The orientation of nestboxes influences their occupation rates and the breeding success of passerine birds

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Abstract Nestboxes are widely provided as nesting sites for hole-nesting birds, yet the relative contribution of nestbox characteristics and habitat quality in determining the occupancy rates and breeding success of birds remains unclear. We provided nestboxes in deciduous woodlands in England and examined if those nestboxes were erected in random orientations and whether the orientation of nestboxes and habitat quality, in the form of tree density, influenced their occupation by, and breeding success of, Blue Tits *(Cyanistes caeruleus)*, Great Tits *(Parus major)* and Pied Flycatchers *(Ficedula hypoleuca)*. We found that first, the nestboxes were erected non-randomly orientated towards the north and east, and away from the south and west. Second, the occupation rates of none of the species was related to nestbox orientation or tree density. Third, the breeding success of neither Blue Tits nor Great Tits varied with tree density but did vary with nestbox orientation. Blue Tit hatching success and fledging success was higher in nestboxes facing south than in other directions whilst in Great Tits, clutch sizes, hatching success and fledging success was higher in nestboxes facing south than nestboxes facing other directions. Our results suggest that nestbox characteristics, such as orientation, have more influence on the reproductive success of passerines than habitat quality. This further suggests that conservationists should orientate nestboxes southwards in order to maximise their benefit to birds in temperate climates during the breeding season.

Keywords: conservation tool; habitat quality; nest site selection; reproductive success; woodland birds

Összefoglalás Az odúban fészkelő madarak költési lehetőségeinek támogatására széles körben használnak mesterségesen kihelyezett költőládákat. A költőládák tulajdonságainak és az élőhely minőségének az elfoglalás gyakoriságára és a madarak költési sikerére gyakorolt hatása azonban további kérdések megválaszolását igényli. Ezért költőládákat helyeztünk ki Anglia több lombhullató erdejébe és megvizsgáltuk, hogy a költőládák vajon véletlenszerű irányokban lettek-e kihelyezve, valamint tájolásuknak és az élőhely minőségének, a környező fák sűrűségében mérve, volt-e hatása azok elfoglalásának arányára és a kék cinege *(Cyanistes caeruleus)*, a széncinege *(Parus major)*, illetve a kormos légykapó *(Ficedula hypoleuca)* költési sikereire. Eredményeink azt mutatják, hogy a költőládák nem véletlenszerűen, hanem többnyire északi és keleti tájolással lettek kihelyezve, ugyanakkor az elfoglalás aránya egyik fajnál sem mutatott összefüggést a tájolással és a fák sűrűségével. A költési sikert nem befolyásolta a környező fák sűrűsége, sem a kék cinegénél, sem pedig a széncinegénél, viszont a költőládák tájolása igen. Míg a kék cinegék kikelési és kirepülési sikere a délre néző költőládákban magasabb volt más tájolású költőládákhoz képest, addig a széncinegéknél ezeken felül még a fészekalj mérete is nagyobb volt a déli tájolású költőládákban. Eredményeink alapján elmondható, hogy a költőládák tájolásának nagyobb hatása van a madarak költési sikerére, mint az élőhely minőségének. Ez azt is alátámasztja, hogy a természetvédelmi tevékenységek során a költőládákat déli irányba érdemes kihelyezni, hogy a mérsékeltövi madarak számára minél több előny származzon ebből a költési időszakban.

Kulcsszavak: erdei madarak, élőhelyminőség, kék cinege, kormos légykapó, költési siker, költőládák, széncinege, tájolás

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Introduction

Nestboxes are widely provided for hole-nesting birds to support their nesting opportunities in temperate woodlands (Lambrechts *et al.* 2010, Culina *et al.* 2021). The frequent occupation of nestboxes by passerine birds such as Blue Tits *(Cyanistes caeruleus)*, Great Tits *(Parus major)*, Collared Flycatchers *(Ficedula albicollis)* and Pied Flycatchers (*Ficedula hypoleuca*) in Europe and species such as Black-capped Chickadees *(Poecile atricapillus)* and Tree Swallows *(Tachycineta bicolor)* in North America has resulted in them becoming some of the most popular model species in ecological and evolutionary research (Lambrechts *et al.* 2010, Culina *et al.* 2021). The provision of nestboxes also helps to provide nesting sites for species of conservation concern. Pied Flycatcher populations have declined (Hewson *et al.* 2007), at least partly, because of climate change induced lethal competition with sedentary Great Tits (Samplonius & Both 2019) and nestboxes help to provide nest sites for the Flycatchers (Goodenough *et al.* 2009).

Nestboxes are not uniformly effective in providing nest sites for birds, though, because occupancy rates vary with respect to their shape (Bellrose *et al.* 1964), age (Mazgajski 2007), colour (Browne 2006), exposure (Charter *et al.* 2010), the size of the entrance holes (Le Roux *et al.* 2016, Stanback *et al.* 2019) and their orientation. In the temperate zone of the northern hemisphere, birds are expected to preferentially occupy nestboxes facing southwards towards the sun in order to increase nest temperatures (Goodenough *et al.* 2008a, 2008b, Butler *et al.* 2009, Lambrechts *et al.* 2020). Illustratively, Tree Swallows in North America occupied warmer nestboxes orientated south and east during the cooler first half of the breeding season yet showed no preference for nestboxes in relation to their orientation in the warmer second half of the breeding season when nest temperatures were unrelated to nestbox orientation (Ardia *et al.* 2006). This agrees with studies showing that passerine birds in temperate woodlands in the northern hemisphere preferentially select nestboxes facing south (Lumsden 1986, Sacilotto & Anderson 2005). However, other studies show that passerine birds preferentially occupy nestboxes facing east (Ardia *et al.* 2006) and the northwest (Navara & Anderson 2011), whilst others show that nestboxes are randomly occupied with respect to orientation (Lumsden 1986, Mennill & Ratcliffe 2004, Goodenough *et al.* 2008a, 2008b). This suggests that further studies are required to understand how nestbox orientation influences their occupation rates.

