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The use of nestboxes by roosting birds during the non-breeding season: a review of the costs and benefits

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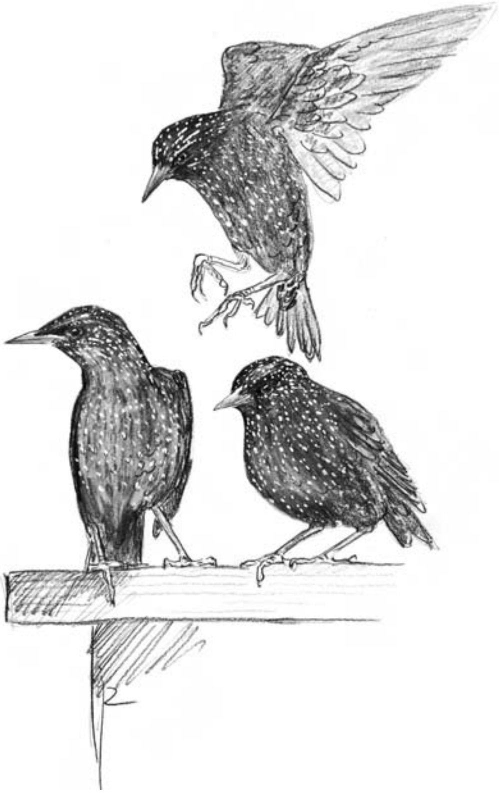

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The advantages and disadvantages of breeding in nestboxes are well known, whilst the merits of roosting in nestboxes during the non-breeding season remain poorly understood. Here I review the advantages and disadvantages of using nestboxes as roosting sites during the non-breeding season. The main advantage of nestboxes is that they increase the number of cavities available for roosting and birds gain considerable thermal benefits and energy savings, when compared to congeners roosting outside of cavities. However, the main disadvantage is that roosting birds are widely targeted by detrimental ectoparasites, and birds actively avoid nestboxes where ectoparasites are abundant. Meanwhile, there is insufficient evidence to make any firm conclusions as to whether roosting in nestboxes increases or decreases predation risk and this is an area, which warrants further research. Consequently, there is a great deal of variation in the quality of individual nestboxes as roosting sites, and interspecific competition results in larger and more dominant species roosting in preferred nestboxes. In summary, this review emphasises the importance of nestboxes to roosting birds during the non-breeding season.

Key words: nestboxes, roosting, energy expenditure, ectoparasites, predation risk, interspecific competition

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The use of nestboxes as breeding sites by secondary hole-nesting birds has advantages and disadvantages for both birds and researchers (Møller 1989, 1992, 1994, Koenig *et al.* 1992, Lambrechts *et al.* 2010). The propensity with which some passerine species breed in nestboxes at high densities, together with their tolerance of routine monitoring activities and experimental manipulations, has established them as some of the classical vertebrate model species. Consequently, species such as Blue Tits *Cyanistes caeruleus*, Great Tits *Parus major*, Eastern Bluebirds *Sialia sialis*, Pied Flycatchers *Ficedula hypoleuca*, and Collared Flycatchers *Ficedula albicollis* have contributed disproportionately to our knowledge in ecological and evolutionary research (Newton 1989, Griffith *et al.* 2008, Clutton-Brock & Sheldon 2010). Moreover, such species show high levels of natal philopatry and the longitudinal nature of such studies have considerably advanced our understanding of both the evolution of life histories in the wild (Newton 1989) and how individuals and populations respond to anthropogenic climate change (Both *et al.* 2006, Charmantier *et al.* 2008). Additionally, the fact that many researchers use the same model species across the species range has provided major insights into the spatial nature of population dynamics and responses to anthropogenic climate change (Visser *et al.* 2003, Sæther *et al.* 2007). Nestboxes are also provided by conservation biologists for endangered birds whose numbers are limited by the availability of suitable nest sites (Newton 1998). For example, when the world population of Seychelles Magpie Robins *Copsychus sechellarum* reached an all time low of just 23 individuals in 1998, a conservation program, including the provision of nestboxes, was initiated and the population had grown to 149 by 2004 (Birdlife International 2005).

