (Alatalo and Lundberg, 1984). Polygynous males are more often fitter and more experienced than monogamous individuals, likely arriving earlier in the season to mate with early arriving females, and then competing with late arriving males for late arriving females (Alatalo *et al.*, 1981). Once paired, females are the sole builders of the nest, which has a loose structure and is typically made out of leaves, grass, roots and moss (Robinson, 2005). Incubated is conducted by the female alone, but both adults feed nestlings post-hatching (Robinson, 2005).

Figure 10. The Pied Flycatcher (*Ficedula hypoleuca*), one of four study species included in the research project examining chick food provisioning in nest boxes at Nagshead Nature Reserve in spring 2022. Images show a female (left) and male (right) in breeding plumage, note the conspicuous sexual dimorphism. Images taken by Joseph Marcus at the time and place of the study.

3.2.5.2. Eurasian Nuthatch

The Eurasian Nuthatch (NH) (Figure 11) is a woodland passerine found throughout Europe and the Palearctic. The UK population has seen a steady increase since the 1970s, currently being common throughout England and Wales, with small populations in southern Scotland. Some local declines have been recorded in western Wales, Kent and Cornwall (Balmer *et al.*, 2013; Woodward *et al.*, 2020b). To date, the species has had a green status on all BoCC reports, and is classified as 'least concern' on the IUCN Red List at a global scale (Birdlife International, 2018b; Stanbury *et al.*, 2021). The Eurasian Nuthatch is a resident breeding species in the UK, and in 2016, there were estimated to be 250,000 breeding pairs nationally (Woodward *et al.*, 2020a).

Figure 11. The Eurasian Nuthatch (*Sitta europaea*), one of four study species included in the research project examining chick food provisioning in nest boxes at Nagshead Nature Reserve in spring 2022. Image taken by Joseph Marcus at the time and place of the study.

Although the species will reside in towns, its preferred habitat is deciduous woodlands, where mature species of oaks provide ample nesting cavities and foraging opportunities. The species will predominantly consume invertebrates, the main food sources fed to young, but will consume various nuts and seeds throughout autumn and winter, which are often stored amongst lichen, moss and bark for later consumption in colder weather (Robinson, 2005). Food items are usually found on tree trunks and branches, but the species will also forage from the ground (Robinson, 2005). Nuthatches are monogamous and sedentary (Matthysen and Schmidt, 1987), and juveniles will disperse from their natal range to establish their own territory (Matthysen, 1987; Pravosudov, 1993). Nests are predominantly built by the female and are typically made out of dead leaves and pieces of bark. Females can also reduce the size of the cavities entrance by plastering mud around the entrance hole (Holden and Gregory, 2021). The females incubate the clutch but both adults feed the nestlings, continuing to feed the chicks after they have fledged until they become independent (Robinson, 2005).

3.2.5.3. Great Tit

The Great Tit (GT) (Figure 12) is common throughout the UK as a resident breeding species, with small numbers of winter migrants from continental Europe (McInerny *et al.*, 2022). The UK population has increased steadily since the 1960s and reached approximately 2.35 million breeding pairs in 2016 (Woodward *et al.*, 2020a; Woodward *et al.*, 2020b). In recent decades, Great Tits have advanced their laying dates in response to phenological changes resulting from climate change (Visser *et al.*, 2009; Bauer *et al.*, 2010; Cole *et al.*, 2015), but this does not appear to be affecting British population trends (Woodward *et al.*, 2020b). The species has had a green status on all BoCC publications (Stanbury *et al.*, 2021), and is classified as 'least concern' by the IUCN Red List (BirdLife International, 2016).

Figure 12. The Great Tit (*Parus major*), one of four study species included in the research project examining chick food provisioning in nest boxes. Image taken by Joseph Marcus at the time and place of the study.

Great Tits can be found in a variety of habitats but typically inhabit open deciduous woodlands, mixed forests, orchards, gardens and parks (Robinson, 2005). Great Tits typically forage by foliage gleaning, where prey is plucked from the leaves and branches of shrubs and trees, but birds will also feed on the ground (Holden and Gregory, 2021). In summer months, the species mainly feeds on insects, but in winter their diet switches to fruits, seeds and nuts, where beechmast can be an important food source that drives adult and juvenile survival (Perdeck *et al.*, 2000; Holden and Gregory, 2021). Great Tits are monogamous and the female builds the nest, which is primarily constructed from moss and lined with hair and feathers (Holden and Gregory, 2021). Incubation of the clutch is conducted by the female, but post-hatching parental care is provided by both parents, where caterpillars are the primary food source fed to nestlings (Holden and Gregory, 2021).

3.2.5.4. Blue Tit

The Blue Tit (BT) (Figure 13) is also a common UK passerine, found throughout the UK as a resident breeding species, with some potential winter migrants (McInerny *et al.*, 2022). The species has had a green status on all BoCC publications (Stanbury *et al.*, 2021), with 2016 UK population estimates reaching 3.4 million breeding territories/pairs (Woodward *et al.*, 2020a). Despite fluctuations, long-term UK population trends show a steady increase in Blue Tit numbers, but, annual productivity has declined in recent years (Woodward *et al.*, 2020b). This is potentially due ecological mechanisms such as phenological disjunction, whereby warmer spring temperatures result in mismatches between hatching dates and peak caterpillar abundance (Cole *et al.*, 2015). European populations are also increasing, being classified as 'Least Concern' on the IUCN Red List of Threatened Species globally (BirdLife International, 2017).

Figure 13. The Blue Tit (*Cyanistes caeruleus*), one of four study species included in the research project examining chick food provisioning in nest boxes. Image taken by Joseph Marcus at the time and place of the study.

Typically, Blue Tits inhabit deciduous woodland habitats, generally preferring forest stands containing oak and birch. However, the species can be found in a variety of habitats, including farmland and urban environments, provided suitable natural/artificial nesting cavities are readily available. Their diet varies with seasonal changes in food availability, but they forage for insects (predominantly caterpillars) and spiders in spring by foliage gleaning, and seeds and fruits in winter (Robinson, 2005). Blue Tits generally breed in monogamous pairs, but extra-pair paternity and polygyny can occur (Vedder *et al.*, 2011). Cup-shaped nests, made from predominantly moss, straw, hair and wool, are built by the female (Tomas *et al.*, 2006). Female-only incubation is exhibited but both adults will provision nestlings, feeding chicks predominantly caterpillars (García-Navas *et al.*, 2012; Bambini *et al.*, 2019).

3.2.6. Field Methods

Data collection took place throughout the breeding season of 2022, and the overall process used is summarised in Figure 14.

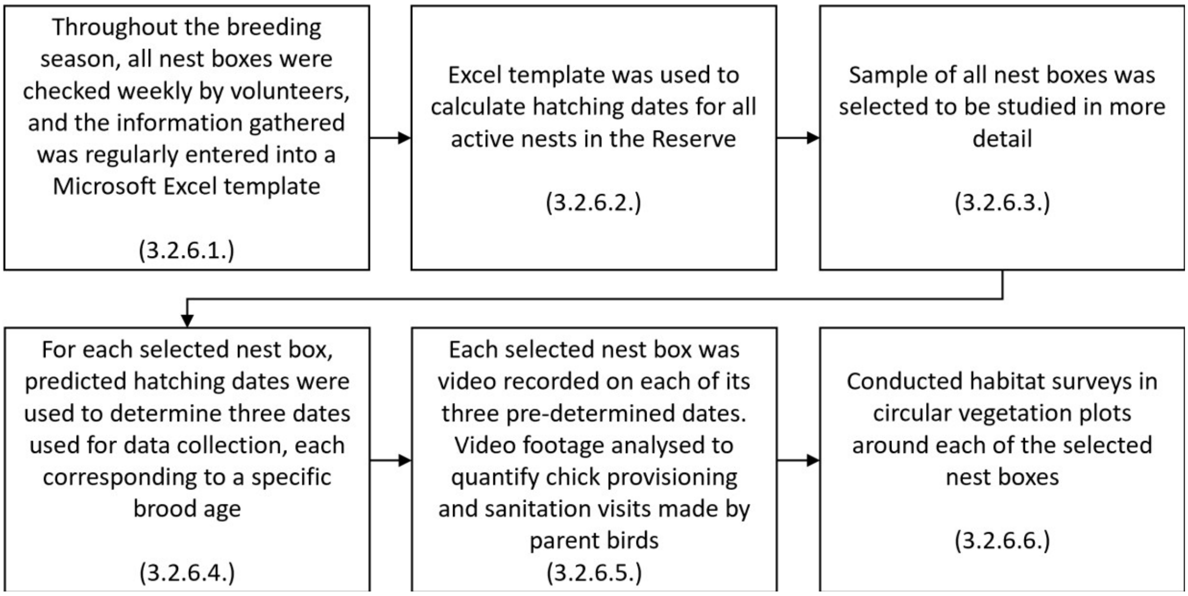
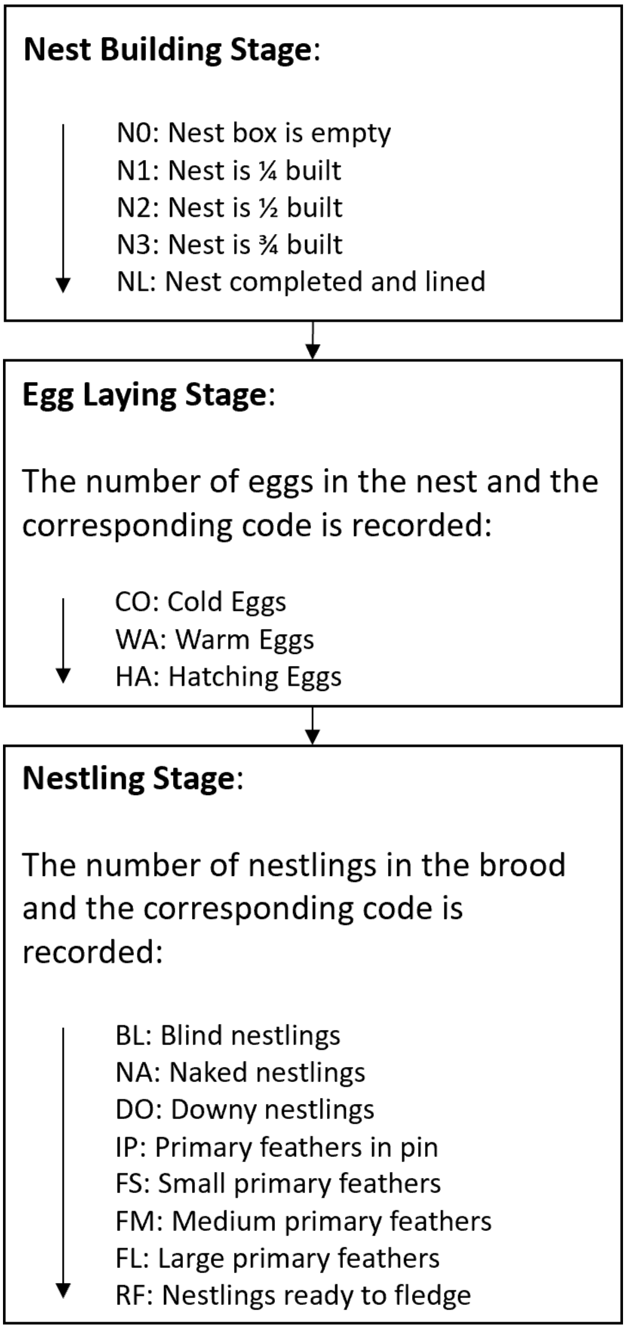


Figure 14. The methodological process used to collect data for a study examining the chick food proviosning in four different nest box types at Nagshead Nature Reserve in 2022. Brackets correspond to the section detailing each step.

3.2.6.1. Weekly Nest Box Checks

Throughout the breeding season in 2022, the nest boxes on each of the 12 nest box routes (see Figure 8) were checked weekly by volunteers who followed the methods and codes of conduct outlined for the BTO’s Nest Record Scheme (NRS) (Crick *et al.*, 2003b). Many scientific studies have shown that, when these guidelines are followed, nest checking has little to no significant effect on a bird’s breeding outcome (Götmark, 1992; MayerGross *et al.*, 1997; Ibanez-Alamo *et al.*, 2012). Volunteers used ladders to gain access to the boxes. Each nest box route had a corresponding weekly datasheet (known as the ‘nest box record sheet’), which was used by the volunteers to record status codes from the NRS, detailing the breeding stages in each nest box (Figure 15).



Nest Building Stage:

N0: Nest box is empty
N1: Nest is ¼ built
N2: Nest is ½ built
N3: Nest is ¾ built
NL: Nest completed and lined

Egg Laying Stage:

The number of eggs in the nest and the corresponding code is recorded:

CO: Cold Eggs
WA: Warm Eggs
HA: Hatching Eggs

Nestling Stage:

The number of nestlings in the brood and the corresponding code is recorded:

BL: Blind nestlings
NA: Naked nestlings
DO: Downy nestlings
IP: Primary feathers in pin
FS: Small primary feathers
FM: Medium primary feathers
FL: Large primary feathers
RF: Nestlings ready to fledge

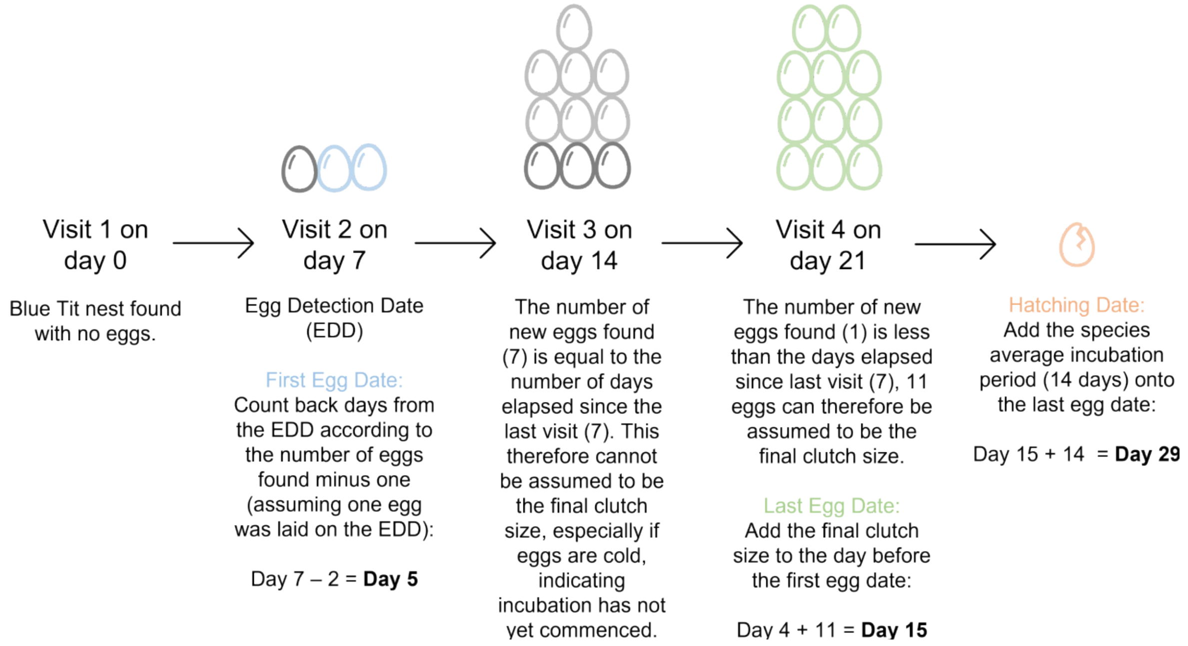
Figure 15. Examples of commonly used Nest-Record-Scheme status codes used to monitor the breeding stages of birds in nests.

To understand breeding progress in all occupied boxes across Nagshead, the weekly nest box record sheets were viewed and data were entered into a Microsoft Excel (Version: 2211) template. This provided a real-time resource containing information about the breeding parameters and nest box type of each active nest box in the Reserve. This was used throughout the breeding season to determine which nest boxes to study in more detail and when.

3.2.6.2. Calculating Hatching Dates

The Excel template was used to predict the hatching dates of each clutch. These calculations were based on the widely-accepted assumption that the female in most species of passerine will lay one egg every 24 hours, usually early in the morning (Gibb, 1950; Hinde, 1952; Perrins, 1996; Lundberg and Alatalo, 2010).

First egg dates (FEDs) were thus determined using the date on which the clutch was first recorded and counting back the same number of days as there were eggs in the clutch. This should be accurate when eggs were cold since incubation usually only begins after all eggs have been laid (Perrins and McCleery, 1989; Crick *et al.*, 2003a). Last egg dates (LEDs) were determined by adding the final clutch size, where one egg represents one day, to the day before the FEDs. Finally, estimated hatching dates were calculated by adding the usual species-specific incubation period to the LEDs. Each species' natural average incubation period was used, which comprised 16 days for the Nuthatch, and 14 days for the other three study species (Snow and Perrins, 1998; Robinson, 2005). A worked example of these calculations is shown in Figure 16.



Blue Tit nest found with no eggs.

Egg Detection Date (EDD)

First Egg Date: Count back days from the EDD according to the number of eggs found minus one (assuming one egg was laid on the EDD):

Day 7 – 2 = **Day 5**

The number of new eggs found (7) is equal to the number of days elapsed since the last visit (7). This therefore cannot be assumed to be the final clutch size, especially if eggs are cold, indicating incubation has not yet commenced.

The number of new eggs found (1) is less than the days elapsed since last visit (7), 11 eggs can therefore be assumed to be the final clutch size.

Last Egg Date: Add the final clutch size to the day before the first egg date:

Day 4 + 11 = **Day 15**

Hatching Date: Add the species average incubation period (14 days) onto the last egg date:

Day 15 + 14 = **Day 29**

Figure 16. Illustrative worked example of the method applied to use weekly nest box checks to calculate the hatching date of a clutch of Blue Tits, one of four focal species investigated in this study examining chick food provisioning at nest boxes at Nagshead Nature Reserve in spring 2022.

3.2.6.3. Selecting Nest Boxes

Due to the scale of the nest box scheme at Nagshead, it was not possible to collect parent visit data from all active nests in the Reserve, and specific boxes were therefore selected for additional study. This selection process was carried out using the Excel template to compare the uptake of each nest box type. As birds started breeding, it became clear there was a low occupancy of all predator-proofed nest box types. Therefore, to ensure similar sample sizes for each box type, a nest box pairing system was used, whereby predator-proofed boxes were selected and then paired with a standard nest box containing the same species.

Each standard nest box was chosen according to which had the most similar geographical location, hatching date and brood size (relative to its paired predator-proofed nest box). Although the subsequent analytical modelling (section 3.2.7.4) did not specifically factor in the pairing, this process helped to control these potentially confounding factors that are known to influence chick provisioning behaviour, and that could have, by chance, skewed the models (Wilkin *et al.*, 2009; García-Navas and Sanz, 2010; Hinks *et al.*, 2015).

3.2.6.4. Determining Observation Periods

Throughout postnatal development there is a general trend from greater to lesser dependence on parental care, which is reflected by the changing behaviour of the adults according to the needs of their offspring (Ricklefs, 1983). Therefore, to account for and measure potential relationships between chick age and provisioning, data for each selected nest box were collected at three stages of nestling development. At each of these stages, a date range of three consecutive days was calculated based on the number of days post-hatching. This consisted of an initial period two to four days post-hatching (young), a second period eight to 10 days post-hatching (mid) and a final period when birds were deemed ready to fledge (old). Because the timing of fledging is species-dependent, the final observation periods were calculated differently for each study species, using each species' average nestling period, thus ensuring nestlings were as close to fledging as possible, but had not fledged prior to observation. The species-specific final observation periods are shown in Table 4.

Table 4. The average nestling period (Snow and Perrins, 1998; Robinson, 2005) of the four focal species in a study examining chick food provisioning at nest boxes, and the corresponding final observation period used to record data when chicks were ready to fledge, at the end of the nestling period.

Species	Average Nestling Period (Days post-hatching)	Final Observation Period (Days post-hatching)
Pied Flycatcher	16 - 17	13 - 15
Eurasian Nuthatch	24 - 25	21 - 23
Great Tit	18 - 21	15 - 17
Blue Tit	18 - 21	15 - 17

Ultimately, only one of the three days for each observation period was used for data collection. The central day was considered optimum and selected whenever possible, with the first or third day being used whenever this was not possible. Overall, for each selected nest box, three dates for data collection were chosen, each corresponding to a different brood age (young, mid and old). The data collection methods deployed on these dates are discussed below (3.2.6.5.).

3.2.6.5. Data Collection

To avoid the presence of a human observer at the nest box disturbing the birds and biasing data collection (Burger, 1981; Frid and Dill, 2002; Blumstein *et al.*, 2005; Price, 2008; Botsch *et al.*, 2018), remote observation was used. The use of internal nest box cameras (Prinz *et al.*, 2016; Surmacki and Podkowa, 2022) was discounted for this study as it was not possible to modify the existing nest box setup to mount the cameras. Therefore, recordings were taken from outside of the nest box, from as great of a distance as possible to minimise disturbance. Afocal photography, commonly referred to as digiscoping, was used to accomplish this. The setup used is shown in Figure 17, and consisted of a 20×–60× magnification spotting scope attached to a *Manfrotto 290 light* tripod. An adapter was then used to attach a digital phone to the scope, allowing footage to be recorded through the eyepiece of the telescope. During periods of rain, a cover was placed around the phone for protection from water damage.

Figure 17. The digiscoping apparatus used to video record nest boxes during the 2022 study at Nagshead Nature Reserve. Video footage was then used to quantify and examine chick food proviosning between nest box types. Image taken by Joseph Marcus at the time and place of the study.

To ensure an adequate distance to minimise disturbance, whilst remaining close enough to record footage with a sufficient resolution, the telescope was positioned approximately 20 m (± 5 m) from the nest box being video recorded. To film a clear view of the adult bird entering the nest box, the telescope was positioned at a 45-80° upwards angle relative to the front panel of each nest box, such that the hole was clearly visible.