Birds may also differentially occupy nestboxes with respect to their surrounding habitat. For example, European Roller's *(Coracias garrulus)* preferentially occupied nestboxes located in olive groves, irrigated crops and holm oaks, whilst actively avoiding nestboxes located in cereals (Avilés *et al.* 2000). Meanwhile, House Wrens *(Troglodytes aedon)* preferentially occupied nestboxes located in areas with sparser woodland understories and were more likely to fledge offspring from nestboxes in sparsely foliated areas (Finch

1989), whilst Bearded Reedlings *(Panurus biarmicus)* preferentially occupied nestboxes located in reed beds over water than over dry land (Wilson 2015). Birds are therefore able to differentiate between nestboxes in relation to the habitat in which they are located (Bloom & Hawks 1983, Belles-Isles & Picman 1986, Finch 1989, Rohrbaugh & Yahner 1997, Monti *et al*. 2019, Mueller *et al*. 2019, but see Le Roux *et al*. 2016). Miller (2010) provided nestboxes for passerine birds in temperate woodlands and suggested that the very low occupancy rates of those nestboxes indicated that habitat structure played a greater role in determining passerine bird populations than the availability of nestboxes. This suggests that habitat quality may well influence nestbox occupancy rates, although our understanding of the relative contributions of nestbox characteristics and habitat quality in determining the occupancy rates of nestboxes and the breeding success of the occupants remains incomplete.

We used data from a long-running nestbox scheme (Smith *et al*. 2011, Briggs & Deeming 2016, 2021, Briggs & Mainwaring 2017, 2019) to examine whether nestboxes were provided randomly with respect to their orientation, whether breeding Blue Tits, Great Tits and Pied Flycatchers occupied nestboxes based on their orientation and/or the density of trees surrounding nestboxes and whether the breeding success of Blue Tits and Great Tits varied in relation to nestbox orientation and tree density. We predict that (1) nestboxes will be placed randomly with respect to their orientation. Meanwhile, given that south-facing nestboxes receive more sunlight than nestboxes facing in other directions (Goodenough *et al*. 2008b, Butler *et al*. 2009, Lambrechts *et al*. 2020), we predict that (2) nestboxes facing south will be preferentially occupied because of the thermal benefits they receive from being exposed to solar radiation. We also predict that (3) birds breeding in nestboxes facing southwards will have higher levels of breeding success than conspecifics in nestboxes facing in other directions because of their high exposure to direct sunlight.

Methods

Study sites and their characteristics

We studied breeding populations of Blue Tits, Great Tits and Pied Flycatchers occupying nestboxes in seven largely deciduous woodlands, two of which contained small areas of coniferous trees. The woodlands were in Lancashire, north-west England (for more information see Briggs & Mainwaring 2017, 2019, Briggs & Deeming 2016, 2021). The woodlands in the Forest of Bowland Area of Outstanding National Beauty (54˚05'N, 02˚ 36'W; altitude 100–250 metres above sea level) on calcium poor gritstone rock types had many oak (*Quercus* spp.) and birch (*Betula* spp.) trees and had an understorey of wavy hairgrass *(Deschampsia flexuosa)*, which was classified as 'W10' (*Quercus robur - Pteridium aquilinum - Rubus fruticosus* woodland) in the National Vegetation Classification (Rodwell 1991).

A total of 187 identical wooden nestboxes with small circular entrance holes were provided for small passerine birds throughout the woodlands by one person (KBB) in 1977, many

years prior to the initiation of this present study. Each year, all the nestboxes were checked for their suitability as breeding sites for passerine birds and were repaired or replaced if they were damaged, so as to ensure that all the nestboxes were available for birds in each breeding season. The orientation of all the nestbox holes was then quantified in April 2021 using a 'Silva Explorer III compass' and in each instance, a bearing of the degrees from due north was recorded.

We quantified the number of trees and shrubs, identified to species, surrounding all the 187 nestboxes in order to give an indication of the number of caterpillars that are likely to have been available for parent birds to feed to their offspring (Wilkin *et al*. 2009). In September 2019, one observer (KBB) quantified the number of trees, shrubs and bushes within a 25-meter radius of all of the nestboxes and identified them to a total of 26 different species including English oak *(Quercus robur)*, ash, sycamore *(Acer pseudoplatanus)*, Scots pine *(Pinus sylvestris)* and birch trees and hazel *(Corylus avellana)*, hawthorn *(Crataegus monogyna)*, bird cherry *(Prunus padus)*, and plum *(Prunus domestica)* bushes as outlined in the guide provided by Mitchell (1974).

Quantifying reproductive parameters

Small passerine birds were provided with wooden nestboxes of identical dimensions (see Briggs & Mainwaring 2017) throughout the study woodlands by one observer (KBB) in order to minimise variation in nestbox design between breeding pairs (Lambrechts *et al*. 2010, Møller *et al*. 2014, Mainwaring *et al*. 2015). All nestboxes were checked at roughly weekly intervals from late March onwards, to establish the beginning of nest building behaviours. After nests were found, regular checks established the date on which the first eggs were laid and if multiple eggs were present in nests, we therefore back-calculated egg laying dates assuming that one egg was laid per day as is usual in the three study species (Lundberg & Alatalo 1992, Cramp & Perrins 1993).