However, breeding in nestboxes can also be disadvantageous for both birds and researchers. Whilst the widespread use of nestboxes by model species is overwhelmingly beneficial for the birds, it has been suggested that studies involving nestbox breeding birds do not accurately reflect wild birds for two main reasons

(Møller 1989, 1992, Wesołowski 2007, Lambrechts *et al.* 2010, but see Koenig *et al.* 1992). First, nest predation rates are significantly higher in natural cavities than in nestboxes, partly because researchers commonly add protective devices to nestboxes to reduce predation rates (van Balen *et al.* 1982, McCleery *et al.* 1996, Mainwaring & Hartley 2008, Griffith *et al.* 2008, Skwarska *et al.* 2009). Second, researchers commonly remove old nests at the end of each breeding season, which reduces the abundance of detrimental ectoparasites when compared to natural cavities (Møller 1989, Mazgajski 2007, Thomás *et al.* 2007). Consequently, results derived from such studies may fail to reflect natural variation and thus lack general validity or applicability (Nilsson 1975, Møller 1989, 1992, 1994, Thomás *et al.* 2007, Wesołowski 2007, Lambrechts *et al.* 2010, but see Koenig *et al.* 1992). Conservation biologists, meanwhile, have commonly provided nestboxes for endangered birds, and although there have been some spectacular success stories (Birdlife International 2005), there have also been some undesired consequences. For example, the global population of Barn Owls *Tyto alba* has declined and the availability of suitable nest sites has been identified as a key limiting factor. Consequently, nestboxes have been provided for the owls across their range, and are often viewed as having a positive effect on the owl population. However, a recent study in Hungary showed that Barn Owl chicks from nestboxes had significantly lower survival rates than those chicks from 'natural' church towers. The nestboxes were effectively acting as ecological traps, which may eventually lead to population instability or decline (Klein *et al.* 2007).

However, the merits of roosting in nestboxes during the non-breeding season remain located in disparate sources and poorly understood. Here I review the advantages and disadvantages of using nestboxes as roosting sites during the non-breeding season.

NESTBOXES AS ROOSTING SITES

Those bird species that use cavities as breeding sites may also use cavities as roosting sites (Newton 1998). Consequently, it follows that there is also a great deal of interspecific variation in the characteristics of cavities used for roosting during the non-breeding season. For example, whilst the majority of species, such as Blue Tits and Nuthatches *Sitta europaea* sleep in empty cavities, others, such as Tree Sparrows *Passer montanus* construct a specifically designed nest like structure in the autumn in order to help keep them warm during cold winter nights (Pinowski *et al.* 2006). Other species, such as Red-cockaded Woodpeckers *Picoides borealis* and Downy Woodpeckers *Picoides pubescens* excavate holes that are purely used as roosting sites (Jackson & Jackson 1994). The fact that some woodpeckers expend a considerable amount of energy excavating their own cavities for roosting gives an indication of the importance of cavities as roosting sites for birds (Jackson & Jackson 1994, Lambrechts *et al.* 2010). In a study which compared Great Spotted Woodpecker *Dendrocopus major* breeding and roosting cavities, there were no differences between them in terms of tree species, condition, girth at breast height, cavity height or cavity orientation. However, behavioural observations suggested that particular holes might be selected as roosting sites, probably based on there being a preferential microclimate and being in a safe location (Mazgajski 2002). Meanwhile, the majority of species that roost in cavities, such as Great Tits and Blue Tits, roost solitarily, whilst other species such as Pygmy Nuthatches *Sitta pygmaea*, Wrens *Troglodytes troglodytes* and Green Woodhoopoes *Phoeniculus purpureus* prefer to roost communally in groups (Kristin *et al.* 2001, Dhondt *et al.* 2010, Vel'ký *et al.* 2010b).

Those species which use nestboxes as breeding sites also use nestboxes as roosting sites. The composition of bird communities that use nestboxes as roosting sites have been the focus of three studies. In the first study, which examined patterns of roosting birds in 44 study areas in Germany, nine bird species were found to be roosting in the nestboxes (Winkel & Hudde 1988). The most frequent occupants were Great Tits (75.8%), Nuthatches (13.3%), Blue Tits (8.0%) and Tree Sparrows (2.7%), whilst Great Spotted Woodpeckers, Lesser Spotted Woodpeckers *Picoides minor*, Starlings *Sturnus vulgaris*, Marsh Tits *Poecile palustris* and Short-toed Treecreepers *Certhia brachydactyla* were only occasional occupants. There were seasonal changes in occupancy rates, with the number of Great Tits and Nuthatches being highest in December and declining as winter progressed through to March, whilst in contrast, the number of Blue Tits was lowest in December and increased as winter progressed through to March. Meanwhile, there were always more adult than juvenile Blue and Great Tits throughout the winter period and joint roosting of two or more individuals in one nestbox was recorded only in the case of Tree Sparrows and Starlings (Winkel & Hudde 1988). In the second study, which examined patterns of roosting birds in an oak–hornbeam forest in Slovakia, the only two species that were recorded roosting in the nestboxes were Great