After the telescope was setup, the device was left to video record a nest box, before moving the scope to another nest box that needed recording that day. When determining the duration for each video recording it was important to ensure a sufficient number of visits to the nest was recorded, whilst also allowing time for multiple nest boxes to be recorded in one day. Chick provisioning rates in the Great Tit for example can range from five to 80 visits per hour (Bengtsson and Rydén, 1983; Wilkin *et al.*, 2009). Object neophobia was also important to account for, whereby a bird may alter its behaviour in response to the novel presence of the telescope (Greenberg, 1990, 2003; Cohen *et al.*, 2020). Therefore, the device was left to record for 40 minutes, where the first 10 minutes of footage was regarded as a settlement period and subsequently disregarded, thus leaving 30 minutes of footage where parent visits to the nest were quantified. This time period allowed for an adequate number of feeding visits to be recorded, whilst also allowing approximately 10 boxes to be monitored in one day whenever needed (accounting for the 40-minute recording time and up to 20 minutes walking time between boxes).

Analysing Video footage:

To allow more boxes to be recorded, video footage was analysed in the field, whilst another nest box was being video recorded. This was possible by rotating the use of two phones. Video footage was analysed using the android application *Video Stopwatch* (Version: 1.6.0.) published by *Seconds Count* and developed by *Mensh Technologies* (Florida, USA). Integrated video scrubbing meant recordings were analysed frame by frame. For each visit a bird made to the nest box, two markers were placed at the frames of the first and last point of contact a bird made with the nest box hole, with the application providing the time between the two points. As footage was recorded at 30 frames per second (fps), this allowed the time that elapsed for a bird to enter and then leave the nest box to be recorded with resolution of $33.\dot{3}$ milliseconds. This period is henceforth termed 'visit duration'.

On occasion, adult birds would enter the nest box after each other, and would therefore be inside the box at the same time. For Pied Flycatchers, this behaviour was not problematic as their clear sexual dimorphism enabled the distinction between individuals as they entered and left the cavity. However, for the other species, it was not always possible to distinguish between individual birds. In such situations, visit durations were recorded according to the order the birds entered and left the nest box. The time between the first bird to enter and the first bird to leave was recorded as one visit duration, and the time between the second bird to enter and the second bird to leave was recorded as another. This assumed birds left the nest box in the order they arrived and, although this may not have always been true, the combined provisioning durations of the two visits would still sum to an accurate total. However, it is worth noting the presence of another bird at the nest box could have affected these visit durations, either directly through physical avoidance, or indirectly via behavioural changes. However, as this behaviour was not common, and occurred naturally throughout data collection, these visit durations were not ignored.

It was important to consider other forms of parental care that could have co-occurred with chick provisioning, especially nest sanitation, whereby adult birds remove faecal sacs produced by the young (Blair and Tucker, 1941). Visit durations were therefore recorded under five headings according to whether the bird entered and/or left the nest box with either food, other materials (e.g. faecal sacs and nest material), both or neither:

1. **Feeding (only)**: Visits where birds were seen entering the nest box with food, and leaving without anything.
2. **Sanitation (only)**: Visits where birds were seen entering the nest box without anything, but leaving with waste material (e.g. faecal sacs).
3. **Feeding and sanitation**: Visits where birds were seen entering the nest box with food, and leaving the nest box with waste material (e.g. faecal sacs).
4. **Motivation unknown**: Visits where birds were not carrying anything into and out of the nest box.
5. **Undeterminable**: Visits where it was not possible to see if birds were carrying food or waste material.

To test the hypothesis that deep and guardian nest boxes may hinder a parent bird's ability to feed nestlings without directly entering the nest box, for each feeding visit a record was made of whether chicks were fed by adults leaning from the entrance or by fully entering the box. This leaning behaviour is shown in Figure 18.

Figure 18. Three successive frames (left to right) from a video recording taken during data collection, of a male Pied Flycatcher feeding nestlings at a standard nest box. Note the leaning behaviour used to accomplish this, whereby the male feeds the brood by leaning in from the entrance hole, without completely entering the nest box. Images taken from video recordings by Joseph Marcus at RSPB Nagshead Nature Reserve in spring 2022.

3.2.6.6. Habitat Surveying

Habitat type and vegetation structure can have various effects on the foraging behaviour of birds (Robinson and Holmes, 1982, 1984), and are therefore likely to have indirect effects on chick provisioning. Due to the possible variation in habitat caused by the old fence line and historic sheep grazing, a habitat survey was conducted to quantify key aspects of vegetation density and species richness. This was done using a survey technique where the trees supporting selected nest boxes were used as the centre point of circular vegetation plots (Lindsey *et al*., 1958; James and Shugart, 1970; Brennan *et al*., 1999). A radius of 5 m from the outer trunk of each focal tree was used for each circular plot, providing an overall plot size of approximately 0.01 ha after the diameter of the focal tree was accounted for. These plots were smaller than the the 0.04 ha plots recommended by James and Shugart (1970). However, unlike James and Shugart (1970), who's aim was to provide an estimate of tree density and dominance for a wider area, my habitat surveys aimed to quantify the vegitation density immidiately surrounding each nest box, assesing what is likley to impact chick provisioning.

Within these plots a variety of habitat variables were measured to provide a rudimentary understanding of the vegetation structure within the breeding territories of studied birds. The 12 variables are listed in Table 5 and were chosen with regards to what is likely to affect prey abundance and diversity, thus affecting foraging times and feeding frequency (Holmes and Robinson, 1981; Robinson and Holmes, 1982, 1984; Wilkin *et al*., 2009). Counts of beech and oak tree were recorded alongside counts of all tree species as these were deemed to be ecologically key food sources for the four avian study species (Gibb, 1954). Habitat surveying was conducted after data collection had finished in late spring, once the final subset of nest boxes with parent visit data was known.

Table 5. Description of the 12 variables measured during habitat surveys at five metre circular vegetation plots surrounding nest boxes in Nagshead Nature Reserve in 2022. Habitat survey results were used as predictor variables in statistical analysis which aimed to examine chick food proviosning in four different types of nest boxes.

Habitat Variable	Description
Number of Mature Trees (All Species)	Frequency counts of mature trees of any species, including the tree at the centre of the plot supporting the nest box. ‘Mature’ was defined as any tree over 2 m tall with a distinguishable established canopy
Number of mature Oak Trees	Frequency counts of mature oak trees, including the tree at the centre of the plot supporting the nest box.
Number of Mature Beech Trees	Frequency counts of mature beech trees. This did not include the centre tree as all nest boxes at Nagshead are located on species of oak.
Number of Saplings (All Species)	Frequency counts of saplings of any species. Saplings were defined as any tree under 2 m tall with a main trunk diameter of less than 5 cm.
Number of Oak Saplings	Frequency counts of oak sapling.
Number of Beech Saplings	Frequency counts of beech saplings.

Percentage Canopy Cover	Percentage canopy cover was recorded using the *CanopyCapture* android application (version: 1.0.2), developed by Nikhil Patel. Once the mobile phone is aligned so that it is level with the ground, the application takes a picture of the forest canopy, from which it accurately calculates the percentage canopy cover. For each vegetation plot, the photo was taken at shoulder height, standing 1 m in front of, but facing away from, the nest box.
Percentage Shrub Cover	From an ariel perspective, an estimation of the percentage of ground covered by vegetation in the shrub layer. This mainly included species of Holly, Bramble and Hawthorn.
Percentage Bracken Cover	From an ariel perspective, an estimation of the percentage of ground covered by bracken species.
Percentage Bare Ground and Leaf Litter cover	From an ariel perspective, an estimation of the percentage of ground left exposed, or covered by leaf litter.
Species Richness of Trees	The number of different species of tree, included both saplings and mature trees.
Species Richness of Shrubs	The number of different species within both the shrub and field layer, not including species of trees/saplings and mosses, or vegetation in the herb and ground layer.

3.2.7. Statistical Analysis

3.2.7.1. Dimension Reduction of Habitat Survey Data

It was not appropriate to include all 12 variables from the habitat survey as predictor variables in statistical models. A dimension reduction technique was therefore used to condense all of the variables into composite 'habitat' variables, where any patterns/trends would still be retained. A principal components analysis (PCA) on all of the 12 habitat variables was therefore conducted in *R studio* (version: 4.2.1 (2022)), using the '*prcomp'* function within the inbuilt '*stats*' package. The PCA was carried out on a correlation matrix of the original variables. Data were therefore scaled to have equal standard deviations before running the PCA, ensuring all variables had the same weight. This was achieved by setting the '*scale*' argument within the '*prcomp*' function to '*TRUE'*.

Because the PCA returned as many principal components as there were original variables (n = 12 here), listed from the highest to lowest percent variance explanation, two selection criteria (Valle *et al.*, 1999) were used to establish how many were appropriate to retain and use in subsequent analysis. These criteria are detailed below, and are visualised with the use of a scree plot (Figure 19).

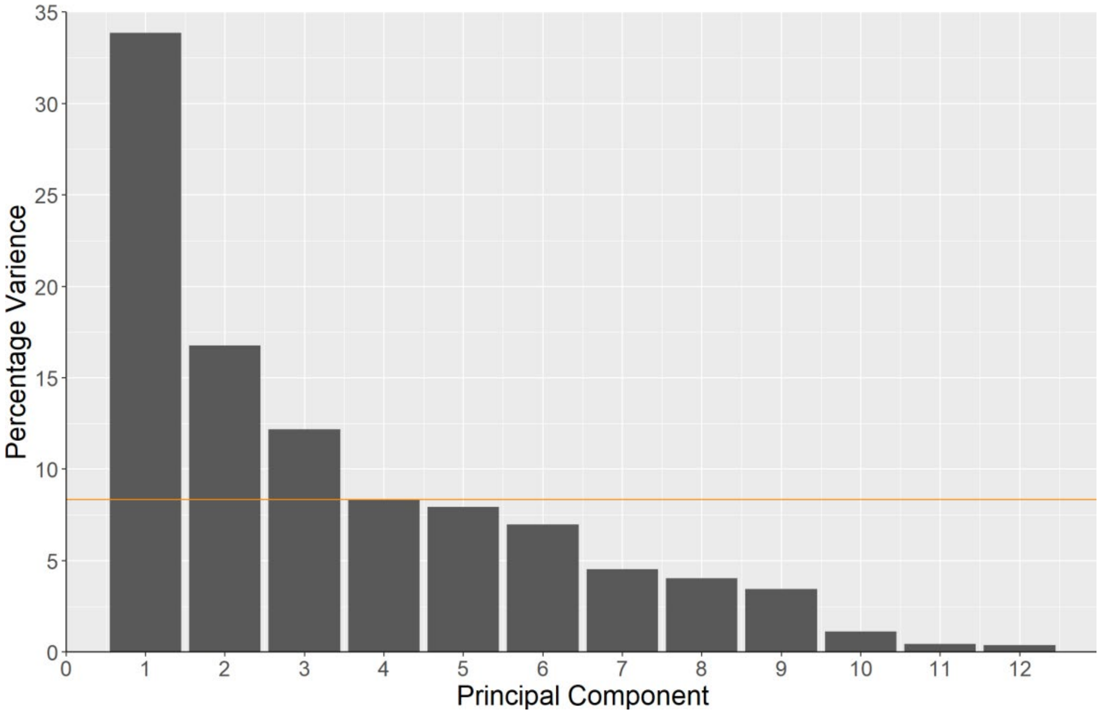


Figure 19. The percentage variance for each principal component computed from a principal component analysis of habitat data collected at circular vegetation plots surrounding nest boxes in Nagshead Nature Reserve in 2022. The orange line shows the average percent variance of 8.33% (100% ÷ 12). Results from the principal components analysis were used as predictor variables in statistical analysis which aimed to examine chick food proviosning in four different types of nest boxes.

1. **Average eigenvalue**: The orange line in Figure 19, shows the average percent variance of 8.33% for all 12 principal components (100% ÷ 12). Principal components five to 12 had a percent variance below this average, and were therefore deemed non-significant as they offered less than one variable's worth of information.
2. **Scree Test on Percent Variance**: The scree plot in Figure 19 shows a clear drop in the percentage variance between principal components one and two, where the rate of change visibly plateaued after this point. This highlights an 'elbow' in the scree plot, and principal component two to 12 were therefore deemed non-significant.

Principal component one (PC1) was therefore considered significant, and included as a predictor variable in statistical models (Section 3.2.7.4). This provided a cumulative percentage variance of 33.85%, which was deemed sufficient due to the large number of habitat variables included in the CA.

The amount each habitat variable contributed to PC1 was assessed using the components factor loadings. Significant factor loadings were determined based on whether they were larger than a calculated threshold. This threshold was calculated using the formula $\sqrt{1/12} = 0.289$ (where 12 referred to the number of habitat variables), and was based on the understanding that the square of all factor loadings sums to one. The value 0.289 therefore represents what all factor loadings would be if each habitat variable contributed the same amount. Computed factor loadings greater than this value were considered significant.

3.2.7.2. Defining Chick Provisioning Visits for Analysis

For each parental visit made to a nest, there are other forms of parental care that could have co-occurred with chick provisioning behaviours, particularly nest sanitation (e.g. removing of faecal sacs) and brooding (Banbura *et al.*, 2001). Therefore, in order to analyse parent visits where only chick provisioning occurred, it was necessary to identify and distinguish these from other visits.

As previously mentioned in section 3.2.6.5, visit durations were recorded under five headings according to whether birds were observed carrying food items and/or waste material. In the cases of visits under headings one ('feeding only') and three ('feeding and sanitation'), was there certainty in the feeding of nestlings (or, more technically, certainty that prey had been taken into the nest box for the purpose of feeding nestlings). However, when analysing the video footage frame by frame, birds were often obscured by motion blur, and by the time they had stopped moving, their bill had already entered the nest box. Therefore, it was often impossible to observe whether birds were carrying food items into the nest box, and the recorded ‘feeding only’ visits were likely an under-representation of the actual feeding events that occurred.

Therefore, the approach taken was to assume a parental visit was solely for chick provisioning only if all other reasons for a visit could be excluded. Assuming there are three main reasons an adult bird would visit the nest (i.e. chick provisioning, nest sanitation and brooding) (Banbura *et al.*, 2001), by excluding visits where sanitation and brooding occurred, it was assumed the remaining visits were for chick provisioning purposes only.

1. **Exclusion of Sanitation only visits**: It was assumed all parental visits where nest sanitation occurred were reliably recorded under headings two (‘sanitation only’) and three (‘feeding and sanitation’). This was reasonable as motion blur was not an issue when birds were leaving the nest box because they exited bill-first, and usually fairly slowly. It was therefore clearly visible when birds were leaving with waste material, especially large and conspicuous white faecal sacs.
2. **Exclusion of visits likely to have involved brooding**: Any visits longer than 30 seconds were assumed to involve brooding behaviours, and were therefore excluded. This upper limit of 30 seconds was chosen based on the assumption that parental visits where food was bought into the box and waste material removed (‘feeding and sanitation’), should have had the longest visit duration compared to visits where these behaviours occurred independently (‘feeding only’ and ‘sanitation only’). Because ‘feeding and sanitation’ visits seldom exceeded 30 seconds, it was assumed the visit durations for parental visits where only chick provisioning occurred should not have exceeded this duration.

Thus, with the exclusion of parental visits that lasted longer than 30 seconds, any visit under headings one (‘feeding only’) and five (‘undeterminable’) were assumed to be for only chick provisioning. Such visits are henceforth termed chick provisioning visits, and were used in data manipulation and analysis (sections 3.2.7.3 and 3.2.7.4).

3.2.7.3. Data Manipulation

As detailed in the field methods (3.2.6) each nest box included in the study was video recorded for 30 minutes at three different stages of brood age. For each of these 30 minute recordings, every visit a parental bird made to the nest box was recorded by measuring the time taken for the bird to land on, enter and then leave the nest box (visit duration).

These raw data were manipulated in Microsoft Excel (version: 2211), providing five different metrics of quantifying parental visits for each nest box and corresponding brood age:

1. **Mean chick provisioning duration**: The mean visit duration of all chick provisioning visits, for each 30 minute recording.
2. **Visit frequency**: All parental visits were tallied, providing the number of times adult birds visited the nest during each 30 minute recording, irrespective of the visit duration.
3. **Chick provisioning frequency**: Chick provisioning visits were tallied, providing the number of times (for each 30 minute recording) adult birds visited the nest to feed nestlings, irrespective of the visit duration.
4. **Total time spent at the nest**: The summation of all visit durations, providing the total time adult birds were at or in the nest box during each 30 minute recording.
5. **Total time spent chick provisioning**: The summation of visit durations for only chick provisioning visits, providing the total time adult birds spent provisioning nestlings during each 30 minute recording.

The above metrics were then analysed as response variables in multivariate models to assess the potential influence of numerous categorical predictors (factors) and continuous predictors (covariates) (section 3.2.7.4). Metrics for fledging success and the expression of leaning behaviours were also assessed and these were calculated as follows:

6. **Leaning behaviour**: The percentage of chick provisioning visits where birds were seen exhibiting leaning behaviours.

7. **Fledging success**: The percentage of hatched eggs that fledged. The number of hatched eggs was used instead of the final clutch size to avoid results being biased by unhatched eggs.

3.2.7.4. Generalised Linear Models

Generalised linear models (GLMs) were used for multivariate analysis to allow for the inclusion of categorical predictors, and to account for various non-parametric distributions amongst response variables. Using *R studio* (version: 4.2.1 (2022)), the '*glm*' function in the in-built '*stats'* package was used to run GLMs on the metrics previously detailed in section 3.2.7.3. All seven models are listed in Table 6.

Akaike's Information Criterion (AIC) was used to compare and select models with different predictor variables, and to determine which of various error distributions and link functions was optimal. The Poisson family with a logarithmic link is typically used for count data (Field *et al.*, 2012), and was therefore applied to GLMs where the number of visits was used as the dependent variable (metrics two and three). All other response variables were continuous with a non-normal positive skew, and gamma error distributions were therefore utilised. In such situations, because GLMs with a Gamma distribution can only be run on positive data greater than zero, a constant of +1 was added to the response variable. Whenever possible, these continuous metrics were normalised using a logarithmic transformation, and a Gaussian distribution was then used for the GLM. This method was applied to metrics one and four, and reduced AIC by 589 and 1,427, respectively. Normality was tested using Shapiro-Wilk tests, as well as assessing skewness and kurtosis.

Overall model significance was assessed using the model Chi-squared statistic, which measured the difference between the model and its corresponding null model, which included no predictors other than the constant/intercept (Field *et al.*, 2012). For significant models, ANOVA tables and corresponding likelihood ratio Chi-squared tests were used to obtain significance levels for each of the included predictor variables.

Table 6. The seven generalised linear models computed in order to analyse the chick food provisioning of four study species nesting in various types of nest boxes at Nagshead Nature Reserve in 2022. The corresponding methods and parameters used for each model are listed.

Dependent Variables (Model I.D.)	Data Transformation	GLM Parameters	
		Family / Distribution	Link Function
Mean Chick Provisioning Duration (1)	Log	Gaussian	Identity
Visit Frequency (2)	N/A	Poisson	Log
Chick Provisioning Frequency (3)	N/A	Poisson	Log
Total Time Spent at the Nest (4)	Log	Gaussian	Identity
Total Time Spent Chick Provisioning (5)	Constant (+1)	Gamma	Log
Leaning Behaviour (6)	Constant (+1)	Gamma	Log
Fledging Success (7)	Constant (+1)	Gamma	Log

For factorial predictor variables, the GLMs only computed comparisons between each level and the first/reference group. Therefore, for significant factors, the '*glht*' function in the '*multcomp'* package was used to run multiple pairwise comparisons of means with Tukey contrasts, providing correlations and significance levels between every level. When running pairwise comparisons it is common to use p-value adjustments as running extra evaluations increases the chances of incorrectly finding statistical significance (type 1 errors leading to false positive results). However, in doing so, the possibility of type 2 errors increases, whereby significant results may be missed (false negative) (Feise, 2002). In this instance, research is exploratory, and it was therefore decided to not adjust p-values for the multiple comparisons. By risking type 1 errors, it is hoped further targeted research, with comparatively larger sample sizes, will clarify any potential relationships found between predictor and response variables. Estimated Marginal Means (EMMs) were also used to provide adjusted averages for each model, which accounted for the effects caused by alternative predictor variables.

Selection of Predictor Variables:

Despite using as many nesting attempts in predator-proof nest boxes at the study site in the focal breeding season as possible, smaller than expected sample sizes were gathered during data collection. Therefore, due to the ratio between the large number of independent variables being considered, and small sample sizes, it was imperative to avoid overfitting the GLMs. Running a full model with all predictor variables was not appropriate as the inclusion of non-significant parameters would have biased estimates (Ginzburg and Jensen, 2004). Stepwise variable selection was therefore used with the intention of producing the most parsimonious models that explain the most amount of variation in a dataset, whilst using the fewest possible number of predictor variables (Aho *et al.*, 2014). Stepwise selection provided a simple, yet objective and reproduceable method of selecting optimal explanatory variables (Murtaugh, 2009; Hegyi and Garamszegi, 2011). Akaike's information criterion (AIC) was used as the information-theoretic measure to assess the model fit at each step of the algorithm (Yamashita *et al.*, 2007; Murtaugh, 2009). To assess the combined predictive ability of all predictor variables (Mantel, 1970), a backward elimination direction was used, whereby the stepwise selection started with the full model and sequentially removed individual predictors that led to the largest reduction in AIC. This process was repeated until the deletion of any remaining variables did not cause a statistically significant reduction in the model's fit. The stepwise selection was conducted using the '*step*' function in the '*stats*' package of *R studio*. Models after stepwise variable selection had been conducted are hereafter referred to as minimum adequate models (MAMs).

All predictor variables included in each of the seven full models, before stepwise selection methods were applied, are listed and described in Table 7. For inclusion in the GLMs, factors were categorised on a discrete numeric scale, where for example, Pied Flycatcher and Eurasian Nuthatch were classified as 1 and 2, respectively.