Further visits established the onset of incubation and close to the date on which eggs were due to hatch, clutch sizes were determined as the number of eggs within nests at that time. The nests were then routinely checked every few days in order to quantify hatching success, which was defined as the number of eggs that hatched. Then, when the eldest offspring within broods were 14 days old, all nestlings were weighed to the nearest 0.1 grams to quantify their mass at pre-fledging (Mainwaring & Hartley 2016). The nests were then left alone in order to prevent the premature fledging of nestlings but were again checked when the eldest nestling/s within broods would have been about 20 days old. It was at this point that we checked for dead nestlings inside the nestboxes, which therefore allowed us to quantify the fledging success of breeding pairs.

Statistical analyses

The data were analysed in the SPSS version 25 (SPSS, Chicago, IL, USA) statistical package. The distribution of the orientation of nestboxes was examined using a one-sample Chi-square test to examine if their orientation differed from a random distribution.

Specifically, the proportion of nestboxes orientated towards the north (315–45 degrees), east (45–135 degrees), south (135–225 degrees) or west (225–315 degrees) was tested against an expected proportion of 0.25 for each direction.

The occupation rates of nestboxes by Blue Tits, Great Tits, Pied Flycatchers and all bird species were examined using general linear models. The 'all bird' species data refers to the occupation of nestboxes by all bird species because in addition to Blue Tits, Great Tits and Pied Flycatchers, we also found very small numbers of Common Redstarts *(Phoenicurus phoenicurus)*, Eurasian Nuthatches *(Sitta europaea)*, Marsh Tits *(Poecile palustris)* and Coal Tits *(Periparus ater)* breeding inside the nestboxes. The assumptions of normality were examined using Kolmogorov-Smirnov one sample tests before separate general linear models for Blue Tits, Great Tits, Pied Flycatchers and all bird species examined the role of nestbox orientation and tree density in determining occupation rates. In each of the models, the dependent variable was occupancy rate (0–6 years occupied), and the explanatory variables were 'orientation' (north, east, south or west: factor), 'tree density' (number of trees: covariate) and their two-way interaction term. The fixed terms, as well as their two-way interaction term, were initially included in the 'full' initial models, before they were sequentially 'removed' in a stepwise manner. For each of the terms, their significance was assessed by their Type I sum of squares and their values were only reported when they were the final terms in the models (Crawley 1993). Terms were dropped from models when their P values were non-significant, meaning that the final minimal models contained only those fixed terms whose P values were significant, or instead were included in a significant two-way interaction term.

Linear mixed models with a Gaussian error structure were used to analyse the breeding success data because the inclusion of random effects allowed us to consider spatially autocorrelated data and so here, 'clutch identity' was included as a random effect in all models. The reproductive success of the Blue Tits and Great Tits in relation to the orientation of nestboxes and tree densities were examined as follows, whilst we had no data on Pied Flycatchers and so they were not included in these analyses. The dependent variables were first egg date, clutch size, hatching success, nestling masses at pre-fledging and fledging success and the explanatory variables were 'orientation' (north, east, south or west: factor), 'tree density' (number of trees: covariate) and their interaction term, whilst 'clutch identity' was fitted as a random term in all models. The full models were simplified as outlined above. Throughout the manuscript, means are presented ± 1 standard error and a critical P value of 0.05 is applied throughout.

Results

A one-sample Chi-square test showed that nestboxes were non-randomly orientated towards the north and east and away from the south and west and so were not randomly distributed with respect to their orientation ($\chi^2 = 9.624$, P = 0.005) *(Figure 1)*. The occupation rates of nestboxes by Blue Tits, Great Tits, Pied Flycatchers and all bird species was not generally related to the orientation of nestboxes, the density of trees within a 25-meter radius
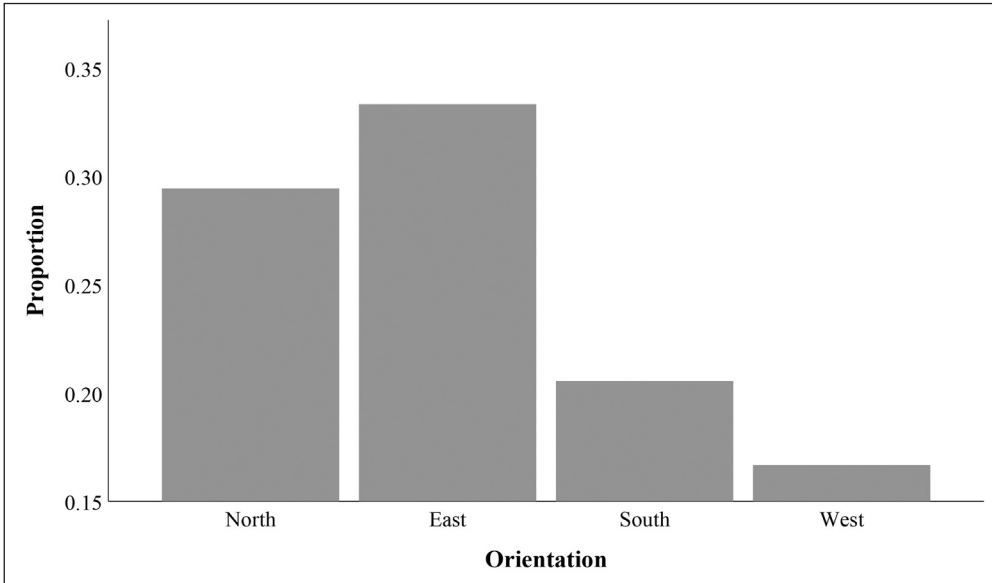
Figure 1. The non-random orientation of nestboxes
1. ábra A költőládák tájolásának nem véletlenszerű megoszlása