Tits and Nuthatches (Kristin *et al.* 2001). Similarly to the study by Winkel & Hudde (1988), there was considerable seasonal variation in the occupancy rates of the birds, with the highest numbers of birds being found in November, before decreasing slightly towards April. There were also sex differences in occupancy rates, with 68% male and 32% female Great Tits and 66% male and 34% female Nuthatches present. Moreover, of the total of 157 roosting birds included in the study, 72% were recaptured again at some point in the study area, implying that roosting site fidelity was very high in that study. Interestingly, whilst the birds roosted in the nestboxes alone, the species and individual birds that occupied a nestbox were found to alternate on a regular basis (Kristin *et al.* 2001), meaning that individual birds did not roost in the same nestbox every night. In the third study, patterns of nestbox occupancy were examined in an urban area of the Czech Republic (Vel'ký 2006). It was found that only two species, Great Tits and Nuthatches, used the nestboxes and occupancy rates in 30 nestboxes during the course of two winters ranged between 3–17%. Birds always roosted alone and whilst the sex ratio of the roosting birds was skewed towards females in November, the sex ratio between December and mid February was even. Interestingly, ring recoveries showed that individual Great Tits used between one and four nestboxes as regular roosting sites and switched among them on a regular basis. The mean distance between two captures was 42 metres for females and 60 metres for males, whilst the maximum dispersal recorded was 231 metres for males and 150 metres for females (Vel'ký 2006). However, there is evidence to suggest that roosting great tits only move between roosting sites when they are disturbed or caught whilst roosting, which suggests that such dispersal was caused by the disturbance from roosting checks. Roosting in nestboxes, or natural cavities, appears to be commonplace amongst a relatively small range of small, secondary cavity-nesting birds. The large amount of seasonal variation in occupancy rates, with respect to the sex and age of the occupants, suggests that there is considerable intraspecific competition for the preferred nestboxes. Therefore, roosting locations may have important consequences for settlement patterns within populations and directly affect the chance of obtaining a future breeding territory. Consequently, individuals are likely to gain long-term benefits from roosting patterns, in addition to the short-term thermal benefits and subsequent energy savings. Such long-term benefits are likely to be most important in species that hold territories, such as nestbox-breeding Great Tits (Kluyver 1957, Drent 1983).

THERMAL BENEFITS AND ENERGY SAVINGS

The main advantage of nestboxes is that during the nights, when temperatures are at their lowest and thus energetic costs for thermoregulation are highest, birds gain considerable thermal benefits and energy savings, when compared to roosting in open sites in the tree canopy (Kendleigh 1961, Dhondt & Eyckerman 1979, Walsberg 1986, Sedgeley 2001, McCafferty *et al.* 2001, Vel'ký *et al.* 2006, 2010a, 2010b, Paclik & Weidinger 2007). More specifically, birds roosting inside nestboxes save energy as a direct result of a reduction in heat loss both by radiation and by convection caused by wind, but also from a reduction of thermal conductance due to additional layers isolating the body from the external environment. Consequently, there is a reduction in the temperature difference between the bird and its direct surroundings (Kendleigh 1961, McCafferty *et al.* 2001, Vel'ký *et al.* 2006). Interestingly, one study found that shelter from the wind provided approximately five times more thermal benefit than any improvement of radiation balance, whilst possible metabolic heating by the bird of air within the roost itself was unimportant (Walsberg 1986). Such energy savings are critical for small birds living in temperate zones, where the short and cold days during the winter months result in birds struggling to find sufficient amounts of food in order to provide energy to stay alive during the long nights. Overnight energy savings of even a few per cent can influence survival (Newton 1998), which means that locating a suitable roosting site is critical, especially for small birds.

One study quantified the pressures which face small birds during winter (Pinowski *et al.* 2006). The body weight of Tree Sparrows in winter varied from 21.4–26.2 g, including 1.46–3.02 g of fat. At an ambient temperature of –10°C, the smallest fat amount was hardly enough for a bird to survive the night, while the fattest tree sparrows would have an energy store for only ~24 hours at that temperature. Therefore, winter fat storage by the sparrows was hardly enough to enable them to survive through the night and then a part of the following day. This means that natural selection promotes optimal energy acquisition during the day in order to facilitate survival through the night. Without storing excessive fat reserves, one way is to roost in nestboxes at night (Pinowski *et al.* 2006), which only serves to highlight the critical importance of nestboxes for facilitating the survival of small birds through the long winter nights.