It was initially planned to include interaction terms in statistical models to account for any effects in the response variables that may be caused by multiple interacting predictors. However, complex models can perform poorly with reduced datasets (Wisz *et al.*, 2008), and compared to main effects, larger sample sizes were needed to predict estimates from interaction terms. Therefore this approach was not undertaken.

Table 7. Description of 13 independent variables used in Generalized linear models which aimed to examine the chick food provisioning of four study species nesting in various types of nest boxes at Nagshead Nature Reserve in 2022. The models each independent variable was included in is shown in superscript with reference to the model I.D. in Table 6

Predictor Variables $^{(\text{Model Inclusion})}$	Description
<u>Factors</u>:	
Species $^{(1,2,3,4,5,6,7)}$	Detailing which of the 4 study species a brood belongs too: Pied Flycatcher (PF), Eurasian Nuthatch (NH), Great Tit (GT) or Blue Tit (BT).
Brood Age $^{(1,2,3,4,5,6)}$	Categorical variable referring to the three brood ages outlined in section 3.2.6.4 (Young, Mid, Old)
Box Type $^{(1,2,3,4,5,6,7)}$	Detailing which of the four box types a brood resides in: Standard (S), Woodcrete (W) Deep (D) and Guardian tube (G).
Nest Box Orientation $^{(1,2,3,4,5,7)}$	The angle from true north the entrance hole of each nest box faces; simplified and categorised according to the 8-point compass.
Rainfall $^{(1,2,3,4,5,6)}$	The predominant rainfall pattern during each video recording. Categorised into dry, intermittent drizzle and raining. The latter was defined as any consistent rainfall more intense than drizzle.
Time of Day $^{(1,2,3,4,5,6)}$	The time of day (British summer time) at the start of each video recording. Split into five categories referring to different periods of the day: early morning (EM: 09.00 to 11.00hrs), late morning (LM: 11.01 to 13.00hrs), early afternoon (EA: 13.01 to 15.00hrs), late afternoon (LA: 15.01 to 17.00hrs) and evening (E: 17.01 to 19.00hrs).

Covariates:	
Hatching Date (1,2,3,4,5,7)	The predicted synchronous hatching date of each clutch. Converted into a continuous scale where the 1st of May equalled 1, and every day thereafter referred to an addition of 1 (e.g. 11th may would equal 11).
Brood Size (1,2,3,4,5,6,7)	For each nest box and corresponding brood age, brood size was calculated based on the number of living chicks last seen during weekly nest box checks. This accounted for unhatched eggs and chicks that had died throughout the breeding season.
Leaning Behaviour (1,2,3,4,5)	The percentage of the total number of visits where birds were seen to feed the chicks by leaning into the nest box from the entrance hole, without directly entering the box.
Habitat (1,2,3,4,5,7)	Composite variable from a principal component analysis (PCA), containing information from 12 habitat variables recorded from vegetation density and richness surveys (Refer to section 3.2.7.1).
Temperature (1,2,3,4,5)	The air temperature (°C) at the start of each video recording. Temperature readings were taken from the *Staverton Private* weather station in Gloucestershire, UK.
Mean Chick Provisioning Duration (2,3)	The mean visit duration of all chick provisioning visits, for each 30 minute recording. Only included in the visit frequency and chick provisioning frequency GLM to determine if increases/decreases in mean visit durations were substantial enough to affect visit frequency.
Visit frequency (7)	The total number of times adult birds visited the nest. Only included in the fledging success GLM to determine if visit frequency affected breeding success.

3.3. Results

3.3.1. Sample Size

A smaller-than-expected sample size was collected throughout the data collection period. A total of 51 active nests were included in the study, 17 of which were in a predator-proof nest box design. The sample sizes according to each species and nest box type are shown in Tables 8, 9 and 10, and the digital terrain model (DTM) in Figure 20, shows their geographic location within the nest box area at Nagshead.

Table 8. The number of nest boxes included in the study which aimed to examine chick food provisioning in different nest box types at Nagshead Nature Reserve in spring 2022. Grouped according to species and nest box type.

Nest Box Type	Number of Nest Boxes Studied			
	Pied Flycatcher	Eurasian Nuthatch	Great Tit	Blue Tit
Standard	13	2	11	8
Woodcrete	1	1	3	2
Deep	0	1	4	3
Guardian Tube	0	0	2	0

3.3.2. Habitat Survey

3.3.2.1. Baseline Results

Table 11 shows the summary statistics from each classification recorded during the habitat survey. The mean number of trees shows a relatively low density of trees in the circular vegetation plots surrounding the nest boxes, with an mean of 2.41 (±1.55). Despite this, canopy cover is still high across the reserve, suggestive of the semi-ancient trees across the site. The low number of oak saplings (0.02 ±0.14) highlights the minimal oak regeneration in the site. Generally, standard deviations for most categories are sizable, especially for measures of percentage ground cover. This suggests variation in the habitat across the nest box area

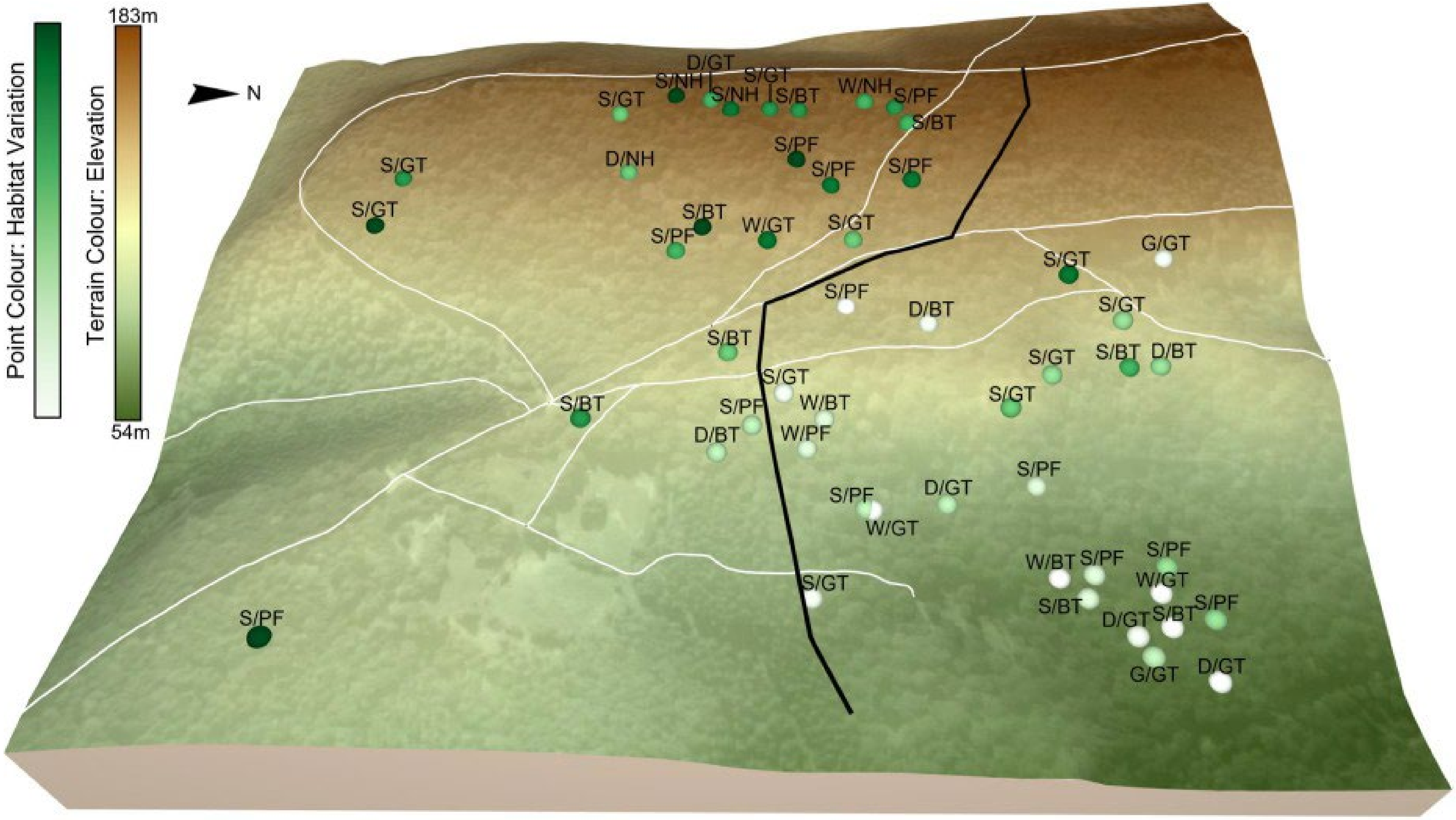


Figure 20. Digital terrain model (2x exaggeration) of the nest box area at RSPB Nagshead Nature Reserve, created using the Qgis2threejs tool in QGIS (version: 3.22.4). Points correspond to each nest included in the 2022 study at Nagshead Nature Reserve in 2022, which examined chick food provisioning in four focal species nesting in four different nest box types. Labels refer to the nest box type (S: Standard, W: Woodcrete, D: Deep and G: Guardian), followed by species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit and BT: Blue Tit). Habitat variation (point colour) corresponds to principal component one, from a dimension reduction analysis of habitat survey data collected from circular vegetation plots surrounding each nest box. White lines are public access footpaths and the black line corresponds to an old fence line, where the North side was historically grazed by sheep. Satellite Image: © Google Earth data (2022). All rights reserved (2020). Elevation Data: OS Terrain 5 [ASC geospatial data], Scale 1:10000, Tiles: so60nw,so61sw, Updated: 26 February 2022, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, <https://digimap.edina.ac.uk>, Downloaded: 2022-07-01 16:09:45.985

Table 9. The number of occupied nest boxes, and the corresponding number of failed and successful (≥1 fledgling) broods, in the Nagshead Nature Reserve nest box scheme in 2022, grouped according to species and nest box type.

	Number of Nest Boxes									
		Species					Box Type			
	Total	Blue Tit	Great Tit	Nuthatch	Pied Flycatcher	Redstart	Standard	Woodcrete	Deep	Guardian Tube
All Boxes	249	132	82	17	17	1	201	28	18	2
Successful Broods	159	76	53	17	13	0	87	14	12	1
Failed Broods	90	56	29	0	4	1	114	14	6	1

Table 10. The number of nest boxes included in a 2022 study at Nagshead Nature Reserve examining the effects of nest box type on the chick provisioning behaviour of woodland passerines. Data for each brood was collected at three different stages post-hatching to account for nestling age, and the number of studied nest boxes where all three stages of brood age was recorded (Full dataset), and where some ages were missed (reduced dataset).

	Number of Nest Boxes									
		Species					Box Type			
	Total	Blue Tit	Great Tit	Nuthatch	Pied Flycatcher	Redstart	Standard	Woodcrete	Deep	Guardian Tube
All Boxes	51	13	20	4	14	0	34	7	8	2
Full dataset	33	6	13	4	10	0	21	5	6	1
Reduced dataset	18	7	7	0	4	0	13	2	2	1

Table 11. Summary statistics for 12 variables collected during habitat surveys at five metre circular vegetation plots surrounding nest boxes in Nagshead Nature Reserve in 2022. Habitat survey results were used as predictor variables in statistical analysis which aimed to examine chick food proviosning of four small woodland passerines in four different types of nest box.

	Habitat Survey Classifications											
	Number of Trees			Number of Saplings			Canopy	Percentage Ground Cover			Species Richness	
	All Species	Oak	Beech	All Species	Oak	Beech	Percentage Cover	Shrubs	Bracken	Bare Ground and Leaf Litter	Trees	Shrubs
Mean	2.41	1.35	0.39	0.96	0.02	0.61	84.31	19.00	37.04	68.73	1.96	2.33
Standard Deviation	1.55	0.62	0.84	2.31	0.14	2.14	9.57	25.46	37.66	29.72	1.05	0.92

3.3.2.2. Ordination of Habitat Variables

The factor loading of each habitat variable on the first principal component axis (PC1) are shown in Table 12. The greater the loading is from zero, the stronger an effect of the variable. Significant factor loadings are shown in bold, and are greater than the threshold calculated in section 3.2.7.1 (i.e., + 0.289). The species richness of trees, the number of mature trees, and the bare ground and canopy cover all have a strong positive correlation to PC1, whereas the bracken cover has a strong negative correlation.

Table 12. Factor loadings from a principal component analysis of 12 habitat variables collected from five metre radius plots around nest boxes in Nagshead Nature Reserve in 2022. The principal component was used as a predictor variable in statistical analysis to examine the chick food proviosning of four small woodland passerines in four different types of nest box. Factor loadings in bold are greater than what all loadings would be if each habitat variable contributed the same amount (± 0.289).

Habitat Variable	Principal Component 1
Number of Mature Trees	**0.385**
Number of Mature Oak Trees	0.091
Number of Mature Beech Trees	0.252
Number of Saplings	0.219
Number of Oak Saplings	0.106
Number of Beech Saplings	0.156
Shrub Cover	0.234
Bracken Cover	**-0.456**
Bare Ground Cover	**0.419**
Canopy Cover	**0.320**
Tree Species Richness	**0.395**
Shrub Species Richness	-0.006

In order to visualise the habitat variation across the nest box area, the PC1 scores for each nest box were added to the DTM in Figure 20. Variation in habitat across the nest box area is evident, with nest boxes located on the grazed side of the old fence line having relatively lower PC1 scores than those located in the un-grazed section (south of the fence line). This habitat difference between the grazed and un-grazed areas is further visualised in Figure 21, where PC1 scores have been plotted against PC2 scores in a biplot. Despite some overlap, this shows two clear groups in the habitat which correlate to the grazed and un-grazed sections. Comparing this with the factor loadings in Table 12, the un-grazed section has more bare ground cover and a higher number and species richness of trees, corresponding with a larger percentage canopy cover. The north side of the fence in the grazed section on the other hand has considerably higher percentage bracken cover.

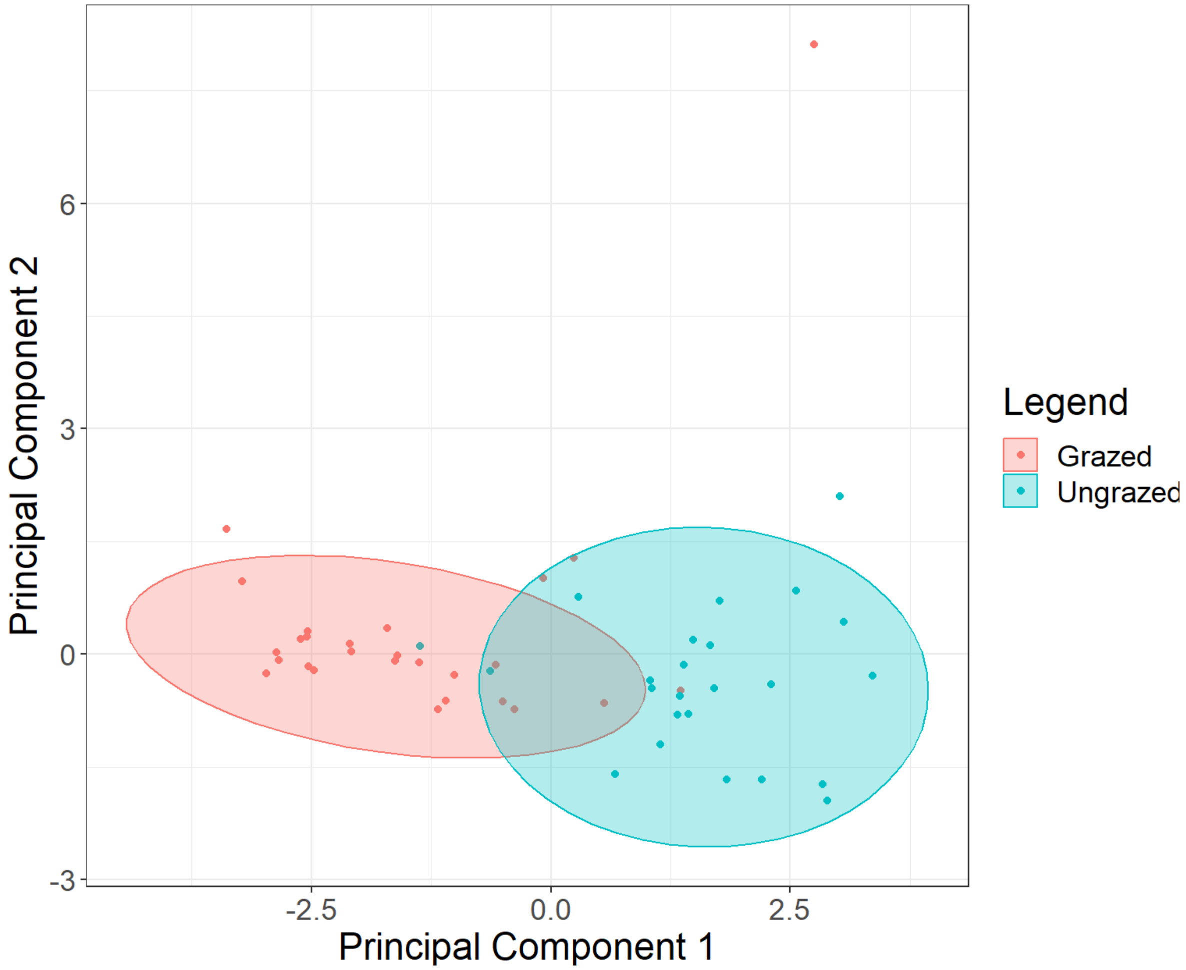


Figure 21. Nest boxes included in the 2022 study at Nagshead Nature Reserve, plotted according to their corresponding principal component one and two score from a principal component analysis of habitat data collected from five metre radius plots around each nest box. Nest boxes are coloured according to whether they are located out of (un-grazed) or in (grazed) a historically grazed section of Nagshead Nature Reserve. Principal component one was used in the study as a predictor variable in statistical analysis which aimed to examine the chick food proviosning of four small woodland passerines in four different types of nest box.

3.3.3. Leaning Behaviour

As shown in the histogram in Figure 22, leaning behaviours were seen infrequently, appearing to be an individual-specific behaviour. Specific birds appeared to either express the behaviour for the majority of visits, or seldom use the behaviour for feeding nestlings (i.e. it seemed to be bird-specific not situation-specific).

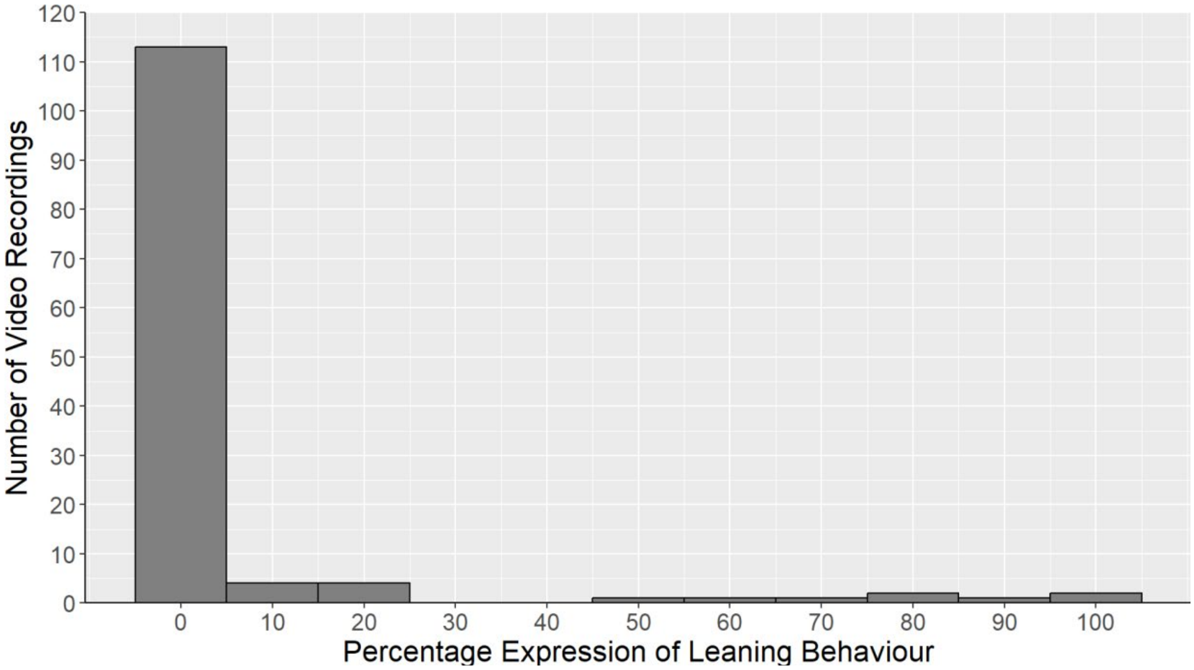


Figure 22. The number of 30 minute video recordings of nest boxes, distributed according to their corresponding percentage expression of leaning behaviour (i.e., the percentage of chick provisioning visits where leaning behaviours were expressed, split into 10% bins). Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines.

Figure 23 shows the mean percentage of leaning behaviours expressed for each species, box type and brood age. These raw means show Eurasian Nuthatches exhibited leaning behaviours the most, whereas Blue Tits and Great Tits seldom provisioned chicks in this manner. Generally, with the exception of guardian tubes (where the prevalence of leaning behaviours is seemingly lower), expression of this behaviour was similar between box types. The prevalence of leaning behaviours increased as the age of the brood increased, being the highest when nestlings were ready to fledge (old). Sizable standard deviations highlight a large spread of data around these means.