Table 1. Summary of general linear models examining variation in the occupancy rate of nestboxes by Blue Tits, Great Tits, Pied Flycatchers and all bird species combined in relation to the orientation of nestboxes and tree densities. The dependent variables were occupancy rate (0–6 years occupied), and the explanatory variables were 'orientation' (north, east, south or west: factor), 'tree density' (number of trees: covariate) and their interaction term. Note that significant terms are highlighted in bold

1. táblázat Az általános lineáris modellek eredményeinek összefoglalása, amelyekkel a költőládák elfoglalási arányának változatosságát (függő változó, 0–6 éven keresztül használt) és azok tájolását (észak, kelet, dél, nyugat – főhatás), valamint a környező fák sűrűségének (a fák száma – kovariáns) és a két magyarázó változó kölcsönhatásának összefüggéseit vizsgáltuk kék cinegék, széncinegék, kormos légykapók és az összes vizsgált faj esetében. A statisztikailag szignifikáns eredményeket félkövér betűtípussal emeltük ki

| Species	Fixed effects	d.f.	F-value	P value
Blue Tit	Orientation	4,186	1.156	0.332
	Tree density	1,186	2.310	0.130
	Orientation × tree density	4,186	0.113	0.978
Great Tit	Orientation	4,186	0.720	0.579
	Tree density	1,186	1.665	0.200
	Orientation × tree density	4,186	0.269	0.897
Pied Flycatcher	Orientation	4,186	0.786	0.535
	Tree density	1,186	0.002	0.963
	Orientation × tree density	4,186	1.449	0.220
All bird species	Orientation	4,186	1.176	0.323
	Tree density	**1,186**	**4.055**	**0.046**
	Orientation × tree density	4,186	0.469	0.759
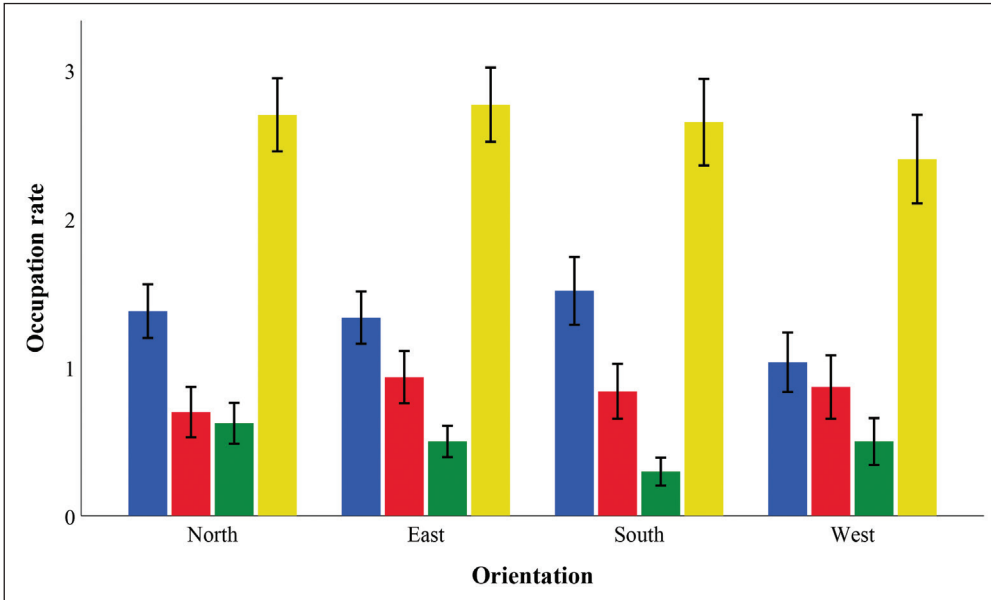
Figure 2. The occupation rates of nestboxes in relation to their orientation. Note that Blue Tits are shown by blue bars, Great Tits by red bars, Pied Flycatchers by green bars and all bird species by yellow bars

2. ábra A költőládák elfoglalásának aránya a tájolásuk szerinti csoportosításban. Kékkel a kék cinegék, pirossal a széncinegék, zölddel a kormos légykapók és sárgával az összes madárfaj adatai láthatóak

of nestboxes or their interaction terms *(Table 1, Figure 2)*, although there was a weakly significant trend for the occupation rates of all bird species to be positively correlated with tree density (P = 0.046) *(Table 1)*.

In terms of the breeding success of Blue Tits, there was no variation in first egg dates or clutch sizes in relation to the orientation of nestboxes or tree density *(Table 2, Figures 3a, 3b)*. Meanwhile, hatching success was higher in nestboxes facing south than in all other directions (P = 0.014) *(Table 2, Figure 3c)*, but it did not vary in relation to tree density *(Table 2)*. The mass of fledglings at pre-fledging did not vary with the orientation of nestboxes or with tree density *(Table 2, Figure 3d)*. Finally, fledging success never varied in relation to tree density *(Table 2)* but did in relation to orientation (P = 0.007) *(Table 2, Figure 3e)*, being lowest in nestboxes facing north and west and higher for nestboxes facing east and higher still for nestboxes facing south.