The selection of nestboxes in relation to their thermal properties has been the attention of several studies.

An observational study of birds roosting in nestboxes in an urban environment in the Czech Republic found that only two species, Great Tits and Nuthatches, used the nestboxes (Vel'ký 2006). Nestbox occupancy rates in 30 nestboxes during the course of 2 winters ranged between 3–17%, with the highest occupancy rates being found when the ambient temperatures were lowest. That study showed that whilst other factors, such as the length of daylight, weather, nestbox cleanliness, predators and human impact were also important, the key factor influencing the nestbox occupancy was the ambient air temperature (Vel'ký 2006). Another study examined the relationships between cavity temperature, ambient temperature outside the cavity and the structural characteristics of 70 cavities (Paclik & Weidinger 2007). It was found that the mean temperature increment of cavities varied between –2.4°C and 4.9°C and increased with higher day-to-night fluctuations in the ambient temperature, smaller cavity entrance and better health status of the cavity tree. Cavities in healthy trees were warmer than those in dead trees, but this difference disappeared with rising mean ambient temperatures. It was concluded that roosting birds selected the warmest natural cavities for roosting and that the predictors of microclimate may provide indirect cues to prospecting birds (Paclik & Weidinger 2007).

Given that birds are able to select those nestboxes which provide the best insulation against the cold winter nights, it is not surprising that the Phainopepla, *Phainopoplnai tens*, was found to increase the temperature of its nestbox by 9.5°C, which resulted in a reduction by 20% of resting energy expenditure (Walsberg 1986). Meanwhile, House Sparrows *Passer domesticus* roosting in nestboxes half filled with nest material saved 13.4% of heat at a temperature of –30°C and 11% at –8°C (Kendleigh 1961). Furthermore, Carolina Chickadees *Poecile carolinensis* reduced their overnight metabolic requirements by 50% by decreasing their body temperature by 10°C by roosting in cavities with higher ambient temperatures than those temperatures outside of cavities (Mayer *et al.* 1982). Furthermore, by using hypothermia, Mountain Chickadees *Poecile gambeli* in America were found to save as much as 50% of their energy overnight, while the larger Juniper Titmouse saved up to 28% (Cooper 2000).

The most detailed study of the thermal benefits and energy savings was made of Barn Owls in Scotland (McCafferty *et al.* 2001). The energy savings made by owls roosting in a nestbox in a rural farm building was compared with the savings made by owls roosting in the canopy of a tree, using a biophysical model via measurements of microclimate. The roost building provided complete shelter from wind and precipitation and the air temperature inside the roost building was 1.4°C greater than the ambient temperature and matched the seasonal change in temperature. Air temperature inside the nestbox was on average only 0.8°C greater than ambient but was 2–3°C warmer when adults and chicks were in the nest during the breeding season. At night, metabolic heat production was greater by 4–12% compared with daytime, depending on location. Heat loss was 30% greater in winter months than in the summer in all locations. The owls were estimated to reduce metabolic heat production by 19% by roosting in the building and by 10% by roosting in a tree, when compared to roosting in the open. In the building and tree, savings of 21% and 9% respectively occurred during the day, compared with 17% and 12% respectively at night. The building used as a roost and nest site had a microclimate that provided thermal advantages for the owls. The building gave complete shelter from wind and precipitation and reduced exposure to the cold radiative temperature in the sky. Metabolic savings were strongly dependent on weather conditions with average metabolic savings of 26% occurring in wet and windy conditions compared with only 12% on dry/calm days. Maximum savings of 29–36% occurred on wet days. Barn Owls appear to compensate for high metabolic demands for heat production by taking advantage of better thermal conditions within buildings, especially during the day when metabolic savings are greatest (McCafferty *et al.* 2001). These energy savings were typical advantages of previously studied night-time roosts where roosts have been shown to reduce wind speeds by 24–100%. The air temperature inside the roost was on average 14°C cooler than ambient due to passive solar heating of the building during the day. Because of the size of the roof space, Barn Owls perched on the roofing beams did not benefit from any localised heating derived from their own body heat. However, the temperature inside the nestbox was 2–3°C above ambient during the breeding season when adults and chicks were present. Barn Owls were estimated to reduce annual metabolic heat production by 19% by roosting in the building, whilst roosting in a spruce tree was predicted to make savings of only 10% (McCafferty *et al.* 2001).