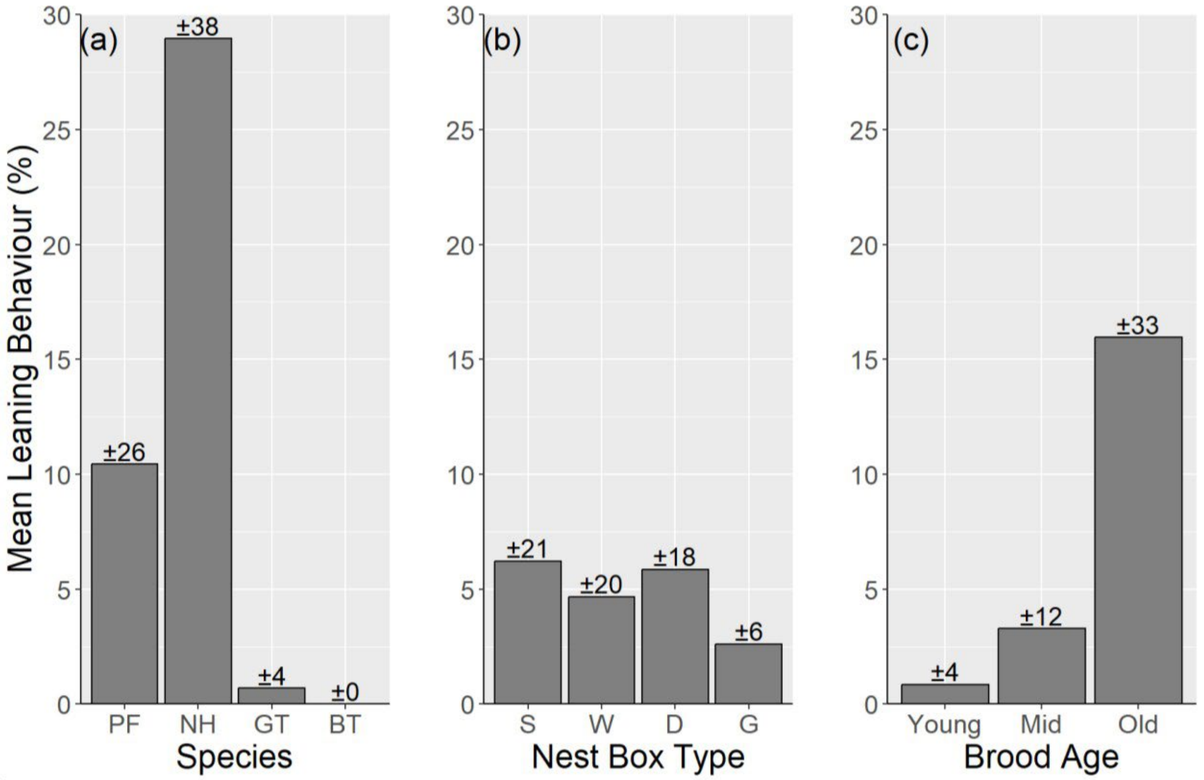


Figure 23. The mean percentage of chick provisioning visits where leaning behaviours were expressed (± standard deviation) according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge). Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines.

The leaning behaviour GLM was significant ($\chi^2_{(5)} = 233.21$, $p < 0.001$, AIC = 534.80) and the results are shown in Table 13. Only species and brood age were included in the MAM, both of which were significant effects. For these two predictor variables, pairwise comparisons are summarised in Table 14, alongside the corresponding EMMs in Figure 24. Generally, the original patterns shown by the raw means in Figure 23 persist, where the expression of leaning behaviours was significantly higher for Eurasian Nuthatch and Pied Flycatcher, and during observation periods when nestlings were ready to fledge.

Table 13. Generalised linear model assessing the influence of various predictor variables on the expression of leaning behaviours. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. p values in bold are greater than 0.05 and deemed significant.

Predictor Variable	d.f.	χ^2	p	Explanation
Factors:				
Species	3	69.11	**<0.001**	Highest for Eurasian Nuthatch and then Pied Flycatcher (Table 14, Figure 24a)
Brood Age	2	24.01	**<0.001**	Highest when chicks were older (Table 14, Figure 24b)

Table 14. Significant pairwise comparisons for significant factors from a generalised linear model assessing the expression of leaning behaviours. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Significance codes: *** < 0.001, ** < 0.01, * < 0.05. †PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit. ‡Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, old: ready to fledge.

Pairwise Comparisons	Test Statistic			
	Standard Error	t	p	Significance
Species†:				
NH > PF	0.46	2.06	0.039	*
NH > GT	0.44	6.00	<0.001	***
NH > BT	0.47	5.89	<0.001	***
PF > GT	0.30	5.62	<0.001	***
PF > BT	0.34	5.33	<0.001	***
Brood Age‡:				
Old > Young	0.30	5.02	<0.001	***
Old > Mid	0.31	3.37	<0.001	***

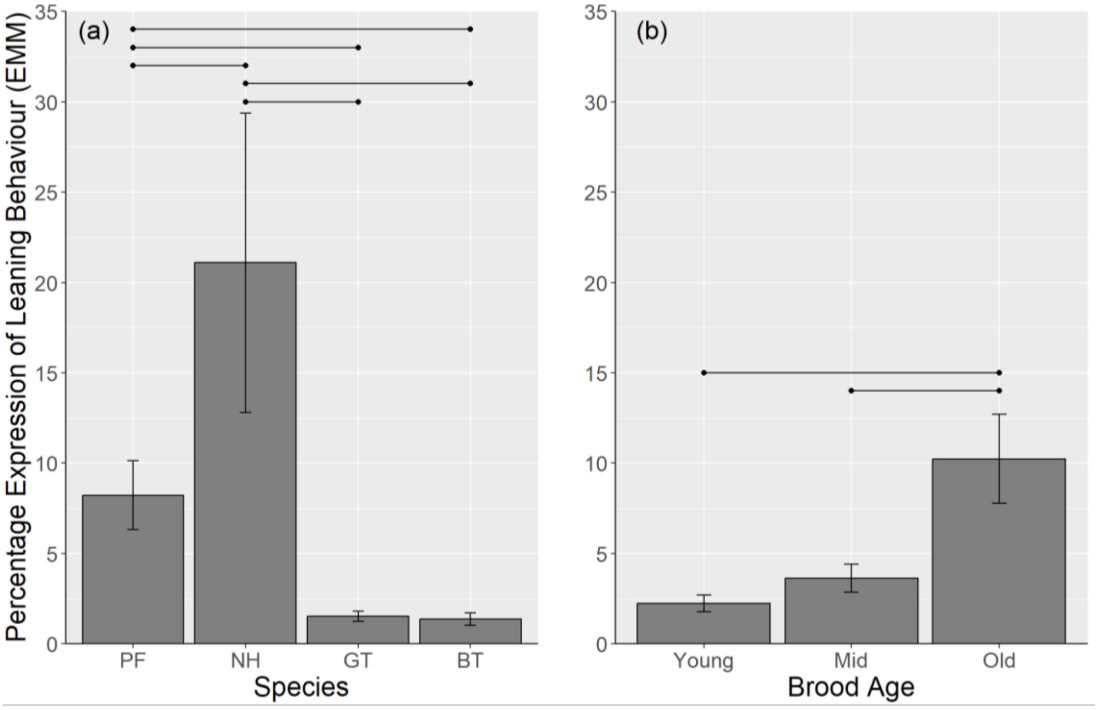


Figure 24. Estimated Marginal Means (EMM) of the percentage of chick provisioning visits where leaning behaviours were expressed, according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit) and (b) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge) from a generalised linear model. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Error bars refer to the standard error, and connecting lines show significant differences from pairwise comparisons.

3.3.4. Mean Chick Provisioning Duration

Boxplots in Figure 25 show the spread of data for the mean chick provisioning durations according to species, nest box type and brood age. Generally, there is some variation amongst the data with outliers mainly being prolonged visits greater than 15 seconds. Chick provisioning durations are higher for Great Tits and deep nest boxes, and seemingly decrease with brood age.

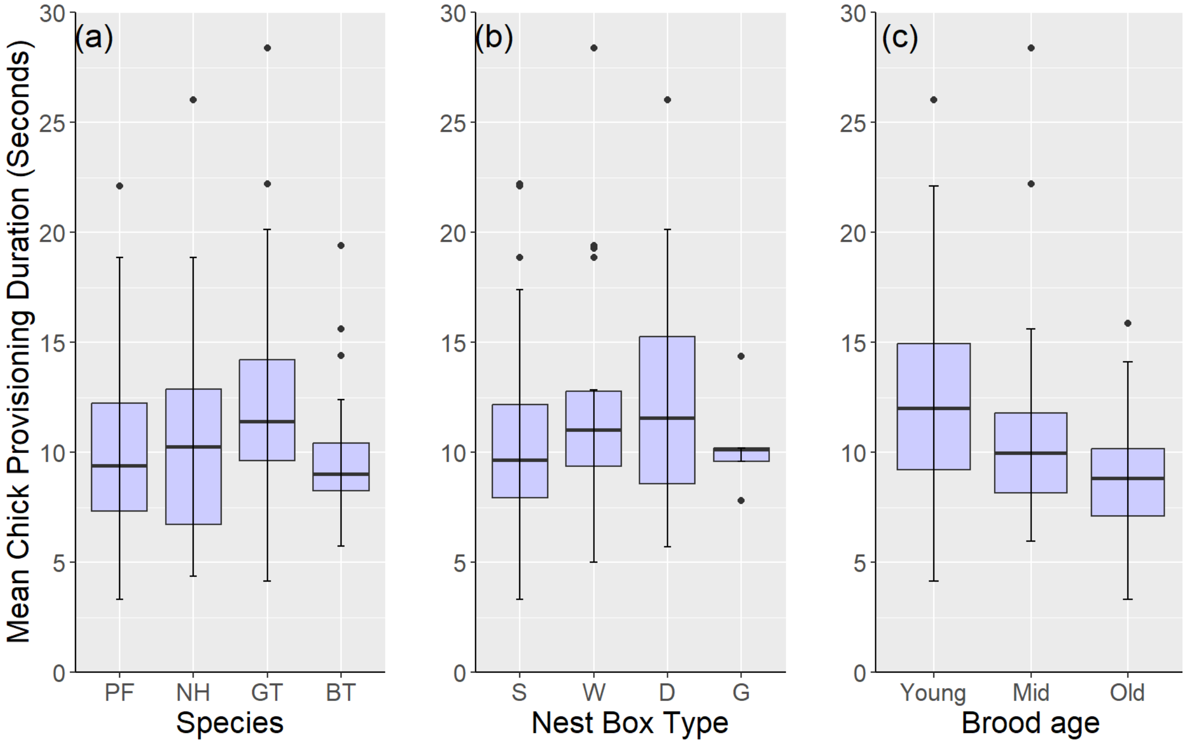


Figure 25. Mean chick provisioning durations according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge). Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. The midline refers to the median value, boxes the 1st and 3rd quartiles and whiskers ± 1.5 times the interquartile range. Values outside these ranges are plotted as outliers.

The GLM for chick provisioning duration was significant ($\chi^2_{(10)} = 6.17$, $p < 0.001$, AIC = 67.68) and the predictor variables included in the MAM are listed in Table 15, all of which were significant. Visit durations were significantly shorter when leaning was used as a feeding method, and had a positive correlation with habitat (i.e. PC1), meaning visit durations were higher in areas with more bare ground and a higher species richness and quantity of trees.

The pairwise comparisons for significant factors (species, box type and brood age) are summarised in Table 16, alongside the corresponding EMMs in Figure 26. Relative to the standard wooden boxes in the Reserve, chick provisioning durations were significantly longer for birds nesting in woodcrete and deep boxes. Great Tits also took significantly longer to provision chicks than Blue Tits. Provisioning durations were negatively correlated to brood age, and were therefore significantly longer when nestlings were presumed to be 2 to 4 days old.

Table 15. Generalised linear model assessing the influence of various predictor variables on the mean chick provisioning duration at nest boxes. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. p values in bold are greater than 0.05 and deemed significant.

Predictor Variable	d.f.	χ^2	p	Explanation
Factors:				
Species	3	10.79	**0.013**	Higher for Great Tit than Blue Tit (Table 16, Figure 26a)
Box Type	3	10.19	**0.017**	Higher in woodcrete and deep boxes relative to standard boxes (Table 16, Figure 26b)
Brood Age	2	15.20	**<0.001**	Higher when nestlings were younger (Table 16, Figure 26c)
Covariates:				
Habitat (PC1)	1	4.82	**0.028**	Higher when PC1 was higher
Leaning	1	13.71	**<0.001**	Higher when the prevalence of leaning was low

Table 16. Significant pairwise comparisons for significant factors from a generalised linear model assessing the influence of predictor variables on mean chick provisioning duration. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Significance codes: *** < 0.001, ** < 0.01, * < 0.05. †PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit. ‡S: Standard, W: Woodcrete, D: Deep, G: Guardian. §Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, old: ready to fledge.

Pairwise Comparisons	Test Statistic			
	Standard Error	t	p	Significance
Species†:				
GT > BT	0.07	3.28	0.001	**
Box Type‡:				
W > S	0.09	2.44	0.015	*
D > S	0.08	2.75	0.006	**
Brood Age§:				
Young > Mid	0.06	2.10	0.036	*
Young > Old	0.07	3.88	<0.001	***
Mid > Old	0.07	2.04	0.042	*

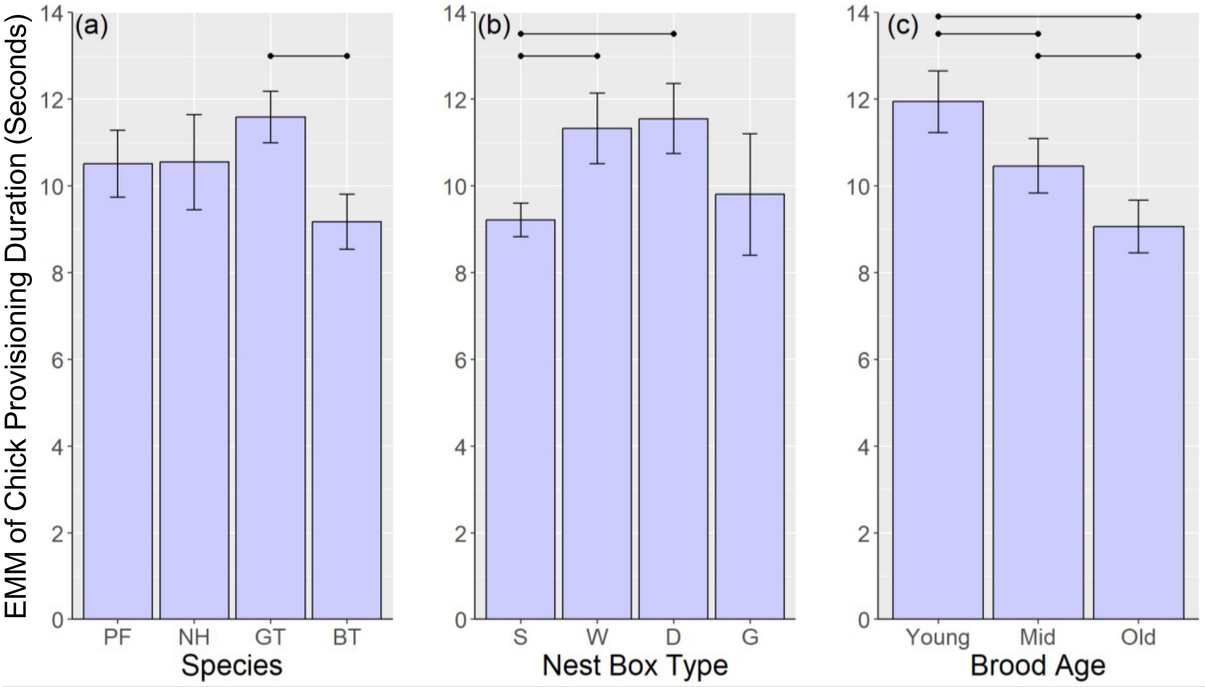


Figure 26. Estimated Marginal Means (EMM) of mean chick provisioning duration according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge) from a generalised linear model. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Error bars refer to the standard error, and connecting lines show significant differences from pairwise comparisons.

3.3.5. Visit frequency

The distribution of the visit frequency data is graphed in the boxplots in Figure 27. A large amount of variation can be seen, with the visit frequency ranging from below 5 to above 40 visits per 30 minutes. Interquartile ranges are also large, especially for nest box type, where woodcrete and guardian boxes have a sizable positive skew. Visit frequency appears to be higher for Pied Flycatchers and Blue Tits, and lower when chicks were youngest (2 to 4 days post-hatch).

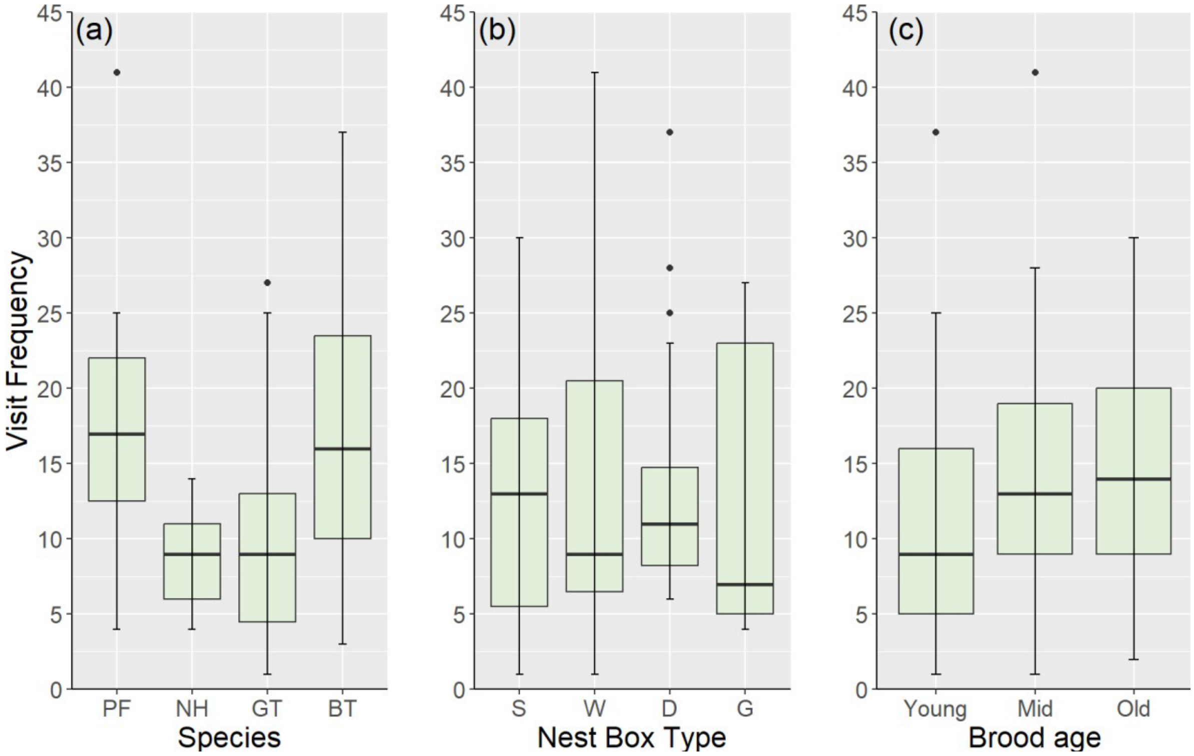


Figure 27. The number of visits within a 30 minute period adult birds made to their nest according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge). Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. The centre line refers to the median value, boxes the 1st and 3rd quartiles and whiskers ± 1.5 times the interquartile range. Values outside these ranges are plotted as outliers.

The visit frequency GLM was significant ($\chi^2_{(26)} = 359.02$, $p < 0.001$, AIC = 817.06) and included all predictor variables except from ambient temperature, however, rainfall and time of day predictors were non-significant (Table 17). The mean chick provisioning duration was negatively correlated with visit frequency, meaning when visit durations were shorter, birds visited the nest more often. However, despite the prevalence of leaning behaviours reducing the mean chick provisioning duration (Table 15), increases in the prevalence of leaning resulted in a lower visit frequency. Similarly, although mean visit durations were higher in areas with more bare ground cover and tree density, the visit frequency was higher in such areas. Visit frequency was also shown to increase significantly when broods were larger and had an earlier hatching dates.

The pairwise comparisons for species, box type, brood age and box orientation are summarised in Table 18, alongside the corresponding EMMs in Figure 28. Overall, Pied Flycatchers visited nests significantly more than all other species, followed by Blue Tits which had a higher visit frequency than both Eurasian Nuthatches and Great Tits. Visit frequency was significantly lower when nest boxes were oriented towards north and were of a standard or woodcrete design. Finally, visit frequency was lower when nestlings were only 2 to 4 days old.

Table 17. Generalised Linear Model assessing the influence of various predictor variables on the number of visits adult birds made to nest boxes within 30 minute periods. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. p values in bold are greater than 0.05 and deemed significant.

Predictor Variable	d.f.	χ^2	p	Explanation
Factors:				
Species	3	54.87	**<0.001**	Higher for Pied Flycatcher, then Blue Tit (Table 18, Figure 28a)
Box Type	3	16.86	**<0.001**	Higher in deep and guardian boxes (Table 18, Figure 28b)
Brood Age	2	14.34	**<0.001**	Higher for older nestlings (Table 18, Figure 28c)
Rainfall	2	5.77	0.056	N/A
Time of Day	4	8.22	0.084	N/A
Box Orientation	7	21.00	**0.004**	Lower when oriented North (Table 18)
Covariates:				
Hatching Date	1	6.74	**0.009**	Higher when hatching dates were earlier
Brood Size	1	26.99	**<0.001**	Higher when brood sizes were larger
Habitat (PC1)	1	7.20	**0.007**	Higher when PC1 was higher
Leaning	1	7.42	**0.006**	Higher when prevalence of leaning was low
Mean Chick Provisioning duration	1	58.36	**<0.001**	Higher when mean chick provisioning durations were lower

Table 18. Significant pairwise comparisons for significant factors from a generalised linear model assessing adult nest visitation during a 30 minute period. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Significance codes: *** < 0.001, ** < 0.01, * < 0.05. †PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit. ‡S: Standard, W: Woodcrete, D: Deep, G: Guardian. §Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, old: ready to fledge. ‖N: north, NE: northeast, E: east, SE: southeast, S: south, SW: southwest, W: west, NW: northwest.