In terms of the breeding success of Great Tits, there was no variation in first egg dates in relation to the orientation of nestboxes or with tree density *(Table 2, Figures 3a)*. Meanwhile, clutch sizes never varied in relation to the density of trees *(Table 2)* but did vary in relation to orientation (P = 0.041) *(Table 2, Figure 3b)*, being higher in nestboxes facing south than in nestboxes facing other directions. Similarly, hatching success was higher in nestboxes facing south than in nestboxes facing all other directions (P = 0.017) *(Table 2 Figure 3c)*, but did not vary with tree density *(Table 2)*. There was no variation in the mass of fledglings at

Table 2. Summary of linear mixed models examining variation in the reproductive success of Blue Tits and Great Tits in relation to the orientation of nestboxes and tree densities. The dependent variables were 'first egg date', 'clutch size', 'hatching success', 'nestling masses at pre-fledging' and 'fledging success' and the explanatory variables were 'orientation' (north, east, south or west: factor), 'tree density' (number of trees: covariate) and their interaction term, whilst 'clutch identity' was fitted as a random term. Note that significant terms are highlighted in bold

2. táblázat A lineáris kevert modellek eredményeink összefoglalása, amelyekkel a kék cinege és a szén-cinege költési sikereinek és a költőládák tájolásának (észak, kelet, dél, nyugat – főhatás), valamint a környező fák sűrűségének (a fák száma – kovariáns) és a két magyarázó változó kölcsönhatásának összefüggéseit vizsgáltuk. Függő változóként az első tojás lerakásának dátuma, a fészekalj mérete, a kikelési siker, a kirepülés előtti fiókák tömege, valamint a kirepülési siker szerepelt, míg a fészekaljak azonosítóit véletlen tényezőként tartalmazták a modellek. A statisztikailag szignifikáns eredményeket félkövér betűtípussal emeltük ki

Species	Breeding parameter	Fixed effects	d.f.	F-value	P value
Blue Tit	First egg date	Orientation	3,40	0.522	0.670
		Tree density	1,40	0.529	0.471
		Orientation × tree density	3,40	0.456	0.715
	Clutch size	Orientation	3,40	0.164	0.920
		Tree density	1,40	0.442	0.510
		Orientation × tree density	3,40	0.481	0.697
	Hatching success	Orientation	3,40	5.662	0.014
		Tree density	1,40	0.654	0.423
		Orientation × tree density	3,40	0.350	0.789
	Nestling mass	Orientation	3,40	0.413	0.302
		Tree density	1,40	0.551	0.477
		Orientation × tree density	3,40	0.469	0.644
	Fledging success	**Orientation**	**3,40**	**8.010**	**0.007**
		Tree density	1,40	0.037	0.849
		Orientation × tree density	3,40	1.351	0.271
Great Tit	**First egg date**	**Orientation**	**3,47**	**2.935**	**0.094**
		Tree density	1,47	1.835	0.173
		Orientation × tree density	3,47	1.582	0.180
	Clutch size	**Orientation**	**3,47**	**4.189**	**0.041**
		Tree density	1,47	0.274	0.694
		Orientation × tree density	3,47	0.124	0.838
	Hatching success	**Orientation**	**3,47**	**6.183**	**0.017**
		Tree density	1,47	0.821	0.573
		Orientation × tree density	3,47	1.744	0.152
	Nestling mass	Orientation	3,47	0.022	0.914
		Tree density	1,47	0.028	0.926
		Orientation × tree density	3,47	0.173	0.727
	Fledging success	**Orientation**	**3,47**	**7.835**	**0.012**
		Tree density	1,47	1.647	0.315
		Orientation × tree density	3,47	1.274	0.239