In addition to roosting in a nestbox, or a natural cavity, birds can make additional energy savings by roosting communally in groups. One study examined the thermal consequences, energy benefits and patterns of night-time communal roosting in Acorn Woodpeckers *Melanerpes formicivorus* during the non-breeding season (du Plessis *et al.* 1994). It was found that the oak limbs in which the woodpeckers roosted, cool more slowly than the surrounding air, which meant that the overnight temperatures inside unoccupied woodpecker roosts averaged 4.3°C higher than the outside ambient temperature, when the later was approximately 0°C. However, the temperature of occupied roosts was further increased as more birds shared the communal roost. For example, a single woodpecker increased the cavity temperature by an additional 1.2°C, whereas four birds increased it an additional 6.0°C. Interestingly, it was found that when placed in a simulated roost-cavity metabolism chamber, the woodpeckers did not huddle together at low air temperatures. This meant that at night-time, their fasted oxygen consumption was independent of group size. Using these two measurements, it was estimated that an outside temperature of 0°C a single cavity-roosting woodpecker would reduce its heat loss by at least 9%, whereas four birds would reduce their heat loss by at least 17%. It was concluded that such large energy savings may contribute to the higher winter survival noted for male Acorn Woodpeckers that live in larger groups (du Plessis *et al.* 1994). Meanwhile, another study examined the energy savings made by roosting with conspecifics in a cavity in Green Woodhoopoes, which is a species that roosts in cavities in groups throughout the year. It was found that a woodhoopoe roosting with four conspecifics was able to reduce its night-time energy expenditure by 30% or more when the minimum ambient temperature was about 5°C. In areas where nocturnal temperatures sometimes drop below freezing, such energy savings were strongly associated with mortality patterns among adults during winter. Consequently, the woodhoopoes conserved considerable amounts of energy by roosting with conspecifics in cavities and it was concluded that such energy considerations might have been important in the evolution and/or maintenance of sociality in this species (du Plessis & Williams 1994).

Surprisingly perhaps, very few studies have experimentally examined the relationship between heat and roosting behaviour. An experimental study in Slovakia examined patterns of roost site selection by Great Tits in relation to experimentally altered thermal properties inside nestboxes. An experimental aviary offered two artificial tree roosts with different micro-climactic conditions, one being insulated and the other being left alone. It was found that the birds actively explored roosts before preferentially selecting those nestboxes with higher ambient temperatures (Vel'ký *et al.* 2010b). In a second experiment, Great Tits were offered a choice of roosting in coniferous or deciduous vegetation, in the absence of a nestbox. The Great Tits were found to thoroughly explore both options before spending more time exploring the coniferous vegetation and eventually showing a preference towards roosting in the warmer coniferous vegetation (Vel'ký *et al.* 2010a).

Another study examined the thermal properties of Tree Sparrow nests that were built in the autumn, which serves as a winter nocturnal roosting site for the pair of sparrows, and is likely to reduce heat losses on frosty winter nights. If nocturnal roosting in nests contributes to energy savings by Tree Sparrows during winter, then the autumn display of building a nest, despite incurring costs (Mainwaring & Hartley 2009), may be prompted by natural selection. Using electronic apparatus in order to simulate a bird roosting in a nest at night, the insulating qualities of tree sparrow nests built in nestboxes under winter conditions were examined. Nests of different construction were compared with an empty box, and with roosting in open air. Energy savings in an empty box accounted for 18%, in boxes with incomplete nests for 23% and in boxes with complete nests up to 36% (Pinowski *et al.* 2006).

Another study examined whether thermal factors are important for the quality of roosts occupied by bats, and whether or not they base their day roost selection directly on roost temperature at night, in colonial female Bechstein's Bats, *Myotis bechsteinii* (Kerth *et al.* 2001). Over one summer, the study examined and tested the roost choice of 21 individually marked female bats, living in one maternity colony. The bats were able to choose between relatively warm vs. cold bat boxes, while controlling for site preferences. It was found that females significantly preferred cold roosts before parturition, whereas post-partum, they significantly favoured warm roosts. This was expected as females should prefer warm roosts during pregnancy and lactation in order to accelerate gestation and shorten the period of growth of the young. Females should also prefer warm roosts as they reduce energy consumption in an energetically costly period of reproduction. Temperature preferences were independent of the roost site, and thus roost selection was based directly on temperature. Boxes with significantly different daytime temperatures did not differ significantly at night. Consequently, bats would have to spend at least one day in a new roost to test it and therefore, information transfer among colony members might facilitate knowledge of roost availability (Kerth *et al.* 2001). These studies provide overwhelming evidence that birds, and other taxa, gain considerable thermal benefits and energy saving from roosting in nestboxes.