Pairwise Comparisons	Test Statistic			
	Standard Error	t	p	Significance
Species†:				
PF > NH	0.18	5.65	<0.001	***
PF > GT	0.13	5.90	<0.001	***
PF > BT	0.14	2.85	0.004	**
BT > NH	0.14	4.25	<0.001	***
BT > GT	0.08	4.86	<0.001	***
Box Type‡:				
D > S	0.09	3.39	<0.001	***
D > W	0.10	3.02	0.003	**
G > S	0.16	2.29	0.022	*
G > W	0.16	2.24	0.025	*
Brood Age§:				
Mid > Young	0.07	2.88	0.004	**
Old > Young	0.08	3.67	<0.001	***
Box Orientation‖:				
NE > N	0.14	3.48	<0.001	***
SE > N	0.14	2.91	0.004	**
S > N	0.21	2.61	0.009	**
W > N	0.15	3.15	0.002	**
NW > N	0.13	2.72	0.007	**
NE > E	0.11	2.08	0.038	*
W > E	0.09	2.11	0.035	*
NE > SW	0.12	2.07	0.039	*

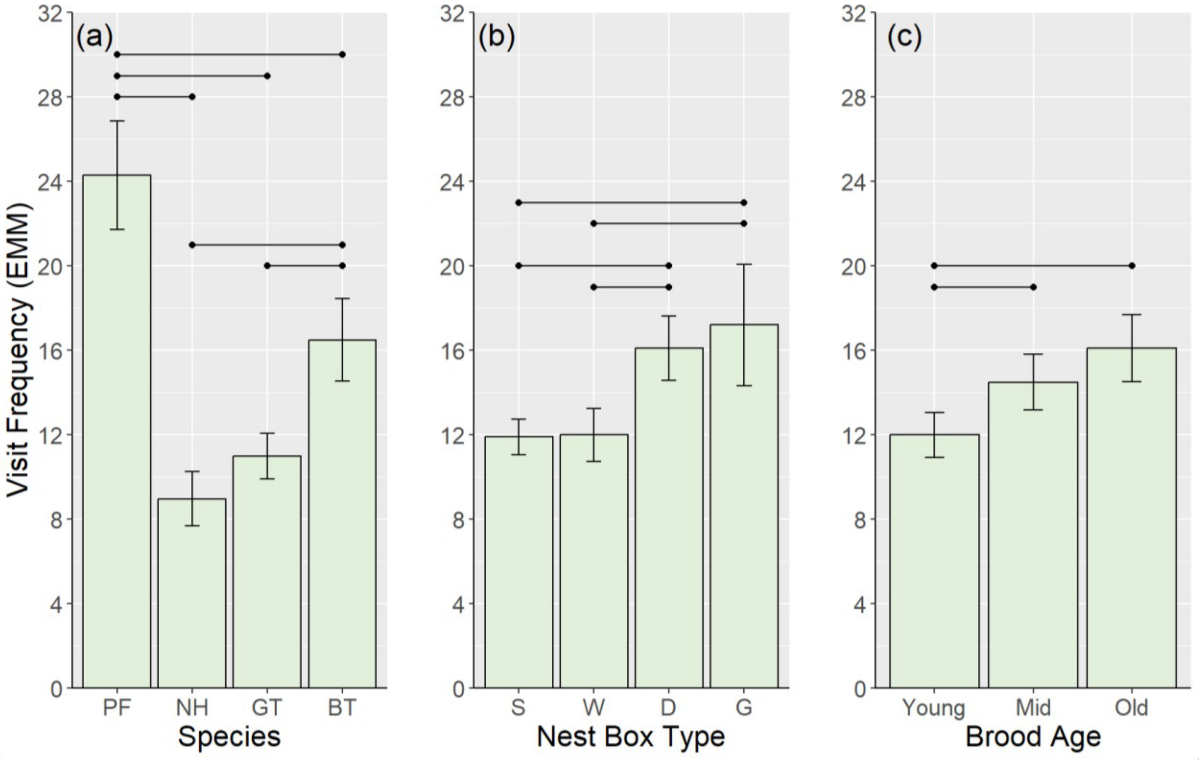


Figure 28. Estimated Marginal Means (EMM) of adult nest visitations during a 30 minute period according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge) from a generalised linear model. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Error bars refer to the standard error, and connecting lines show significant differences from pairwise comparisons.

3.3.6. Chick provisioning frequency

Figure 29 shows the number of chick provisioning visits according to species, nest box type and brood age. Generally, distributions and patterns are similar to the boxplots in Figure 27, which show the total number of nest visitations (visit frequency). It is worth mentioning, on occasion no chick provisioning visits were seen.

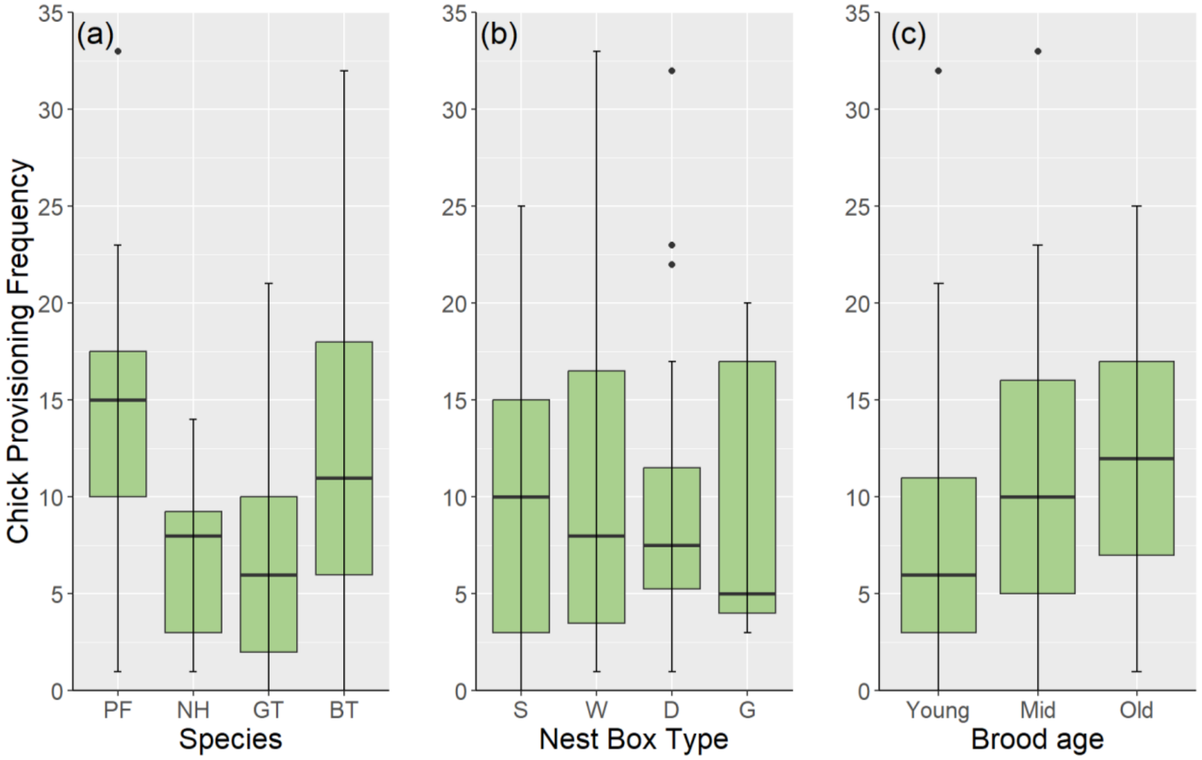


Figure 29. The number of chich provisioning visits within a 30 minute period adult birds made to their nest according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge). Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. The centre line refers to the median value, boxes the 1st and 3rd quartiles and whiskers ± 1.5 times the interquartile range. Values outside these ranges are plotted as outliers.

The GLM for chick provisioning frequency was significant ($\chi^2_{(26)} = 368.13$, $p < 0.001$, AIC = 788.19) and results are shown in Table 19. Similarly to the visit frequency GLM, the only predictor variable not included in the MAM was ambient temperature, but, in this model all independent variables were significant. The pairwise comparisons for significant factors are summarised in Table 20, alongside the corresponding EMMs in Figures 30 and 31. Generally, aside from the inclusion of rainfall and time of day predictors, patterns in GLM results are analogous with those from the visit frequency GLM (Figure 28 and Tables 17 and 18). Provisioning frequency was consistent throughout the morning and into the early afternoon, followed by a significant peak in the late afternoon (15.01 to 17.00hrs) and a significant drop in the evening (17.01 to 19.00hrs). chick provisioning frequency significantly increased during periods of more intense rainfall.

Table 19. Generalised Linear Model assessing the influence of various predictor variables on the number of chick provisioning visits birds made to nest boxes within a 30 minute period. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. p values in bold are greater than 0.05 and deemed significant.

Predictor Variable	d.f.	χ^2	p	Explanation
Factors:				
Species	3	43.63	**<0.001**	Higher for Pied Flycatcher then Blue Tit (Table 20, Figure 30a)
Box Type	3	20.86	**<0.001**	Higher in deep and guardian boxes (Table 20, Figure 30b)
Brood Age	2	31.77	**<0.001**	Higher for older nestlings (Table 20, Figure 30c)
Rainfall	2	10.37	**0.006**	Higher with more intense rainfall (Table 20, Figure 31a)
Time of Day	4	16.36	**0.003**	Higher in the late afternoon and lower in the evening (Table 20, Figure 31b)
Box Orientation	7	19.79	**0.006**	Lower when oriented towards North and East (Table 20)
Covariates:				
Hatching Date	1	6.59	**0.010**	Higher when hatching dates were earlier
Brood Size	1	25.30	**<0.001**	Higher when brood sizes were larger
Habitat (PC1)	1	7.09	**0.008**	Higher when PC1 was higher
Leaning	1	5.11	**0.024**	Higher when prevalence of leaning was low
Mean Chick Provisioning Duration	1	63.05	**<0.001**	Higher when mean chick provisioning durations were lower

Table 20. Significant pairwise comparisons for significant factors from a generalised linear model assessing the influence of predictor variables on the frequency of chick provisioning during a 30 minute period. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Significance codes: *** < 0.001, ** < 0.01, * < 0.05. [†]PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit. [‡]S: Standard, W: Woodcrete, D: Deep, G: Guardian. [§]Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, old: ready to fledge. [‖]EM: early morning (09.00 to 11.00 hrs), LM: late morning (11.01 to 13.00 hrs), EA: early afternoon (13.01 to 15.00 hrs), LA: late afternoon (15.01 to 17.00 hrs), E: evening (17.01 to 19.00 hrs). [¶]N: north, NE: northeast, E: east, SE: southeast, S: south, SW: southwest, W: west, NW: northwest.

Pairwise Comparisons	Test Statistic			
	Standard Error	t	p	Significance
Species[†]:				
PF > NH	0.20	5.52	<0.001	***
PF > GT	0.16	5.52	<0.001	***
PF > BT	0.16	3.23	0.001	**
BT > NH	0.16	3.66	<0.001	***
BT > GT	0.10	3.54	<0.001	***
Box Type[‡]:				
D > S	0.10	3.94	<0.001	***
D > W	0.12	3.53	<0.001	***
G > S	0.19	2.10	0.036	*
G > W	0.19	2.07	0.038	*
Brood Age[§]:				
Mid > Young	0.08	4.45	<0.001	***
Old > Young	0.09	5.39	<0.001	***
Old > Mid	0.07	2.10	0.036	*
Rainfall:				
Drizzle > Dry	0.08	2.18	0.029	*
Raining > Dry	0.22	2.80	0.005	**
Raining > Drizzle	0.22	2.04	0.041	*
Time of Day[‖]:				
LA > EM	0.15	2.43	0.015	*
LA > LM	0.08	2.07	0.039	*
LA > EA	0.08	2.27	0.023	*
LM > E	0.18	2.29	0.022	*
EA > E	0.18	2.27	0.023	*
LA > E	0.18	3.24	0.001	**
Nest Box Orientation[¶]:				
NE > N	0.16	2.96	0.003	**
SE > N	0.16	2.96	0.003	**
S > N	0.25	2.12	0.034	*
W > N	0.17	2.33	0.020	*
NE > E	0.13	2.53	0.012	*
NE > SW	0.14	1.97	0.049	*
SE > E	0.15	2.26	0.024	*
W > E	0.11	2.14	0.032	*

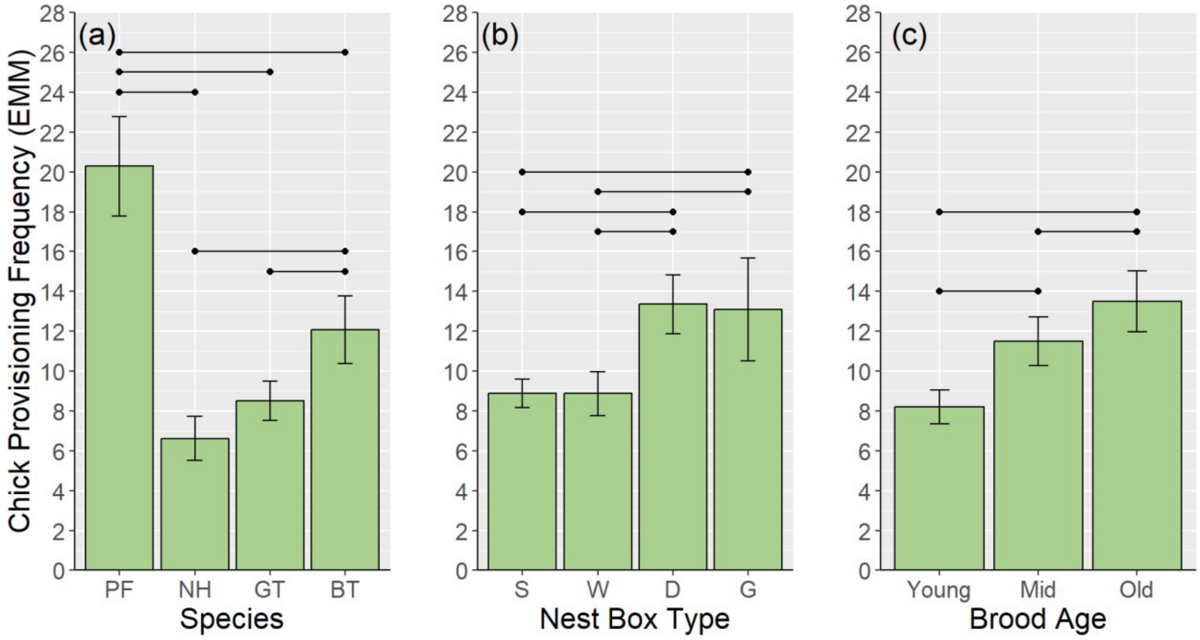


Figure 30. Estimated Marginal Means (EMM) of chick provisioning frequency during a 30 minute period according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge) from a generalised linear model. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Error bars refer to the standard error, and connecting lines show significant differences from pairwise comparisons.

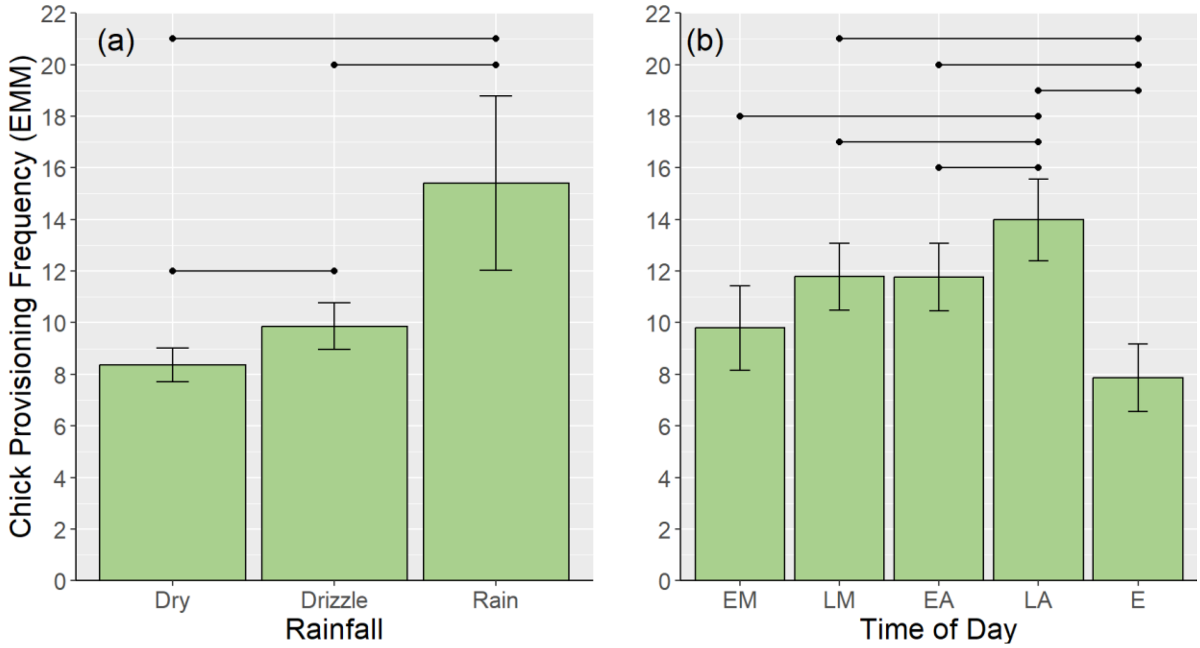


Figure 31. Estimated Marginal Means (EMM) of chick provisioning frequency during a 30 minute period, according to (a) rainfall patterns, and (b) time of day (EM: early morning (09.00 to 11.00 hrs), LM: late morning (11.01 to 13.00 hrs), EA: early afternoon (13.01 to 15.00 hrs), LA: late afternoon (15.01 to 17.00 hrs), E: evening (17.01 to 19.00 hrs)) from a generalised linear model. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Error bars refer to the standard error, and connecting lines show significant differences from pairwise comparisons.

3.3.7. Total Time Spent at the Nest

Boxplots in Figure 32 show the total time the birds spent at the nest boxes within the 30 minute periods. Generally, times were below 10 minutes, although there were a few prolonged outliers where birds were at the nest box for the majority of the 30 minute period. Times appear to be longer when nestlings were presumed to be 2 to 4 days old, but large boxes and whiskers show large variations in the time spent at the nest for this brood age.

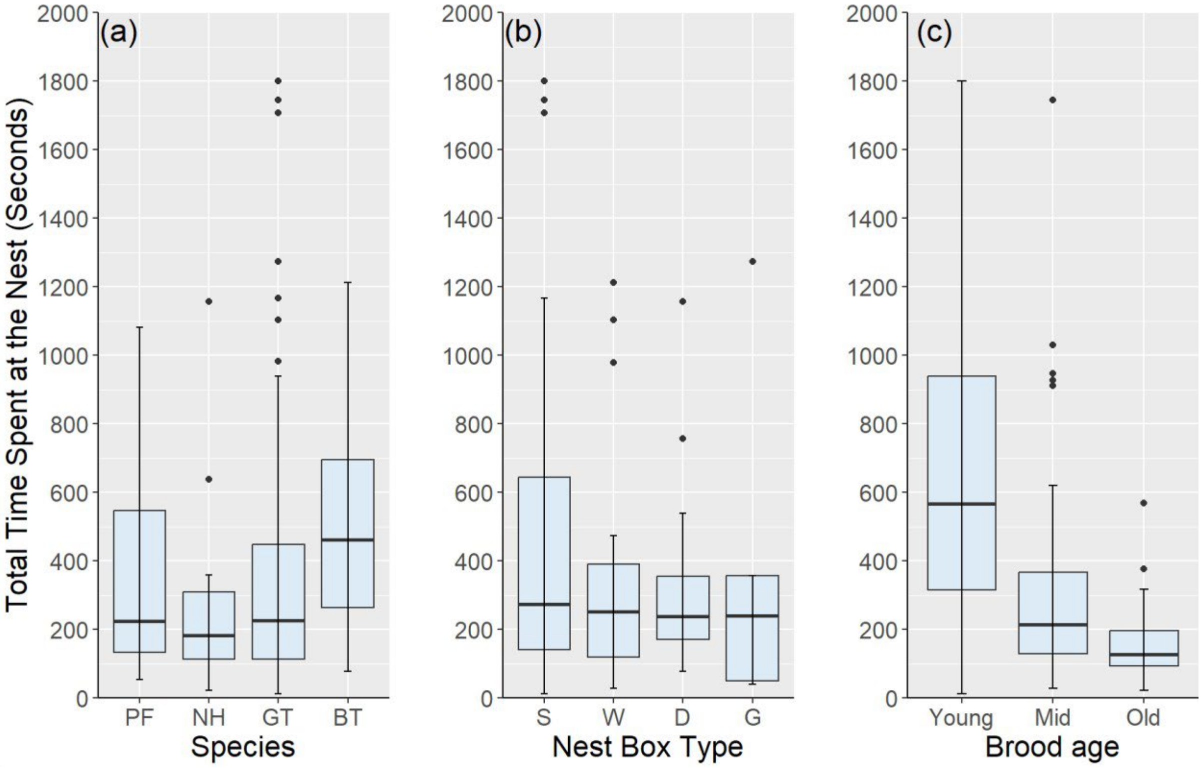


Figure 32. The total time birds spent at nests within a 30 minute period according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge). Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. The centre line refers to the median value, boxes the 1st and 3rd quartiles and whiskers ± 1.5 times the interquartile range. Values outside these ranges are plotted as outliers.

The GLM was significant ($\chi^2_{(10)} = 59.26$, $p < 0.001$, AIC = 307.77) and the predictor variables included are listed in Table 21, alongside their significance in the model. Aside from habitat, all other predictor variables included in the MAM were significant. Both the leaning behaviour and temperature predictors were negatively correlated, meaning birds spent more time at the nest when ambient temperatures were colder, and prevalence of leaning behaviours was low. For significant factors (species, brood age and rainfall), the pairwise comparisons between levels are summarised in Table 22, alongside the corresponding EMMs in Figure 33. Whereas Pied Flycatchers had the highest visit and chick proviosning frequency, Blue Tits spent the most time at the nest overall. Similarly, whereas visit frequency was higher when nestlings were older (Figures 28 and 30), the total time spent at the nest reduced as brood age increased.