Figure 3.
A. First egg date
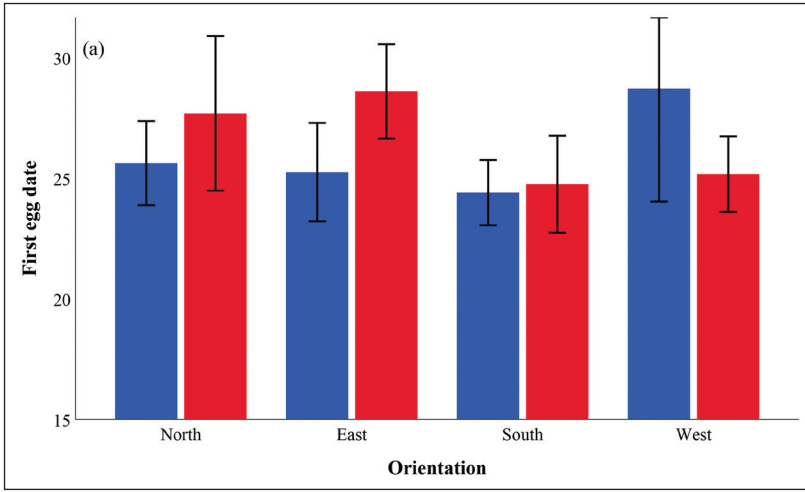
Figure 3.
B. Clutch size
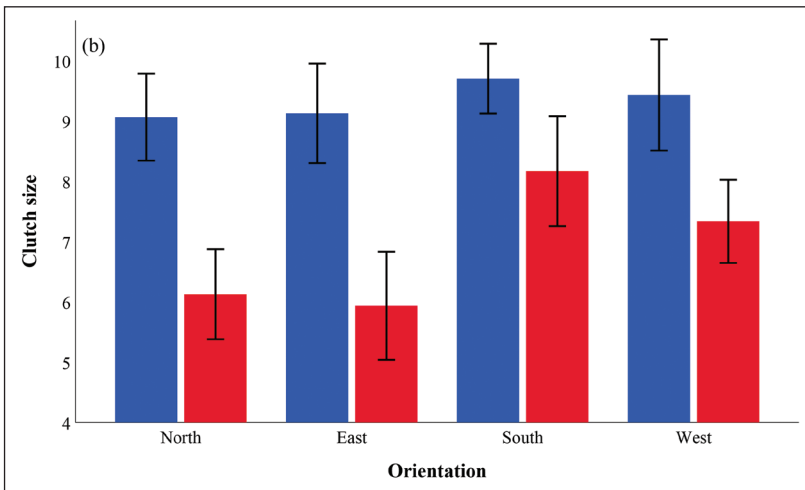
Figure 3.
C. Hatching
success
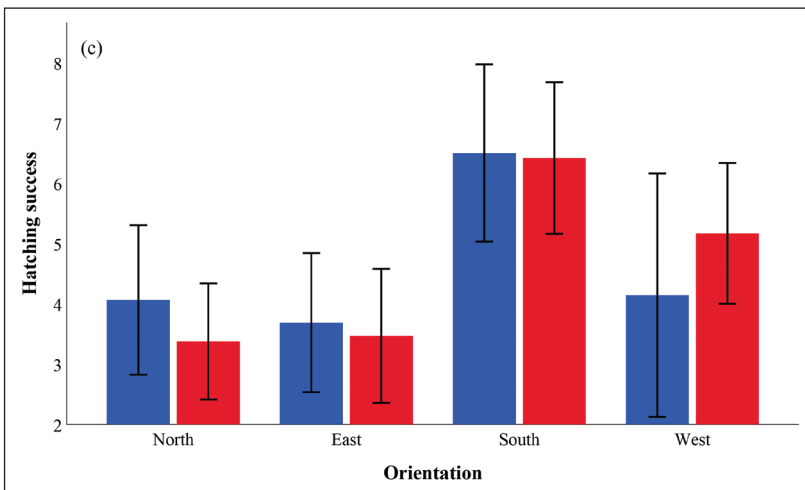
Figure 3.
D. Mass at day 14
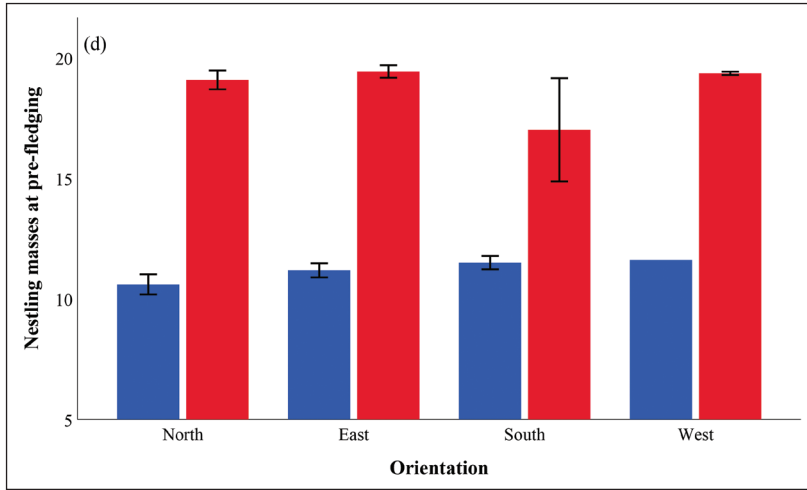
Figure 3.
E. Fledging
success
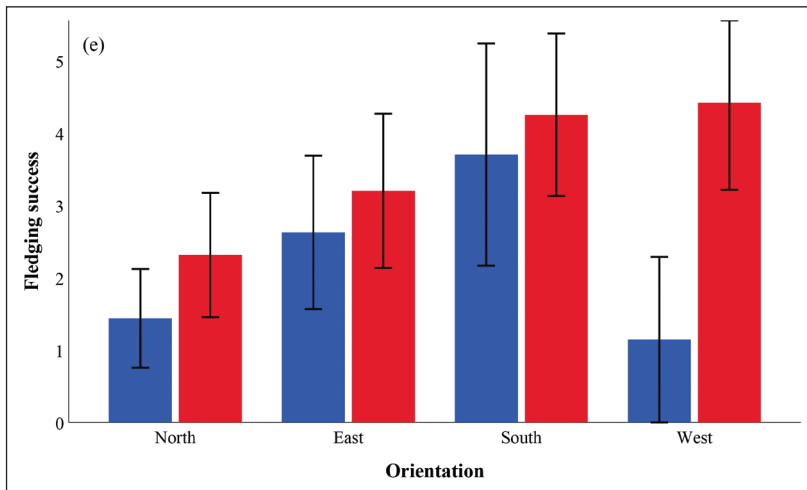
Figure 3. The reproductive success of Blue Tits and Great Tits, in terms of their (a) first egg date, (b) clutch size, (c) hatching success, (d) nestling masses at pre-fledging and (e) fledging success in relation to the orientation of nestboxes. Note that Blue Tits are shown by blue bars and Great Tits are shown by red bars

3. ábra A kék cinegék (kék) és a széncinegék (piros) költési sikereinek alakulása a költőládák tájolá-sa szerinti csoportosításban: (a) az első tojás lerakásának dátuma, (b) fészekalj-méret, (c) ki-kelési siker, (d) a kirepülés előtti fiókák tömege, valamint (e) a kirepülési siker

pre-fledging in relation to orientation or tree density *(Table 2, Figure 3d)*. Finally, fledging success never varied in relation to tree density *(Table 2)* but did vary in relation to orientation (P = 0.012) *(Table 2, Figure 3e)*, being lowest in nestboxes facing north and getting ever higher in nestboxes facing east, south and west.