However, the regular occurrence of potential hosts does not go unnoticed by ectoparasites.

ECTOPARASITE ABUNDANCE

Ectoparasites can have severe negative impacts on the fitness of hosts during both the breeding and non-breeding seasons (Toft 1991). For example, a study which experimentally increased the abundance of the hematophagous Hen Flea *Ceratophyllus gallinae* in the nests of nestbox-breeding Great Tit hosts found that when compared to controls, experimental pairs laid eggs later in the year, deserted their nests during incubation more frequently and had lower hatching and fledging success (Oppliger *et al.* 1994). Nestboxes used in academic studies are routinely cleaned out at the end of each breeding season, partly to reduce or limit the number of ectoparasites present (Møller 1989, 1992, 1994, Koenig *et al.* 1992, Wesolowski & Stańska 2001). This is generally successful as removing old nests does reduce the number of ectoparasites present, although it is unlikely to ever be completely effective as ectoparasites can survive over long time intervals, such as from one summer to the next, inside their cocoons. Their emergence is then triggered by rapid increases in temperature and by mechanical stimulation which can be provided either by a roosting or nestling bird (Humphries 1968). Nevertheless, in areas where there are no nestboxes and roosting cavities are therefore limited, the presence of a used nest will not prevent birds from roosting in that cavity, even though the birds face a trade-off between the thermal benefits gained from roosting inside a cavity and the disadvantages of being parasitized by ectoparasites. The abundance of ectoparasites is known to influence the location of roost sites in a range of bird species, whether they are cavity nesting species or not. For example, Great Horned Owls *Bubo virginianus* in Canada exhibit a seasonal shift in roost site selection due to ectoparasites (Rohner *et al.* 2000). During the winter months, the owls roosted on concealed perches at the mid-canopy level, which is typical for forest inhabiting owls, but during the summer months, the owls roosted close to the ground or on the open ground. It was found that the shift from roosting in the canopy to roosting on or close to the ground coincided with the emergence of ornithophilic Black Flies *Simulium yahense*, which transmit avian malaria. Black Fly activity was highest at the mid-canopy level and they were almost non-existent either on or close to the ground. Therefore, it was concluded that the presence of Black Flies and avian malaria can influence the vertical distribution of roosting owls (Rohner *et al.* 2000). Given that parasites exert strong selection pressure on their hosts, it is not surprising that a number of studies have investigated roost site selection by birds in relation to ectoparasite abundance. An observational study showed that whilst Blue Tits roosted in nestboxes in southern France, they did not on the nearby island of Corsica. The reason for this discrepancy was thought to be that the Blue Tit nests on Corsica were very heavily parasitized and hence the birds avoided roosting in them (Dhondt *et al.* 2010).

Meanwhile, an experimental study in Switzerland examined if Great Tits preferred to roost in natural cavities or in nestboxes with varying levels of ectoparasite abundances (Christe *et al.* 1994). In the first experiment, single nestboxes were placed in territories to test if birds would roost in a heavily infested nestbox, if that nestbox was the only place to roost in, and in the absence of another suitable roosting site, may have to roost outside. It was found that whilst Great Tits roosted in the heat-treated nestboxes, which contained nests but no ectoparasites, they avoided the highly infested nestboxes in favour of natural cavities or in the tree canopy (Christe *et al.* 1994). Therefore, Great Tits preferred to roost in ectoparasite free nestboxes rather than natural cavities and in natural cavities rather than in nestboxes, where ectoparasites were abundant. In the second experiment, pairs of nestboxes were provided within territories, in order to test whether the Great Tits preferred to roost in empty nestboxes or in nestboxes that had a nest, but had been heat-treated so that it contained no ectoparasites. The birds showed no preference for either type of nestbox, indicating that the presence of an old nest without ectoparasites did not alter the roosting preferences of the birds. In the third experiment, pairs of nestboxes were provided within territories, in order to test whether Great Tits preferred roosting in nestboxes containing old nests which had either been infested with approximately 20 fleas or had been heat-treated to remove fleas. The Great Tits were found to prefer roosting in the nestboxes that were free of ectoparasites (Christe *et al.* 1994).

In another experimental study, roost site selection by Great Tits was examined in relation to ectoparasite abundance in Sweden. First, an observational study showed that Great Tits roosting in nestboxes with an old nest, preferentially chose those nestboxes with the fewest ectoparasites present (Merilä & Allander 1995). Also, in that first observational study, every second nestbox was provided with an old Great Tit nest, whilst the remainder were cleaned and left empty. Subsequent monitoring showed that Great Tits preferred roosting in empty boxes. In the second experiment, a choice was offered between empty nestboxes and nestboxes containing old Collared Flycatcher nests and the Great Tits showed no preference for either kind of nestbox (Merilä & Allander 1995). Therefore, the birds were avoiding nestboxes with ectoparasites, regardless of the type of nest in the nestbox.