Table 21. Generalised Linear Model assessing the influence of various predictor variables on the total time birds spent at their nest within a 30 minute period. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. p values in bold are greater than 0.05 and deemed significant.

Predictor Variable	d.f.	χ^2	p	Explanation
Factors:				
Species	3	11.93	**0.008**	Higher for Blue Tit (Table 22, Figure 33a)
Brood Age	2	51.43	**<0.001**	Higher for younger nestlings (Table 22, Figure 33b)
Rainfall	2	6.39	**0.041**	Higher when Dry (Table 22, Figure 33c)
Covariates:				
Habitat (PC1)	1	3.07	0.080	N/A
Leaning	1	5.17	**0.023**	Higher when prevalence of leaning was low
Temperature	1	6.37	**0.012**	Higher when ambient temperatures were colder

Table 22. Significant pairwise comparisons for significant factors from a generalised linear model assessing the influence of predictor variables on the total time birds spent at nests within a 30 minute period. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Significance codes: *** < 0.001, ** < 0.01, * < 0.05. †PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit. ‡Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, old: ready to fledge.

Pairwise Comparisons	Test Statistic			
	Standard Error	t	p	Significance
Species†:				
BT > NH	0.30	2.41	0.016	*
BT > GT	0.18	2.95	0.003	**
Brood Age‡:				
Young > Mid	0.16	5.04	<0.001	***
Young > Old	0.19	6.88	<0.001	***
Mid > Old	0.18	2.56	0.010	*
Rainfall:				
Dry > Drizzle	0.19	2.50	0.012	*

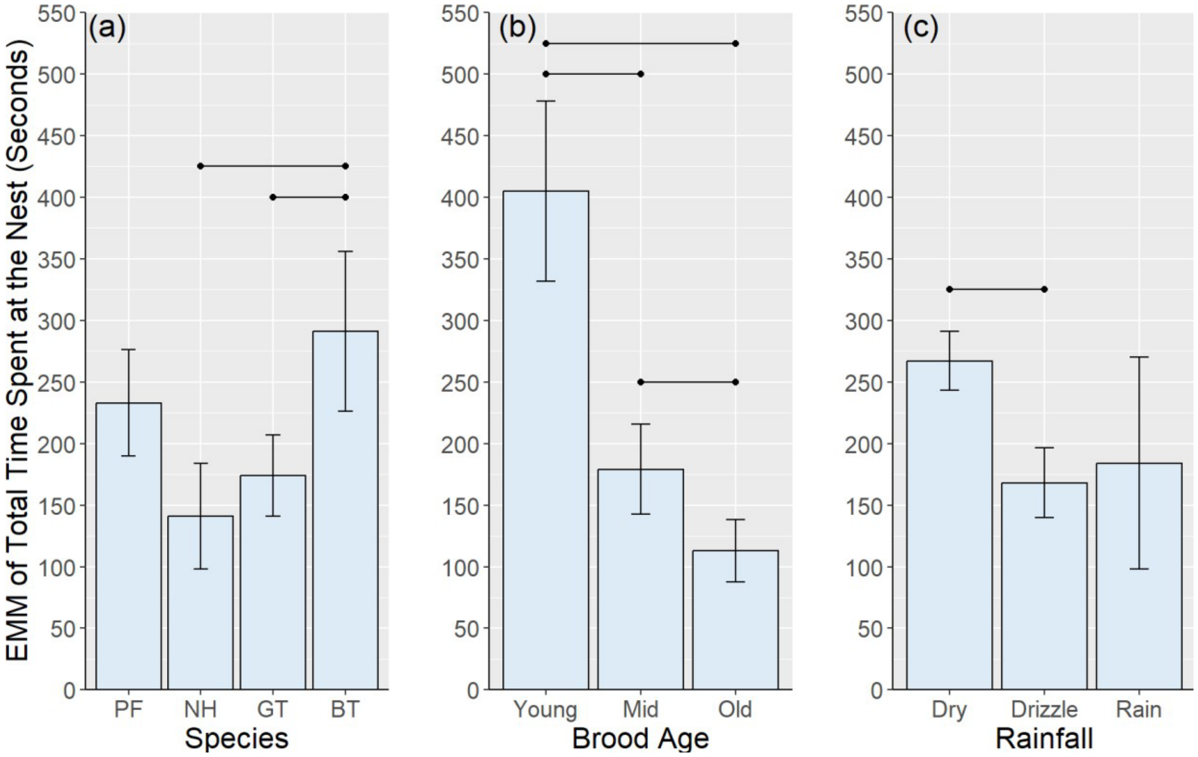


Figure 33. Estimated Marginal Means (EMM) of the total time birds spent at their nests in a 30 minute period, according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge) and (c) rainfall patterns, from a generalised linear model. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Error bars refer to the standard error, and connecting lines show significant differences from pairwise comparisons.

3.3.8. Total Time Spent Chick Provisioning

When comparing the box plots in Figures 32 and 34, the time spent chick provisioning was generally lower than the total time spent at the nest, and fewer outliers are seen. Variations according to brood age are seemingly less pronounced, and times are higher for Pied Flycatchers.

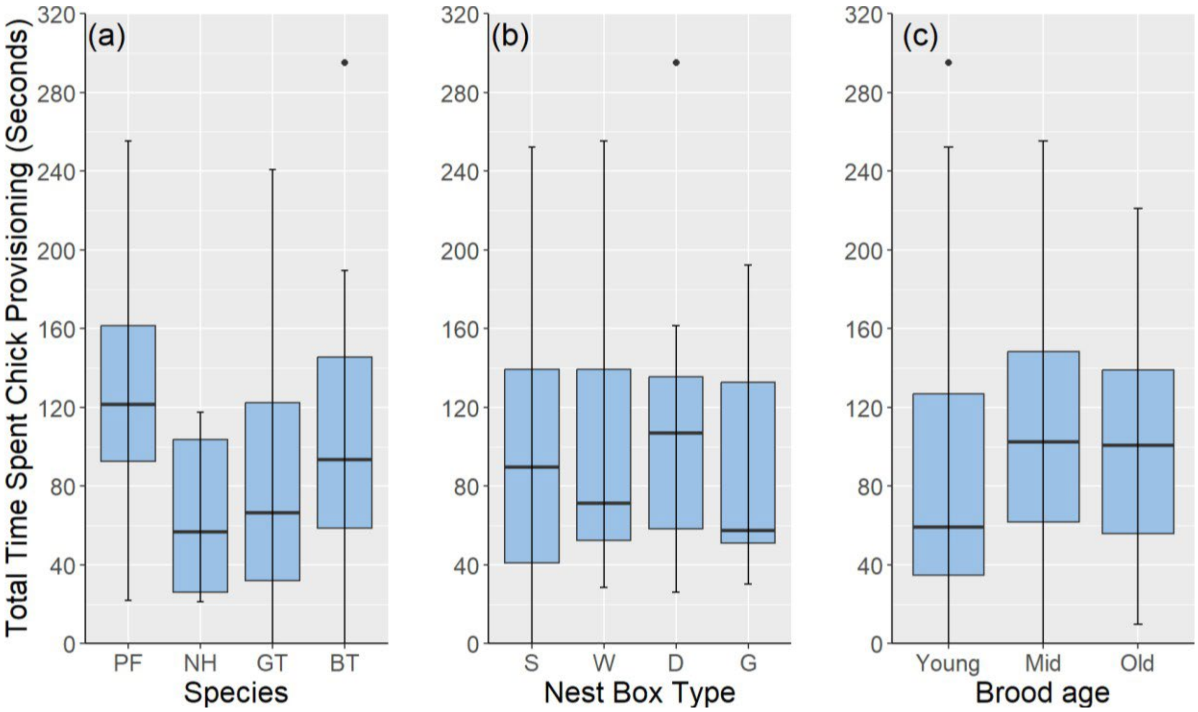


Figure 34. The total time birds spent chick provisioning within a 30 minute period according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge). Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. The centre line refers to the median value, boxes the 1st and 3rd quartiles and whiskers ± 1.5 times the interquartile range. Values outside these ranges are plotted as outliers.

The GLM for total time spent chick provisioning was significant ($\chi^2_{(11)} = 22.14$, $p < 0.001$, AIC = 1391.60) and predictor variables included are listed in Table 23. Unlike the total time spent at the nest GLM (Table 21), box type and temperature were not included in the MAM, but rainfall and brood size were. Habitat (i.e. PC1) was also significant, where more time was spent chick provisioning in habitats with more bare ground cover, a larger density of trees and higher species richness. More time was spent chick provisioning when the brood size was larger.

For significant factors (species, box type and brood age), the pairwise comparisons between levels are summarised in Table 24, alongside the corresponding EMMs in Figure 35. Similar to the visit frequency and chick provisioning frequency GLMs, more time was spent at the nest for Pied Flycatchers and Blue Tits, and when nestlings were older.

Table 23. Generalised Linear Model assessing the influence of various predictor variables on the total time birds spent chick provisioning within a 30 minute period. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. p values in bold are greater than 0.05 and deemed significant.

Predictor Variable	d.f.	χ^2	p	Explanation
Factors:				
Species	3	31.70	**<0.001**	Higher for Pied Flycatcher (Table 24, Figure 35a)
Box Type	3	10.62	**0.014**	Higher for deep compared to standard (Table 24, Figure 35b)
Brood Age	2	24.29	**<0.001**	Higher for older nestlings (Table 24, Figure 35c)
Covariates:				
Brood Size	1	23.41	**<0.001**	Higher when brood sizes were larger
Habitat (PC1)	1	4.37	**0.037**	Higher when PC1 was higher
Leaning	1	7.40	**0.007**	Higher when prevalence of leaning was low

Table 24. Significant pairwise comparisons for significant factors from a generalised linear model assessing the influence of predictor variables on the total time birds spent chick provisioning during a 30 minute period. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Significance codes: *** < 0.001, ** < 0.01, * < 0.05. †PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit. ‡S: Standard, W: Woodcrete, D: Deep, G: Guardian. §Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, old: ready to fledge.

Pairwise Comparisons	Test Statistic			
	Standard Error	t	p	Significance
Species†:				
PF > NH	0.23	3.45	<0.001	***
PF > GT	0.14	5.48	<0.001	***
PF > BT	0.15	3.13	0.002	**
BT > GT	0.14	2.15	0.032	*
Box Type‡:				
D > S	0.16	2.98	0.003	**
Brood Age§:				
Mid > Young	0.12	3.40	<0.001	***
Old > Young	0.15	5.04	<0.001	***
Old > Mid	0.14	2.38	0.017	*

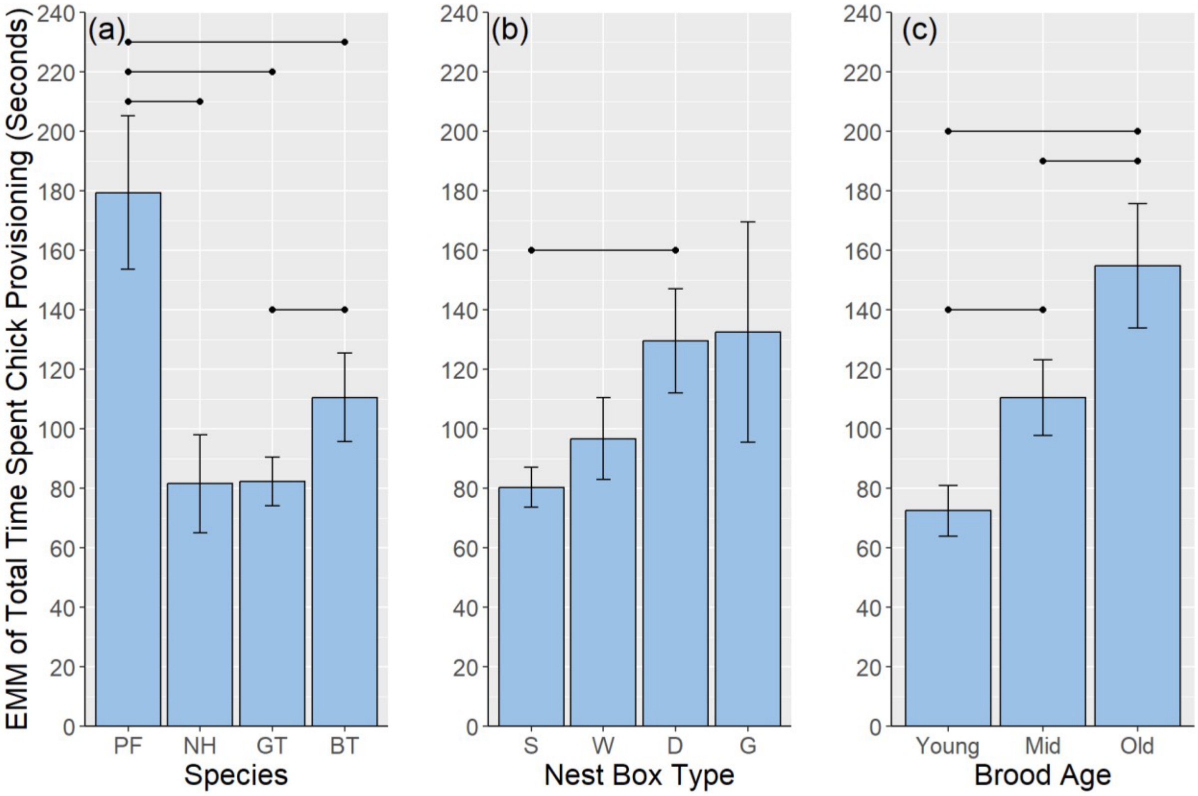


Figure 35. Estimated Marginal Means (EMM) of the total time birds spent chick provisioning during a 30 minute period, according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge) from a generalised linear model. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines. Error bars refer to the standard error, and connecting lines show significant differences from pairwise comparisons.

3.3.9. Fledging Success

Overall, the interquartile ranges shown in the box plots in Figure 36 highlight the sizable variability in the fledging success of broods in nest boxes. They also show how many of the nests completely failed.

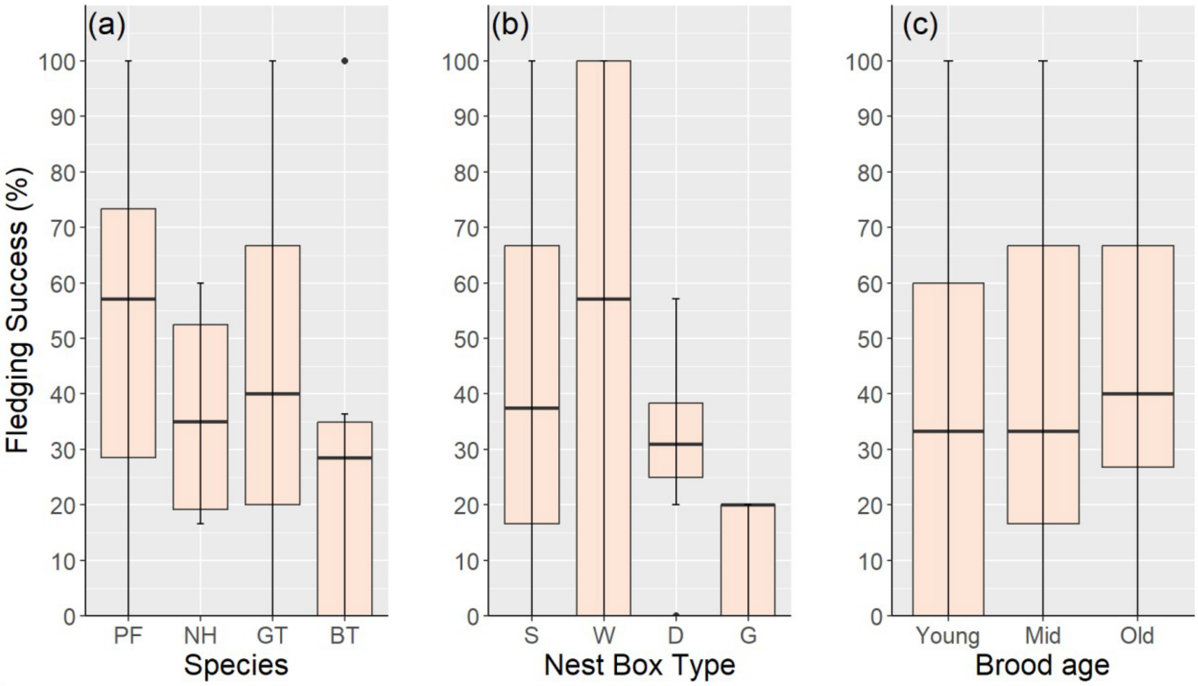


Figure 36. The percentage fledging success (% hatched to fledged) of four woodland passerines, according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) and (c) brood age (Young: two to four days post-hatching, Mid: 8 to 10 days post-hatching, Old: ready to fledge). Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning. The centre line refers to the median value, boxes the 1st and 3rd quartiles and whiskers ± 1.5 times the interquartile range. Values outside these ranges are plotted as outliers.

The GLM for fledging success was significant ($\chi^2_{(15)} = 37.71$, $p < 0.001$, AIC = 1228.32) and the predictor variables included in the MAM are shown in Table 25. Habitat was non-significant, whereas fledging success was higher for broods that hatched earlier in the breeding season. All included factors were significant, and their corresponding pairwise comparisons are summarised in Table 26, alongside their EMMs in Figure 37. Pied Flycatchers had the highest fledging success, followed by Great Tits. Guardian tube nest boxes had the lowest fledging success, as well as boxes oriented towards north and east. Finally, clutches that hatched earlier had a higher fledging success.

Table 25. Generalised Linear Model assessing the influence of various predictor variables on the percentage fledging success of four woodland passerines. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning. p values in bold are greater than 0.05 and deemed significant.

Predictor Variable	d.f.	χ^2	p	Explanation
Factors:				
Species	3	15.27	**0.002**	Higher for Pied Flycatcher then Great Tit (Table 26, Figure 37a)
Box Type	3	10.01	**0.019**	Lower for guardian (Table 26, Figure 37b)
Box Orientation	7	26.06	**<0.001**	Lower for North and East (Table 26)
Covariates:				
Habitat (PC1)	1	2.58	0.108	N/A
Hatching Date	1	6.91	**0.009**	Higher when hatching dates were earlier

Table 26. Significant pairwise comparisons for significant factors from a generalised linear model assessing the influence of predictor variables on the percentage fledging success four woodland passerines. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning. Significance codes: *** < 0.001, ** < 0.01, * < 0.05. †PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit. ‡S: Standard, W: Woodcrete, D: Deep, G: Guardian. §N: north, NE: northeast, E: east, SE: southeast, S: south, SW: southwest, W: west, NW: northwest.

Pairwise Comparisons	Test Statistic			
	Standard Error	t	p	Significance
Species†:				
PF > NH	0.43	3.46	<0.001	***
PF > GT	0.33	2.51	0.012	*
PF > BT	0.35	4.34	<0.001	***
GT > NH	0.29	2.22	0.026	*
GT > BT	0.20	3.36	<0.001	***
Box Type‡:				
S > G	0.44	3.72	<0.001	***
W > G	0.44	2.56	0.011	*
D > G	0.44	2.82	0.005	**
Box Orientation§:				
NE > N	0.32	2.86	0.004	**
SE > N	0.32	4.32	<0.001	***
S > N	0.50	3.58	<0.001	***
SW > N	0.35	3.34	<0.001	***
W > N	0.32	2.55	0.011	*
NW > N	0.28	3.74	<0.001	***
SE > E	0.36	2.61	0.009	**
S > E	0.48	2.77	0.006	**
SW > E	0.34	2.11	0.035	*
NW > E	0.26	2.28	0.023	*
S > W	0.44	2.21	0.027	*

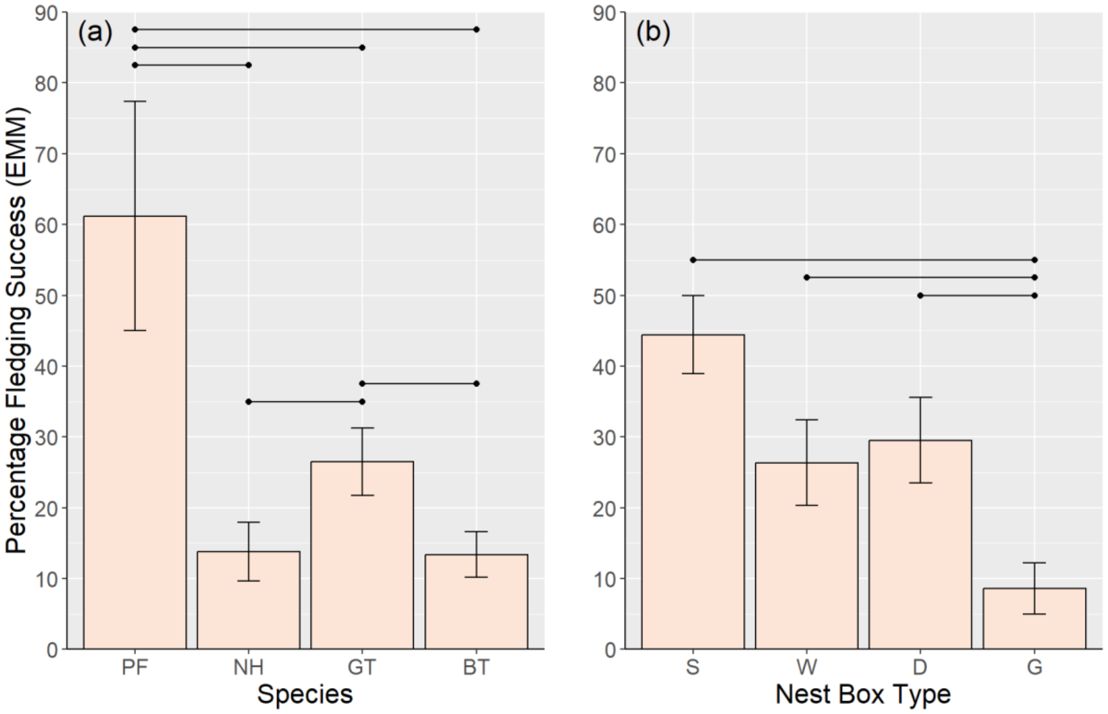


Figure 37. Estimated Marginal Means (EMM) of the percentage fledging success of four woodland passerines according to (a) species (PF: Pied Flycatcher, NH: Eurasian Nuthatch, GT: Great Tit, BT: Blue Tit), (b) nest box type (S: Standard, W: Woodcrete, D: Deep, G: Guardian) from a generalised linear model. Data was compiled from 30 minute video recordings of nest boxes at Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning. Error bars refer to the standard error, and connecting lines show significant differences from pairwise comparisons.