Discussion

The main findings of this study were that nestboxes were non-randomly positioned on trees in relation to their orientation, being orientated towards the north and east and away from the south and west. Meanwhile, although the occupation rates of nestboxes by all three study species was unrelated to the orientation of nestboxes or tree density, Blue Tit and Great Tit breeding success was affected by the orientation of nestboxes, but not to tree density. Blue Tit hatching success and fledging success was higher in nestboxes facing south than in nestboxes facing any other directions. However, Great Tit clutch sizes and hatching success were higher in nestboxes facing south than in nestboxes facing other directions, whilst fledging success was higher in nestboxes facing west and south than in nestboxes facing east and north. Our results suggest that the orientation of nestboxes have more influence on the reproductive success of passerine birds than tree density. They further suggest that nestboxes in the temperate zone of the northern hemisphere should be preferentially orientated southwards.

    The orientation of nestboxes never influenced their occupation rates by Blue Tits, Great Tits or Pied Flycatchers, but did affect the reproductive success of Blue Tits and Great Tits. Fledging success in both species was highest in nestboxes facing southwards, presumably because they received more sun than nestboxes facing in other directions, which thus maximised internal nest temperatures (Lumsden 1986, Sacilotto & Anderson 2005, Ardia *et al*. 2006, Goodenough *et al*. 2008a, 2008b, Butler *et al*. 2009, Mainwaring & Hartley 2012, Lambrechts *et al*. 2020). Birds inhabiting temperate environments in the northern hemisphere experience ambient temperatures below the threshold at which embryos develop optimally (Salaberria *et al*. 2014), and so they are likely to prefer nestboxes orientated towards the sun to reduce the energy required to keep the embryos warm (Goodenough *et al*. 2008b, Butler *et al*. 2009). Whilst birds breeding in nestboxes that faced south had the highest levels of breeding success, the majority of nestboxes were positioned on trees so that they faced north or east. This suggests that those nestboxes facing north may have been acting as an ecological trap because whilst the passerine birds readily occupied them, they ultimately suffered reduced levels of reproductive success by occupying them, when compared to conspecifics occupying nestboxes facing southwards (O'Connor 1984).

    The density of trees surrounding nestboxes had no effect on the occupation rates of nestboxes or on the reproductive success of Blue Tits and Great Tits. This is perhaps surprising because previous studies show that the habitat surrounding nestboxes influences their occupation rates (Bloom & Hawks 1983, Belles-Isles & Picman 1986, Finch 1989, Rohrbaugh & Yahner 1997, Avilés *et al*. 2000, Wilson 2015, Mueller *et al*. 2019, but see Le Roux *et al*. 2016) and the reproductive success of the occupants (Finch 1989, Goodenough *et al*. 2008a). It is unclear why tree density never influenced occupancy rates or breeding

success, but it may be that caterpillar abundance was unrelated to tree density. Alternatively, territories with fewer trees are likely to have more open canopies than territories with more trees, meaning that they may well have received a higher amount of solar radiation (Wachob 1996). The temperature inside nestboxes is positively correlated with ambient temperatures (Lambrechts *et al.* 2020) and so birds occupying nestboxes with fewer trees may therefore have benefitted from having relatively warm nest microclimates. Determining the mechanisms underlying this pattern deserves further research attention.

We have shown that hole-nesting passerine birds occupying nestboxes facing south had higher levels of breeding success than conspecifics occupying nestboxes facing in other directions. This is likely to be a result of those nestboxes facing south receiving a greater amount of solar radiation than nestboxes facing other directions, which thus increased the temperatures inside nestboxes and enabled birds to save energy keeping offspring warm. Our findings suggest that ornithologists should provide nestboxes that face south in temperate woodlands in the northern hemisphere. Further research is needed to examine the patterns described here. First, studies show that nestboxes provide less insulation that natural cavities (Maziarz *et al.* 2017) and so it would be interesting to examine if these patterns occur in species breeding in natural cavities (Lundberg & Alatalo 1992). Second, the patterns we have reported here are observational and thus may have been confounded by alternative factors. It would be useful to experimentally disassociate the relationship between the occupation of nestboxes and the density of trees by cutting trees to examine the influence of tree density on nestbox occupation rates. Third, south facing nestboxes provide thermal benefits for birds and research that quantifies how nest microclimates are influenced by the orientation of nestboxes in a changing climate may help ornithologists provide nesting sites for birds in the future.

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References

Ardia, D. R., Pérez, J. H. & Clotfelter, E. D. 2006. Nestbox orientation affects internal temperature and nest site selection by Tree Swallows. – Journal of Field Ornithology 77(3): 339–344. DOI: 10.1111/j.1557-9263.2006.00064.x

Avilés, S. M., Sánchez, J. M. & Parejo, D. 2000. Nest-site selection and breeding success in the Roller *(Coracias garrulus)* in the Southwest of the Iberian peninsula. – Journal of Ornithology 141(3): 345–350. DOI: 10.1007/BF02462244

Bellrose, F. C., Johnson, K. L. & Meyers, T. U. 1964. Relative value of natural cavities and nesting houses for Wood Ducks. – Journal of Wildlife Management 28(4): 661–676. DOI: 10.2307/3798781

Belles-Isles, J. C. & Picman, J. 1986. Nesting losses and nest preferences in House Wrens. – Condor 88(4): 483–486. DOI: 10.2307/1368275

Bloom, P. H. & Hawks, S. J. 1983. Nest box use and reproductive biology of American Kestrel in Lassen County, California. – Raptor Research 17(1): 9–14.