A similar experimental study involving bats examined whether colonial female Bechstein's Bats adapted their roosting behaviour to the life cycle of the Bat Fly *Basilia nana* in order to decrease their contact with the infective stages of the parasite (Reckardt & Kerth 2007). First, an observational study on the natural roosting behaviour of female bats indicated that the bats largely avoided occupying roosts when highly contagious pupuria were likely to be present. However, some infested roosts were occupied, and it was assumed that in such cases, those roosts provided advantages to the bats, such as a beneficial microclimate, that outweighed the negative effects associated with bat fly infestation (Reckardt & Kerth 2007). Second, suitable day roost locations were either experimentally non-contagious or contagious and it was shown that the bats overwhelmingly preferred the non-contagious sites (Reckardt & Kerth 2007). These results suggest that roost selection in Bechstein's Bats, like birds, is the outcome of a trade-off between the costs of parasite infestation and beneficial roost qualities (Reckardt & Kerth 2007).

Together, these studies provide good evidence that roost site selection by birds is strongly influenced by the abundance of ectoparasites. The mechanism by which the birds avoid flea infestation at nestboxes has been examined. Two identical nestboxes designed for Blue Tits were erected in an English garden and one had about 200 simulated fleas around the entrance hole and the other had none. Blue tits made more visits to the plain box than to the box with fleas (du Feu 1992). Therefore, the prime way of avoiding infestation at a potential roosting site thus seems to be by avoiding sites where parasites are seen (du Feu 1992). Together, these studies provide strong evidence that birds actively gauge the number of ectoparasites present at a potential roost site and preferentially select those roost sites containing the lowest number of ectoparasites. Therefore, there is good evidence that birds face a trade-off between the thermal benefits gained from roosting inside a cavity and the disadvantages of being parasitized by ectoparasites.

PREDATION RISK

The thermal benefits and subsequent energy savings associated with roosting inside nestboxes usually make nestboxes advantageous roosting locations for small passerines during the non-breeding season (Newton 1998). Whilst birds roosting inside nestboxes generally have a lower risk of predation than individuals roosting in tree canopies, there is nonetheless a risk that small predators such as Weasels *Mustela nivalis*, Stoats *Mustela erminea*, Martens *Martes* spp., various snakes and small rodents can prey upon birds roosting in cavities (Dhondt *et al.* 2010). Consequently, it may be expected that predators also influence the choice of a roost site and roosting in cavities. One study provided support for this idea, when it was found that owl pellets more often contained the rings of Great Tits that did not roost in nestboxes than of birds that were regularly observed roosting in nestboxes. Consequently, birds roosting in nestboxes had higher levels of overwinter survival when compared to those birds roosting in the tree canopy (Drent 1987). However, it is important to remember that such a pattern may also be explained by the fact that only higher-quality birds had access to nestboxes and predators caught disproportionally more lower- than higher-quality birds.

In contrast, an observational study showed that whilst Blue Tits roosted in nestboxes in southern France, they did not on the nearby island of Corsica (Dhondt *et al.* 2010). This difference in behaviour was thought to have originated because on mainland Europe, various owl species are widespread whereas in Corsica, owls are rare but Weasels are abundant. Furthermore, Corsica Black Rats *Rattus rattus* are very arboreal and nest in boxes, thereby potentially competing with birds, but not preying on them. In Corsica, therefore, predation pressure on cavity users could be severe while predation pressure in tree canopies is much lighter (Dhondt *et al.* 2010). Also, a study in Poland suggested that predators strongly influence the roosting patterns of birds during the non-breeding season (Ekner & Tryjanowski 2008). In an experimental study, fur and mangled feathers were placed in half of 100 randomly selected nestboxes. Nestboxes were then checked every ten days from January–March and the birds showed a significantly stronger preference towards 'clean' nestboxes without predator traces (Ekner & Tryjanowski 2008). Consequently, the paucity of research makes it very difficult to make any general conclusions as to whether roosting in nestboxes increases or decreases levels of predation risk and is clearly an area that requires further research.