3.4. Discussion

As previously discussed, predator-proof nest boxes are often assumed to provide a net benefit to birds, however, there is a significant lack of scientific literature testing their efficacy and there are potentially unintended negative consequences of their use. One aim of this study was to contribute towards filling this knowledge gap by testing the hypothesis proposed by Blunsden (2020), who suggested that certain predator-proof nest box designs, such as guardian tubes, may adversely influence chick proviosning by preventing adult birds from feeding nestlings at the entrance hole (i.e., leaning behaviour). Results showed that nest box type did not affect the prevalence of such learning behaviours, however, despite this chick provisioning durations were still significantly longer in woodcrete and deep nest boxes. The study also set out to and has identified various life-history (e.g. brood size and nestling age) and environmental (e.g. habitat and rainfall) factors that influenced the chick provisioning behaviours of the four studied secondary cavity-nesting species. The following discussion is structured according to the variables explored within the study, followed by a section detailing the main limitations (3.4.9). Generally, the research was exploratory, and therefore, analysis of results may at times be speculative. However, it is important to note the principal goal was to generate hypotheses that will drive future research into this relatively understudied topic.

3.4.1. Leaning Behaviours

3.4.1.1. Expression of Leaning as a Learned Behaviour

As previously stated, the expression of leaning behaviours appeared to be bird-specific, rather than situation-specific. Leaning behaviours were rarely observed at the majority of nest boxes, whereas some individuals were seen frequently adopting the technique. A potential explanation for this is that the action of leaning is a learned behaviour which increases the efficacy of chick provisioning. Therefore, similar to the temporal development of foraging strategies in young birds (Wunderle, 1991), the ability of parental birds to effectively feed chicks at the nest may also improve with age and experience. There is therefore the possibility that older and more experienced birds were the ones expressing these leaning behaviours. This could be assessed in future research, whereby studied birds could also be caught, and plumage characteristics used to differentiate between yearlings and older individuals (Jenni and

Winkler, 2020). Statistical modelling could then identify potential relationships between age and the expression of leaning behaviours.

It can be important to consider the potential adaptive value of a behaviour (Tinbergen, 1963), and although speculative, there are three possible benefits of provisioning nestlings by leaning into the nest box:

1. As hypothesised, the expression of leaning behaviours significantly reduced mean chick provisioning durations, likely due to time being saved as a result of birds not needing to completely enter the nest box. Leaning could therefore reduce the energy expenditure of parental birds. There was also a strong negative correlation between mean chick provisioning duration and visit frequency, where shorter chick provisioning visits significantly increased the number of times a bird was able to visit the nest. This highlights the importance of a bird's ability to feed chicks efficiently at the nest.
2. The decision-making process when feeding nestlings greatly depends on begging behaviour, and nestlings will often compete for the best positions within the nest cup (Teather, 1992; McRae *et al.*, 1993; Kolliker *et al.*, 1998). Expression of leaning by parent birds could therefore be a method of assessing hunger levels by encouraging chicks to reach up to the entrance hole.
1. In daylight, light levels can fall from 4.5 log lx outside, to a mesopic level of 0.74 log lx inside of a standard nest box (Reynolds *et al.*, 2009). Therefore, diurnal cavity-nesting birds have to be able to adjust their eyesight to the darker conditions within nest boxes (Wesołowski and Maziarz, 2012). However, the process of dark adaptation is relatively slow in birds, taking up to 40 minutes (Blough, 1955), and upon entering the nest chamber adult birds will experience vison that is inadequately adapted to the ambient light levels (Reynolds *et al.*, 2009). Feeding nestlings at the entrance hole therefore means birds do not need to completely enter the mesopic nest chamber, minimising the need to adjust eyesight and thus improving the speed of a chick provisioning visit.

Despite this, the exclusion of the leaning behaviour predictor from the fledging success analysis (Section 3.3.9) during variable selection, suggests that the expression of leaning behaviours did not significantly affect the survival of nestlings. Although it is worth mentioning the below average breeding success across the whole reserve could have offset positive effects caused by the behaviour. Alternatively, it is also possible that nestling body condition and weight for example was directly affected, potentially affecting post-fledgling survival instead of fledging success.

3.4.1.2. Leaning Behaviour and Predation Risk

It is also important to note that parental activity at the nest can increase predation (Martin *et al.*, 2000). When compared to entering the nest box completely, birds leaning at the entrance are exposed to predators for a prolonged period of time. There is therefore the potential that this increases predation risk by increasing the chances of predators observing parental care and discovering the nest. This therefore highlights a potential trade-off between chick provisioning and predation risk.

3.4.1.3. Leaning Behaviour and Chick Provisioning

The expression of leaning behaviours significantly reduced mean chick provisioning durations (Table 15). Subsequently, shorter chick provisioning durations significantly increased the number of times birds visited the nest (Table 17). When comparing these two results, it could be hypothesized that a higher expression of leaning behaviours would cause increases in visit frequency, as a direct result of decreased visit durations. However, the opposite was seen, where results show the expression of leaning behaviours resulted in a lower visit frequency (Table 17).

There are a few potential explanations as to why increased prevalence of leaning reduced the number of times birds visited the nest. First, the lack of interaction terms in modelling could be causing considerable bias, Nuthatches expressed the majority of observed leaning behaviours, yet also had a significantly lower visit frequency. If the latter is a species-dependent trait (e.g. due to variations in interspecific foraging strategy), this link may have been a driver in this result. Secondly, flaws regarding the use of feeding frequency as a measure of chick provisioning may cause bias. Generally, variations in provisioning and foraging strategy have been shown to affect feeding frequency significantly, whereby parent birds that provision chicks relatively infrequently, typically deliver the same amount of food by increasing prey selectivity and delivering larger food items (Nour *et al.*, 1998; Grieco, 2002a; Grieco, 2002b). Therefore, even when leaning behaviours were common, birds may be spending more time foraging, thus diluting the effects of the leaning behaviour.

Expanding on this notion of variations in foraging time, parental age and experience could again be an influencing factor. Proficiency in prey recognition and selection is shown to increase with age in many avian species (Wunderle, 1991), and older, more dominant birds, will usurp others from the best foraging patches (Gustafsson, 1988). It could therefore be hypothesised that birds with a lower feeding frequency but delivering prey of a higher energetic/nutritional quality, could be more experienced birds foraging at a greater efficacy. Such negative relationships between feeding frequency and parental age have been observed in seabirds (Ratcliffe and Furness, 1999) and corvids (Roskaft *et al.*, 1983), but has seemingly not been investigated in insectivorous passerines. Overall, the notion of older birds leaning more, but chick provisioning less frequently, could explain the negative correlation found between these two variables.

3.4.2. Species' Differences

3.4.2.1. Species and Leaning Behaviours

The prevalence of leaning behaviours varied significantly between species, being considerably higher in the Eurasian Nuthatch, and is therefore suggestive of the behaviour being a species-specific trait. The Eurasian Nuthatch will characteristically narrow the entrance hole of cavities by plastering mud around the openings, a behaviour theorised to protect against predation (Yu *et al.*, 2021). As shown in Figure 38, this was seen at this species' boxes included in my study, and the expression of leaning behaviours could therefore be an adaptive trait to counteract decreased entrance hole sizes and thus improve visit duration efficacy.

Eurasian Nuthatches were also seen habitually landing atop the nest box for multiple seconds prior to provisioning nestlings (shown in Figure 38). Avian species are known to assess predation risk and adjust reproductive strategy throughout the breeding season (Fontaine and Martin, 2006a), and it is therefore possible this 'nest box topping' behaviour aims to assess the predation risk surrounding the nest box. If leaning behaviours increase the risk of predators detecting a nest (3.4.3.2), parental birds may have been more likely to lean after making an assessment of the predation risk. Overall, a more detailed study categorizing and quantifying the behaviours seen at nest boxes could provide more insight and assess the potential reasons for them.

Figure 38. A Eurasian Nuthatch atop a standard nest box, before feeding nestlings. Note the plastering of mud around and into the entrance hole of the nest box. Image taken from video recordings by Joseph Marcus at RSPB Nagshead Nature Reserve.

3.4.2.2. Species and Chick Provisioning durations

Chick provisioning durations were significantly longer for Great Tits than for Blue Tits (Table 15), and this could simply be a result of their larger morphology, rendering it physically harder for the species to enter and exit the boxes. This hypothesis would also suggest the visit durations of Eurasian Nuthatches should have also been longer compared to those of Blue Tits because they are also physically larger; however, no such significant difference was found. Although the increased prevalence of leaning behaviours by Eurasian Nuthatches may have considerably reduced the mean chick provisioning duration for the species, thus counteracting the effect of their larger morphology.

3.4.2.3. Species and Visit frequency

Overall, visit frequency and chick provisioning frequency significantly varied between species (Figure 28 and 30) and the strongest potential driver of this variation is interspecific differences in foraging strategy. Niche separation and habitat partitioning results in avian species foraging at different tree species and at various positions within the tree (Peck, 1989). For example, Eurasian Nuthatches are typically bark foragers (Adamik and Kornan, 2004), moving up and down branches searching for food, whereas Pied Flycatchers frequently hunt by hawking (Norberg, 1986), typically leaving a perch to catch flying insects. If different foraging methods are more effective when finding food, or there was variation in the food availability of different prey species, this is likely to affect foraging times, and therefore chick provisioning frequency. This could be tested by using published relationships between the biodiversity of prey species and the species/age of trees on which the focal species foraged.

Secondly, feeding frequency is generally governed by the food requirements of chicks (Royama, 1966), and species differences in chick provisioning frequency could therefore be affected by interspecific differences in brood size. Research has shown how chick feeding frequency increases alongside increases in brood size (García-Navas and Sanz, 2010), and the results from my study match these findings, where significant positive correlations between brood size and chick provisioning frequency were found (Table 19). Furthermore, the average brood size was higher in Pied Flycatchers and Blue Tits, and lowest in Eurasian Nuthatches, and these patterns therefore match the results from the chick provisioning frequency analysis (Table 19). These values are shown in Table 27 and highlight the occurrence of a potential interaction between species and brood size.

Table 27. The average brood size and estimated marginal means (EMM) from a generalised linear model assessing chick provisioning frequency (the number of chick provisioning visits during 30 minute video recordings of nest boxes), split according to species. Data is compiled from Nagshead Nature reserve as part of a 2022 study examining how nest box type affects chick provisioning in four woodland passerines

Species	Average Brood Size	EMM of Chick Provisioning Frequency
Pied Flycatcher	7.03	20.29
Eurasian Nuthatch	5.50	6.62
Great Tit	6.71	8.51
Blue Tit	8.55	12.07

Pied Flycatchers are poly-territorial and adopt a mating system termed staggered simultaneous polygyny. Alatalo, Lundberg and Stahlbrandt (1982) stated how secondary females can only partially compensate for the lack of parental care provided by the male. It was therefore hypothesised that secondary females would have a relatively lower provisioning frequency, but because sex was excluded as a factor from analyses to maintain sample sizes, this was not possible to assess.

3.4.2.4. Species and Fledging Success

Overall, Pied Flycatchers had significantly higher fledging successes compared to all other species, and there are a number of potential reasons for this. The significant increase in chick provisioning frequency could be the central explanation, whereby the species was simply provisioning more often, thus improving nestling body condition. This could be linked to the species-specific foraging strategy described above, where if there was minimal niche overlap between study species, habitat characteristics and availability of specific prey types may have better suited the food preferences and hunting techniques of the Pied Flycatcher, allowing for an increased provisioning frequency and fledging success (Ulfstrand, 1977).

Interestingly, hatching date was negatively correlated to both chick provisioning frequency and fledging success, meaning broods that hatched earlier in the season were fed more often and had increased fledging success. However, despite Pied Flycatchers breeding later in the season (relative to the other study species), analyses showed that the species had the highest chick provisioning frequency and fledging success, thereby directly contrasting with the effects of hatching date alone. This suggests that the other three study species drove the correlations for the hatching date predictor variable. Although speculative, earlier hatching dates could have increased visit frequency and fledging success for the other species due to the above average temperatures in 2022 advancing the peak abundance of caterpillars (e.g. Visser *et al*., 1998, 2006; Burger *et al*., 2012; Cole *et al*., 2015; Hinks *et al*., 2015). Data from frass counts at the reserve could be used examine caterpillar availability and determine its peak. Therefore, Blue Tit, Great Tit and Nuthatch broods that hatched later in the season may have had access to a relatively lower abundance of prey, decreasing foraging efficiency and reducing breeding success. Pied Flycatchers on the other hand have a more generalist diet, consuming other insects such as Aranea, Hymenoptera, Diptera and Coleoptera (Lundberg and Alatalo, 2010; Burger *et al*., 2012; Nicolaus *et al*., 2019), and are therefore not as reliant on caterpillar abundance and may have exploited these alternative food sources later in the season.

3.4.3. Nest Box Type

3.4.3.1. Nest Box Occupancy

The nest box dyads across the reserve provided breeding birds with a choice of a standard or adjoining predator-proofed nest box. Overall, out of 180 dyads occupied in 2022, the predator-proofed nest boxes were only inhabited at 48 (27%), suggesting a preference for standard boxes. Research analysing nest box occupancy at Nagshead is recommended to identify if the differences observed in my current study are statistically significant. This preference for standard boxes contrasts with the literature on predator-proofed nest boxes (discussed in Chapter 2), where studies have observed relatively higher occupancy of woodcrete and deep nest boxes. Nest box preference could therefore be geographically constrained, being dependent on local conditions such as temperature. For example, due to the improved insulative properties in woodcrete boxes compared to standard nest boxes, they typically have warmer internal temperatures (García-Navas *et al.*, 2008, 2010). Woodcrete boxes could therefore be preferred in cooler locations to minimise heat loss, but avoided in warmer areas where internal nest box temperatures may become too high. In order to identify patterns in nest box preference in relation to spatial location, future research could assess nest box occupancy at an international scale, with analogous and differing habitat characteristics and meteorological conditions.

3.4.3.2. Nest Box Type and Expression of Leaning

Generally, leaning behaviours were seen at all types of nest boxes, and this did not support the hypothesis that deep boxes and guardian tubes entirely prevent the expression of this behaviour. However, it is worth mentioning that leaning behaviours were seen at only one of the two occupied guardian tube boxes, and an enlarged entrance due to prior damage could have made leaning feasible, as shown in Figure 39.

Nest box type was also excluded from the leaning behaviour model by stepwise selection, suggesting it did not have a significant effect. However, it is worth mentioning the zero-inflated nature of the leaning variable (Figure 22), combined with low sample sizes for predator-proofed nest boxes will have resulted in a low statistical power.

Figure 39. A Great Tit feeding nestlings in a guardian tube nest box by leaning in through the entrance. Note the damage to the top-side of the guardian tube. Image taken from video recordings by Joseph Marcus at RSPB Nagshead Nature Reserve

3.4.3.3. Nest Box Type and Chick Provisioning

Mean chick provisioning durations were higher in deep boxes compared to standard designs (Figure 26). As hypothesised, this was likely due to nest cup and nestlings being further away from the entrance hole, making it more difficult for parental birds to enter and exit the nest box when feeding chicks. The same was observed in woodcrete boxes, likely for the same reason, where the offset entrance hole in these particular *Vivara* boxes (as seen in Figure 9) acts a form of guardian tube, extending the entrance and increasing the distance from the box's entrance to the nest.

Visit frequency and chick provisioning frequency was also lower in woodcrete boxes (Figure 28 and 30), and this could be a direct result of lower mean chick provisioning durations, enabling birds to feed nestlings more often. Alternatively, parental care patterns could be affected by the improved insulation and warmer microclimates found in woodcrete nest boxes (García-Navas *et al.*, 2008, 2010; Bueno-Enciso *et al.*, 2016). Improved insulation for example can reduce nestling heat loss (Larson *et al.*, 2018), promoting nestling growth and suggesting less parental care is required. However, if nest box temperatures exceed critical thresholds, nestling growth can be significantly reduced (Cunningham *et al.*, 2013; Andreasson *et al.*, 2018). In comparison, visit and chick provisioning frequency were higher in deep boxes. Deep boxes can have significantly higher ectoparasite loads (Blunsden, 2020; Blunsden and Goodenough, 2023), and potential reductions in nestling body condition could give rise to increased parental care and nest sanitation to compensate. However, Sudnick, Brodie and Williams (2021) found parental behaviour and feeding frequency in Eastern Bluebirds was not affected by Blow Fly (*Protocalliphora* spp.) parasitism. Although it is important to note that parasite virulence and host resistance can vary (De Lope and Møller, 1993; Richner *et al.*, 1993; Clayton and Tompkins, 1994).

Overall, both woodcrete and deep boxes did not have significantly lower fledging success, suggesting these variations in parental visits were not sufficient to affect nestling survival. However, it is worth noting, variation in nestling body condition can affect post-fledging survival, and thus fledgling success is not always an appropriate indicator of nestling survival (Streby *et al.*, 2009; Vitz and Rodewald, 2011). Guardian tube boxes, however, had a significantly higher visit and chick provisioning frequency, but significantly lower fledging successes, and reasons for this are unclear. However, it is again worth noting the low sample size for guardian tube boxes.

3.4.3.4. Nest Box Orientation

Results show a lower visit frequency and lower fledging success for nest boxes oriented towards north and east (Tables 17 and 25). Because the visit frequency was not statistically significant in the fledging success analysis (i.e. it was excluded from the model by stepwise variable selection), it is unlikely the lower fledging success was caused by the reduction in visit frequency. It is again important to note sample sizes were low, especially when further subdividing data according to eight ordinal points on a compass.

Generally, the literature exploring nest box orientation highlights the subsequent effects of sun expose and temperature, where south-facing boxes are generally warmer (Ardia *et al.*, 2006b; Goodenough *et al.*, 2008). Decreased fledging success in north-facing boxes could therefore be due to increased shade and colder temperatures. However, these findings contradict those found by Goodenough *et al.* (2008), also at Nagshead, when data from 1990-2004 revealed a lower fledging success in south-southwest-facing Pied Flycatcher nest boxes. It is possible different 2022 weather patterns, such as the above average ambient temperature, were drivers behind this disparity (Met Office, 2022a,b).

Another possible influencing factor is exposure to prevailing wind. Although cavity-nesting species can be protected from external weather (Kendeigh, 1961; Collias, 1997), wind speeds can still directly affect nestling growth (Mainwaring and Hartley, 2016) and increase corticosterone levels, a hormone related to the avian stress response (Crino *et al.*, 2020). Heightened exposure to prevailing rain may also increase the risk of nest soaking. Therefore, if nest boxes are frequently exposed to prevailing wind, nestling survival may be negatively affected (Goodenough *et al.*, 2008). Whilst UK prevailing winds are generally south-westerly, short-term local wind patterns during the 2022 breeding season may have varied from this, meaning north-facing boxes were more often exposed. Wind could have also influenced feeding frequency, either directly through flight and foraging ability, or indirectly through nestling body condition and food requirements.

3.4.4. Brood Age

The prevalence of leaning behaviours was significantly higher when nestlings were ready to fledge, compared to when they were two to four and eight to 10 days old (Figure 24). This was expected as older and larger nestlings will typically stand and reach up to the entrance hole when begging, likely helping the adults feed nestlings at the entrance hole and thus increasing the incentive for adult birds to express leaning behaviours. This relationship between the prevalence of leaning and brood age is likely the main driver behind the significant reduction in chick provisioning durations when nestlings were the oldest (Figure 26), especially since the prevalence of leaning was negatively correlated to the mean chick provisioning duration metric (Table 15). (if leaning was more prevalent during visits to the oldest broods, and leaning increased the speed of chick provisioning visits, visit durations when nestlings were the oldest should be lower compared to when they were the youngest).

The visit frequency, chick provisioning frequency, and total time spent chick provisioning significantly increased with the age of the brood (Figures 28, 30 and 35). Similarly, increases in the frequency of food delivery and prey size alongside nestling age have been recorded in a variety of species such as the Gray Catbird (*Dumetella carolinensis*) (Johnson and Best, 1982), Bachman's Sparrow (*Peucaea aestivalis*) (Haggerty, 1992) and Blue Tit (*Cyanistes caeruleus*) (García-Navas *et al.*, 2012). This is likely due to the increasing daily energy requirements as nestlings develop and gain weight (Weathers, 1992), meaning parents may increase prey delivery to compensate for higher nestling food demands (Johnson and Best, 1982). In contrast to these results, the total time spent at the nest was significantly higher when broods were the youngest in my study, relative to the older brood ages. This is likely because this metric includes visit durations longer than 30 seconds, and therefore, although visit frequency was lower for the youngest broods, visit durations were longer. This reflects the differences in the type of parental care provided to chicks at different ages: despite older nestlings requiring more food due to higher energy requirements, the lower thermoregulatory capabilities of younger nestlings results in a higher demand for brooding behaviours to prevent heat loss (Johnson and Best, 1982).