INTERSPECIFIC COMPETITION

A good roost site may increase the bird's chance of survival as it protects them against severe weather and predators. Nestboxes are the preferred roosting sites as a higher proportion of dominant adult males than subdominant juvenile female birds use them. Nestboxes vary in their quality as roosting sites, and interspecific competition results in dominant species roosting in preferred nestboxes. An experimental study was carried out in Belgium, where both Great Tits and Blue Tits use nestboxes for roosting during the non-breeding season (Kempenaers & Dhondt 1991). Blue and Great Tits always sleep alone in roost sites and if the number of available roost sites is limited, then competition for nestboxes should be expected to occur, given that the two species compete for nestboxes during the breeding season (Perrins 1979). In the study area, two types of nestbox were available: large-holed nestboxes, which can be used by both Great and Blue Tits, and small-holed boxes, that can only be used by Blue Tits. An observational study showed that when both large and small-holed nestboxes were available, Blue Tits preferentially roosted in small-holed nestboxes, but when only large-holed boxes were available, few boxes were occupied by Blue Tits, despite many empty boxes being left by Great Tits. In the absence of Great Tits, Blue Tits preferred larger-holed nestboxes for roosting. In the presence of a Great Tit, Blue Tits changed to a small-holed nestbox. Meanwhile, an aviary experiment showed that in the absence of Great Tits, Blue Tits prefer large-holed nestboxes. Over half of the Blue Tits changed to small-holed box in the presence of a Great Tit. It was concluded that blue tits were forced to use the small-holed nestboxes, because they are kept out of the large-holed ones by the dominant Great Tit (Kempenaers & Dhondt 1991). These findings support the prediction that the smaller Blue Tits were forced to use the small-holed nestboxes due to competition from the larger Great Tits. If only large-holed boxes are available in the wild, then Blue Tits may be forced to roost outside, which may affect winter survival. Blue Tits were thought to prefer large-holed boxes because they may incur less cost wear on the wing feathers (Kempenaers & Dhondt 1991). Consequently, the lack of research makes it very difficult to make any general conclusions as to whether roosting in nestboxes increases or decreases levels of interspecific competition and is clearly an area that requires further research.

CONCLUSIONS

In summary, this review emphasises the importance of nestboxes to roosting birds during the non-breeding season. Birds gain considerable thermal benefits and subsequent energy savings, when compared to congeners roosting in the tree canopy, and the evidence strongly suggests that birds actively choose those roosting locations that provide the greatest thermal benefits. However, roosting birds are targeted by detrimental ectoparasites, and there is also strong evidence that birds actively avoid nestboxes where ectoparasites are abundant. Meanwhile, there is insufficient evidence to make any firm conclusions as to whether roosting in nestboxes either increases or decreases predation risk or is strongly affected by interspecific competition. Whilst the limited evidence suggests that roosting in nestboxes does come with predation risks and that interspecific competition exerts a strong influence of roost site selection, further studies are required before any general conclusions can be made. Further research could also usefully examine the trade-off between competing selecting pressures, as birds must trade the principle benefit of increased insulation against the principal cost of parasitism, and a single experiment which manipulated both temperature and ectoparasite abundance simultaneously may be enlightening. Further research could also usefully examine the relationships between various aspects of roosting, such as the frequency of nestbox use and the timing of any changes in roosting location, that are collected via regular nestbox checks during the non-breeding season, and the subsequent reproductive success of individuals and population dynamics of a species.

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SAMENVATTING

Een aantal vogelsoorten gebruikt nestkasten niet alleen als nestgelegenheid, maar ook als slaapplaats buiten de broedtijd. Over de consequenties van het gebruik van nestkasten buiten het broedseizoen is echter weinig bekend. Deze review beschrijft de voor- en nadelen van het slapen in nestkasten. Het verstrekken van nestkasten door mensen heeft het aantal mogelijke slaapplaatsen voor vogels sterk vergroot. Het grootste voordeel van slapen in nestkasten is dat het vogels een belangrijke energiebesparing oplevert. Hier staat echter tegenover dat de vogels blootstaan aan een verhoogde druk van parasieten. Vogels vermijden dan ook nestkasten met een hoge dichtheid aan ectoparasieten. Natuurlijk is er een grote variatie in de kwaliteit van nestkasten als slaapplaats. Inter-specifieke concurrentie zorg er daarbij voor dat de grotere en dominante soorten de nestkasten van hogere kwaliteit bezetten. Vanwege een gebrek aan veldonderzoek is het niet te zeggen of het voor een individu een voor- of nadeel voor de fitness oplevert om van nestkasten gebruik te maken als slaapplaats. Toekomstige studies over het gebruik van nestkasten als slaapplaats dienen zich daarom daarop te richten. (KvO)

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