3.4.5. Habitat

Results from the PCA of habitat survey data showed there were clear differences in the vegetation structure between the historically sheep grazed and un-grazed sections of the nest box area, highlighting the habitat modification caused by the sheep grazing, which ceased in 2001, has had long-lasting effects on the habitat (Figures 20 and 21). Grazing pressure from deer, and the rooting behaviour of Wild Boar, where they overturn soil to feed on belowground flora, are known to have significant ecological effects. They greatly impact plant communities by modifying soil chemistry, reducing plant cover and influencing species richness (Kirby, 2001; Massei and Genov, 2004; Barrios-Garcia and Ballari, 2012). It is therefore possible the continued habitat modification caused by these species has influenced the study area's ecological succession since the livestock grazing stopped (Putman *et al.*, 1989). The most apparent difference in the habitat was the significantly higher density of Bracken in the grazed section of the Reserve. This is likely due to the species' ability to withstand grazing pressure and readily colonise disturbed habitats, usually occurring in plagioclimax communities (Dyer, 1990; Cherrill and Lane, 1994; Marrs *et al.*, 2000). It is therefore unsurprising the species has thrived following the relief of grazing from livestock, and the continued pressure from high densities of Wild Boar and deer. More thorough and detailed habitat surveying at RSPB Nagshead is recommended to quantify the variation in vegetation structure in more detail.

This variation in habitat between the grazed and un-grazed areas had clear effects on the ability of parental birds to feed nestlings. The visit frequency and chick provisioning frequency, and the total time spent chick provisioning were all positively correlated to PC1 (Tables 17, 19 and 23): nests in territories with a lower density of Bracken and a higher species richness and density of trees, had a significantly higher chick provisioning frequency. It is most likely the increased density of ecologically important tree species (such as oaks and beeches) and the larger canopy cover in these territories provided better quality foraging patches with a larger prey abundance, thus increasing foraging proficiency and resulting in higher chick proviosning frequency. Such relationships between habitat quality, foraging duration and feeding frequency have been recorded at the habitat level, between evergreen and deciduous woodlands, for example (Blondel *et al.*, 1991), and the territory level, whereby fine-scale patchy distributions of caterpillars occur between territories within the same habitat (Wilkin *et al.*, 2009). However, habitat had no effect on fledging success, highlighting that although chick provisioning frequency was lower in some territories, it was not sufficiently detrimental to nestling survival. It is possible the deciduous woodland habitat at RSPB Nagshead is of overall high quality, providing ample food for local insectivores bird communities. Therefore, although foraging times may have been longer in relatively lower quality territories, the food abundance might still have been sufficient to produce fledglings. Additionally, birds on lower quality territories may have compensated for reduced foraging ability by increasing parental effort and prey selectivity, as described by Tremblay *et al*. (2005).

Mean chick provisioning duration was also positively correlated to habitat characteristics (Table 15), whereby birds in habitats with a higher density of trees and shrubs took longer feeding chicks per nest visit. Reasons for this are unclear but a possible explanation is that birds in these potentially higher quality territories were delivering larger/more prey items, thus taking longer to feed chicks and increasing chick provisioning durations. Alternatively, a higher density of trees and low-level shrubs (e.g. large and dense Holly tress) could have directly obstructed birds as they approached the nest boxes.

3.4.6. Meteorological Conditions

3.4.6.1. Rainfall

Studies have shown that visit frequency can decrease with increasing amounts of rainfall in the Great Tit (Radford *et al.*, 2001), Northern Wheatear (*Oenanthe oenanthe*)

(Oberg *et al.*, 2015), Eurasian Wryneck (*Jynx torquilla*) (Geiser *et al.*, 2008), Eurasian Hoopoe (*Upupa epops*) (Arlettaz *et al.*, 2010) and Gray Catbird (Johnson and Best, 1982). Mechanisms behind this are believed to be due to reductions in insect prey abundance and increased brooding requirements (to compensate for heightened thermoregulatory demands of nestlings) during periods of rainfall. However, results from my study found the opposite, whereby chick provisioning frequency was significantly higher during periods of rainfall, further increasing with rainfall intensity (Figure 31). These results align with those found by Cox *et al.*, (2019), who studied the Tree Swallow (*Tachycineta bicolor*) in Ontario, Canada. The authors suggested a likely explanation is parental birds counteracting the low food availability during adverse weather conditions by increasing their foraging effort, possibly at the expense of their own body condition. Studies artificially increasing parental workload both support and oppose this hypothesis: in response to increased work load parents can increase feeding frequency (e.g. Dijkstra *et al.*, 1990; Martins and Wright, 1993; García-Navas and Sanz, 2010; Lendvai *et al.*, 2018), or show reductions/no differences in feeding frequency (e.g. Winkler and Allen, 1995; Moreno *et al.*, 1999). The ability of parents to increase foraging effort could therefore be spatially constrained according to local food abundance, whereby in habitats with low prey availability, parental birds are already working at their maximum capacity. It is therefore possible the native, semi-ancient woodland habitat that comprises RSPB Nagshead provides ample prey for insectivorous passerines, thus allowing the study species to increase foraging effort during periods of rainfall. Additionally, the resulting large canopy cover may reduce the amount of rainfall reaching the understory, reducing the negative effects caused by intense precipitation. It is also possible the above average spring temperatures in 2022 minimised the heat loss of nestlings, thus reducing the demand for brooding behaviours during rainy periods. Overall, rainfall had no effect on fledging success, unlike the literature which shows marked reductions on both nestling growth and fledging success (Radford *et al.*, 2001; Geiser *et al.*, 2008; Oberg *et al.*, 2015; Cox *et al.*, 2019). This disparity could be due to below average rainfall in 2022 (Met Office 2022a,b).

3.4.6.2. Ambient Temperature

Out of all metrics analysed, the temperature only had significant effects on the total time birds spent at the nest, whereby more time was spent at the nest when temperatures were colder (Table 21). This metric includes visit durations longer than 30 seconds, and this result is therefore most likely linked to brooding behaviours. Particularly at hatching, altricial nestlings generally do not have thermoregulatory capabilities, and therefore struggle to generate heat in low ambient temperatures (Ricklefs and Hainsworth, 1968). As a result parental birds will increase brooding when temperatures are low to minimise the chances of hypothermia (Johnson and Best, 1982). Therefore, when temperatures were colder, the prevalence of brooding behaviours may have been higher, thus increasing the total time spent at the nest. Overall, it is worth mentioning the temperatures included in the models were not directly recorded at the Reserve but were taken at the *Staverton Private* weather station in Gloucestershire. It is therefore possible local temperatures differed from these values.

3.4.7. Time of Day

Out of all metrics analysed, the time of day only had significant effects on chick provisioning frequency (Figure 31 and Tables 19 and 20). Results from my study found a consistent chick provisioning frequency throughout the morning and into the early afternoon (09.00 to 15.00hrs), followed by a significant peak in the late afternoon (15.01 to 17.00hrs) and a sizable drop in the evening (17.01 to 19.00hrs). Other studies however, have found temporal consistency in feeding frequency throughout the course of the day (e.g. Goodbred and Holmes, 1996; Sethi and Bhatt, 2007; Barba *et al.*, 2009), constant declines from early morning to nightfall (Low *et al.*, 2008; García-Navas and Sanz, 2012; Pagani-Nunez and Senar, 2013), peaks at dawn and dusk (Knapton, 1984), and a lower frequency in the morning (Olson *et al.*, 2009). There is therefore large disparity in the literature regarding the daily variations in chick feeding frequency, and this may be attributed to differences in factors between study sites (e.g. prey diversity, predation risk and temperature). Although Pagani-Nunez and Senar (2013) found daily declines in provisioning frequency, an increase in prey size over the course of the day was also found, highlighting that parent birds may counteract daily variations in feeding frequency by altering prey selectivity.

3.4.8. Observed Predation events

The only predator observed in video footage was Great Spotted Woodpeckers, where seven predation attempts were seen, each occurring at different nest boxes. This is unsurprising as woodpeckers are a common and effective predator of natural and artificial cavity nests (Walankiewicz, 2002; Czeszczewik and Walankiewicz, 2003; Mainwaring and Hartley, 2008). No predation by mammals, including Pine Martens, was recorded, despite them being common nest predators and the focus of a species recovery effort across the Forest of Dean (Stringer et al., 2018). The lack of observation was likely due to the species' crepuscular nature.Woodpeckers would most frequently lean in through the entrance hole in attempts to grab nestlings (Figure 40), but, all seven observed predation attempts failed. On one occasion, a nestling reaching up to and out of the box's entrance hole was grabbed by a woodpecker's bill, but escaped the bill before retreating back into the cavity; it was unclear whether the chick was injured.

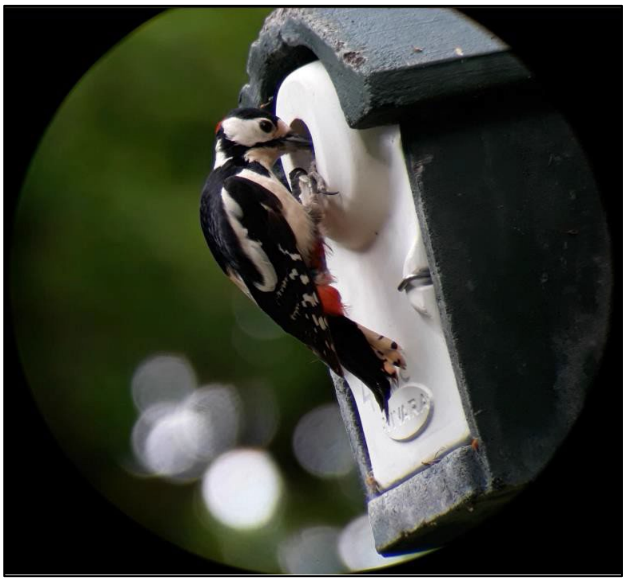


Figure 40. A Great Spotted Woodpecker attempting to access a woodcrete nest box by leaning in through the entrance hole. Image taken from video recordings by Joseph Marcus at RSPB Nagshead Nature Reserve.

No predation events were seen when chicks were two to four days old, likely because nestlings are smaller and less likely to reach up to the entrance hole at these younger ages (Nuhlíčková *et al.*, 2021), ultimately making it more difficult for predators to reach the nestlings. Woodpeckers were also seen pecking at the side and front panels of the nest boxes, but were never seen to excavate sufficiently large holes to access the nest boxes. Their failure to access the standard nest boxes is likely due to their design, where gaps between wooden panels were small and the front panels cover the edges of the side walls, thereby limiting weak points which the woodpeckers could otherwise exploit, as explained by Skwarska et al. (2009).

3.4.9. Study Limitations

3.4.9.1 Sample Size and Study Power

Due to the large scale of the nest box scheme, the overarching aim of the study design was to maximize the number of nest boxes included in the study. However, a low occupancy of predator-proofed nest boxes and overall low breeding success greatly reduced the maximum possible sample size. Therefore, with only 51 nesting attempts being included in the study, 17 of which were in predator-proofed nest boxes, a smaller-than-expected dataset was collected. It is generally important to discuss the reasons behind the collection of a small sample size, and consider the potential effects caused during statistical procedures. As shown in Table 9, out of the 249 nest boxes used by breeding birds in the reserve, only 48 were of a predator-proofed design, of which just 27 had at least one presumed successful fledgling. The uptake of guardian tube boxes was particularly low, with only two occupied across the whole reserve. Productivity (percentage of total eggs to successful fledglings) across all 249 nests was only 35%, which is comparatively low when compared to previous years (Figures 41 and 42). Low productivity in 2022 could be due to short bouts of rainfall followed by above average spring and summer temperatures (Met Office, 2022a, 2022b). Low breeding success also resulted in many of the selected nests failing as the season progressed. This often meant entire broods died after one or two observations.

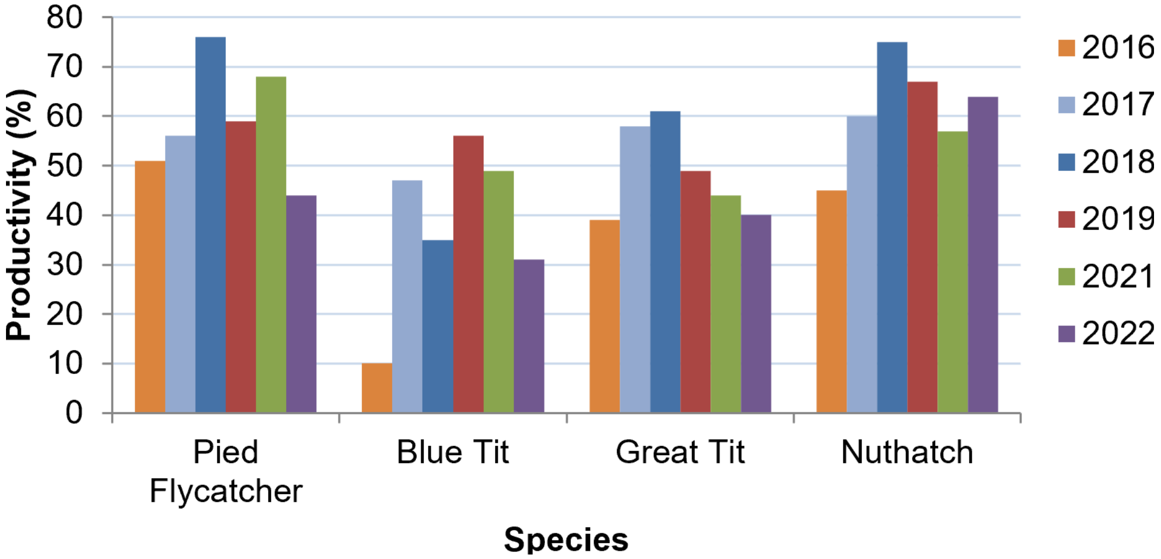


Figure 41. The annual productivity (percentage of total eggs to successful fledglings) of nests from the RSPB Nagshead Nature Reserve nest box scheme between 2016 and 2022. Graph provided by Lewis Thompson.

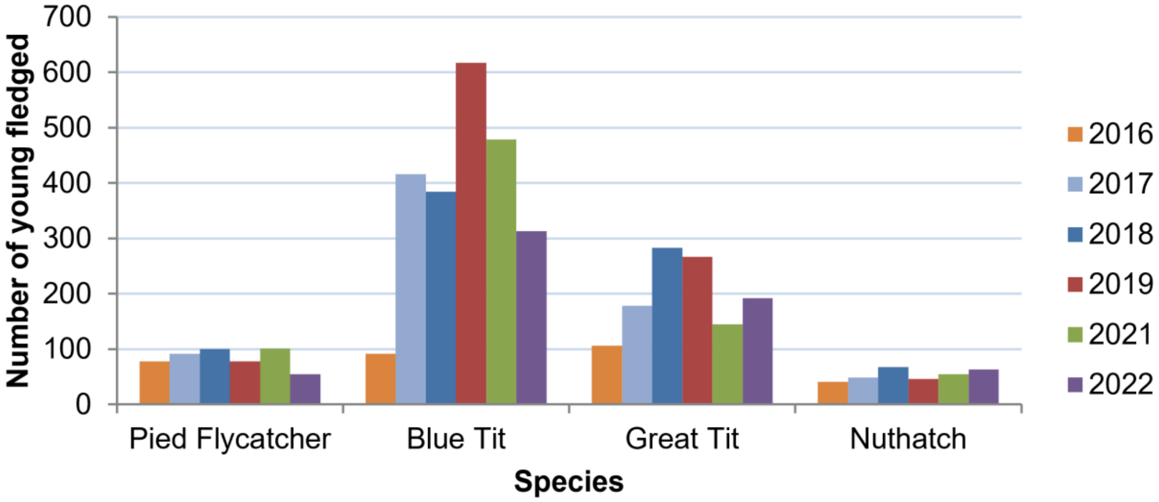


Figure 42. The annual number of nestlings fledged from the RSPB Nagshead Nature Reserve nest box scheme from 2016 to 2022. Graph provided by Lewis Thompson.

Generally, the reduced dataset collected will have caused a variety of limitations when analysing results. G*Power (Version: 3.1.9.6) was used to run a power analysis in order to compute the optimal sample size needed for similar linear multiple regression analyses (Kang, 2021). In this instance, the risk of a type 1 error is preferable (Di Stefano, 2003). For example, the hypothetical conclusion that a predictor variable such as nest box type has no effect on chick provisioning, when they actually do (false negative), could lead to the installation of nest boxes that are having unknown negative consequences. As increasing the power of a test decreases the type 2 error risk, whilst simultaneously increasing the type 1 error risk, a relatively high power of 90% was chosen for this sample size calculation (Di Stefano, 2003). The medium effect size for a linear multiple regression of 0.15 was used, as described by Cohen (1988). Overall, the output of these calculations reveal that a sample size of 157 or 123 would be required, with the inclusion of 12 or six predictor variables, respectively. With only 51 nests being included in this study, there is certainly the potential the computed GLMs did not have sufficient power to detect true effects, especially when subdividing data according to factors (e.g. nest box type, orientation). Any bias caused by uncontrolled variables, such as parental care patterns (divorced or widowed females), predator presence, and individual fitness/experience, may therefore be intensified due to small sample sizes. Many of the statistical approaches used (e.g. exclusion of interaction terms and stepwise variable selection) were taken with the aim of reducing model complexity and minimising these effects.

It is also worth mentioning a methodological procedure that resulted in the missing of some brood ages, and although it did not cause substantial issues, it is still important to discuss in order to streamline future research. As outlined in the NRS code of conduct, in order to avoid disturbance and reduce the chances of desertion, whenever parent birds were sitting on the nest during nest box checks, the nest was left undisturbed until the following week (Crick *et al.*, 2003b). Sitting is common during egg laying and incubation, and the occurrence of this behaviour was widespread during early nest box checks. Therefore, whenever nests were left un-checked for multiple weekly checks, the breeding parameters needed to calculate hatching dates were left unknown until later in the breeding season. In such situations, the hatching dates of these nests were often missed. More frequent nest box checks would increase the likelihood of visiting a nest when parent birds are away from a nest. Although this would increase disturbance, research has shown nests that are visited more frequently (up to three day intervals), actually have a higher breeding success, where the increase in human presence significantly reduces predation (Ibanez-Alamo and Soler, 2010). However, with nest box schemes as large as the one at Nagshead, organising large groups of volunteer work to routinely check sizable numbers of nest boxes on a more than weekly basis may not always be feasible.

3.4.9.2 Presumed Feeding Visits

Visit durations were recorded under five headings according to whether birds were observed carrying food items and/or waste material. However, when analysing video footage, motion blur meant it was often impossible to discern whether birds were carrying food items into the nest box. This issue is reflected in the results, where only 13% of all parent visits were recorded under heading one (‘feeding only’), and this is unlikely to be an accurate representation of the actual number of feeding events that occurred. Furthermore, species-dependent behaviours also caused bias in the number of these observed feeding visits. The Eurasian Nuthatch would often land atop the nest box, appearing to assess the surroundings before dropping down through the entrance hole. Compared to the other three species, it was easier to identify whether Eurasian Nuthatches were carrying food.

Therefore, a novel method of presuming feeding visits was implemented, whereby visits were assumed to be exclusively for chick provisioning only if all other reasons for a visit could be excluded. This method allowed the inclusion of visits under heading five (‘undeterminable’) and therefore provided a more statistically robust method by improving sample sizes and removing species-dependent observation bias. However, because the method was based on assumptions, there is the possibility that non-feeding visits were assumed to be for chick-provisioning (vice versa), and it is therefore important to assess the method’s reliability. Because video footage was recorded from outside of the nest boxes, it cannot be said for certain what behaviours occurred inside the nest chamber during each parent visit. Therefore the method’s reliability cannot be assessed from the current study and testing is recommended. The comparison of footage from the method described in my study and internal nest box cameras (where the number of chick provisioning visits can be directly observed with minimal imprecision) could be used to validate the presumed chick provisioning visits.

Regarding the failure of the initial method, increasing the frame rate and resolution of video recordings would decrease motion blur and improve clarity. This would serve to increase the chances of detecting food items, whilst also allowing for a higher precision when calculating visit durations. However, as was the case with this study, this can be restricted by the storage capacity of the cameras in use. The rapid movement of small passerine species may also mean the frame rate required to prevent motion blur when analysing footage frame by frame may not be achievable without specialist equipment (e.g. professional digital single-lens reflex camera). The use of Internal nest box cameras can also be costly and impractical for large-scale nest box schemes. Therefore, the use of external video recordings or direct observation, alongside the implementation of this novel procedure for identifying chick provisioning visits, could provide an effective and cheap method of quantifying chick feeding.

3.5. Conclusion

Relative to the widespread and common use of the nest box predator-prevention methods discussed in chapter 2, there is a considerable lack of literature testing both their effectiveness and biological effects on breeding birds. Some preliminary research has tested the efficacy of deep and woodcrete nest box designs, relative to standard wooden boxes, and although provide a rudimentary insight into their biological effects, it has given rise to further questions that are yet to be fully explored. There is an absence of recent and dedicated research, with substantial samples sizes and robust statistical analysis, testing the use of nest box modifications, such as baffles, metal protection plates and guardian tubes. It is likely their cost-effective design, combined with their simplistic and logical functionality have resulted in many researchers and landowners assuming their effectiveness.

Results from the research project in chapter 3 support the hypothesis originally proposed by Blunsden (2020). Although predator-proof nest boxes did not prevent birds from exhibiting leaning behaviours, they had clear negative effects on chick provisioning durations. Therefore, it cannot be concluded that nest box design had no effect on a bird’s ability to effectively enter and exit the nest box to feed nestlings, and further research is warranted.

Overall, there is little scientific evidence to advise against the use of predator-prevention methods for nest boxes. However, it is clear there are unintended negative consequences, and their severity on individual fitness and productivity is uncertain. Whether these methods provide a net benefit to birds remains unclear, and concrete conclusions cannot be drawn until further research is conducted. Despite this, nest boxes have been, and will likely to continue to be, a crucial tool in both conservation and ornithological research, especially for threatened species. It is therefore important to note the ethical implications of erecting ill-conceived nest boxes, and reiterate that there use is a responsibility. It is recommended that until there is a better understanding of their effects on the bird’s breeding behaviour, nest box predator-prevention methods should be used potently, as a last resort to stabilize and reverse population trends of threatened species where nest predation and nest-site availability is proven to be a significant issue affecting their populations.

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