Briggs, K. B. & Deeming, D. C. 2016. Use of materials in nest construction by Pied Flycatchers *Ficedula*

hypoleuca reflects localised habitat and geographical location. – Bird Study 63(4): 516–524. DOI: 10.1080/00063657.2016.1238867

Briggs, K. B. & Deeming, D. C. 2021. Localized habitat affects size and materials used in the construction of Common Redstart *Phoenicurus phoenicurus* nests. – Bird Study 68(1): 9–20. DOI: 10.1080/00063657.2021.1958197

Briggs, K. B. & Mainwaring, M. C. 2017. Habitat geology influences intraspecific variation in the speckling patterns of Blue Tit *Cyanistes caeruleus* and Great Tit *Parus major* eggs. – Acta Ornithologica 52(1): 11–20. DOI: 10.3161/00016454AO2017.52.1.002

Briggs, K. B. & Mainwaring, M. C. 2019. Experimental evidence of non-random nest material selection in Pied Flycatchers. – Behavioural Processes 164: 59–64. DOI: 10.1016/j.beproc.2019.04.008

Browne, S. J. 2006. Effect of nestbox construction and colour on the occupancy and breeding success of nesting tits *Parus* spp. – Bird Study 53(2): 187–192. DOI: 10.1080/00063650609461432

Butler, M. W., Whitman, B. A. & Dufty, A. M. Jr. 2009. Nest box temperature and hatching success of American Kestrels varies with nest box orientation. – Wilson Journal of Ornithology 121(4): 778–782. DOI: 10.1676/08-124.1

Charter, M., Meyrom, K., Leshem, Y., Aviel, S., Izhaki, I. & Motro, Y. 2010. Does nest box location and orientation affect occupation rate and breeding success of Barn Owls in a semi-arid environment? – Acta Ornithologica 45(1): 115–119. DOI: 10.3161/000164510X516164

Cramp, S. & Perrins, C. M. 1993. The birds of the Western Palearctic, Vol. 7: Flycatchers to Shrikes. – Oxford University Press, Oxford

Crawley, M. J. 1993. GLIM for Ecologist. – Blackwell Scientific Publications, Oxford

Culina, A., Adriaensen, F., Bailey, L. D., Burgess, M. D., Charmantier, A., Cole, E. F., Eeva, T., Matthysen, E., Nater, C. R., Sheldon, B. C., Sæther, B-E., Vriend, S. J. G., Adamík, P., Aplin, L. M., Angulo, E., Artemyev, A., Barba, E., Barišić, S., Belda, E., Can Bilgin, C., Bleu, C., Both, C., Bouwhuis, S., Branston, C., Broggi, J., Burke, T., Bushuev, A., Camacho, C., Campobello, D., Canal, D., Cantarero, A., Caro, S. P., Cauchoix, M., Chaine, A., Cichoń, M., Ćiković, D., Cusimano, C. A., Deimel, C., Dhondt, A., Dingemanse, N. J., Doligez, B., Dominoni, D. M., Doutrelant, C., Drobniak, S. M., Dubiec, A., Eens, M., Erikstad, K. E., Espín, S., Farine, D. R., Figuerola, J., Gülbeyaz, P. K., Grégoire, A., Hartley, I. R., Hau, M., Hegyi, G., Hille, S., Hinde, C. A., Holtmann, B., Ilyina, T., Isaksson, C., Iserbyt, A., Ivankina, E., Kania, W., Kempenaers, B., Kerimov, A., Komdeur, J., Korsten, P., Král, M., Krist, M., Lambrechts, M., Lara, C. E., Leivits, A., Liker, A., Lodjak, J., Mägi, M., Mainwaring, M. C., Mänd, R., Massa, B., Massemin, S., Martínez-Padilla, J., Mazgajski, T. D., Mennerat, A., Moreno, J., Mouchet, A., Nakagawa, S., Nilsson, J-Å., Nilsson, J., Norte, A. C., van Oers, K., Orell, M., Potti, J., Quinn, J. L., Réale, D., Reiertsen, T. K., Rosivall, B., Russel, A. F., Rytkönen, S., Sánchez-Virosta, P., Santos, E. S. A., Schroeder, J., Senar, J. C., Seress, G., Slagsvold, T., Szulkin, M., Teplitsky, C., Tilgar, V., Tolstoguzov, A., Török, J., Valcu, M., Vatka, E., Verhulst, S., Watson, H., Yuta, T., Zamora-Marín, J. M. & Visser, M. E. 2021. Connected data landscape of long-term ecological studies: the SPI-Birds data hub. – Journal of Animal Ecology 90(9): 2147–2160. DOI: 10.1111/1365-2656.13388

Finch, D. M. 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in House Wrens. – Condor 91(4): 848–859. DOI: 10.2307/1368069

Goodenough, A. E., Elliot, S. L. & Hart, A. G. 2009. The challenges of conservation for declining migrants: are reserve-based initiatives during the breeding season appropriate for the Pied Flycatcher *Ficedula hypoleuca*? – Ibis 151(3): 429–439. DOI: 10.1111/j.1474-919X.2009.00917.x

Goodenough, A. E., Hart, A. G. & Elliot, S. L. 2008a Variation in offspring quality with cavity orientation in the Great Tit. – Ethology Ecology and Evolution 20(4): 375–389. DOI: 10.1080/08927014.2008.9522518

Goodenough, A. E., Maitland, D. P., Hart, A. G. & Elliot, S. L. 2008b Nestbox orientation: a species-specific influence on occupation and breeding success in woodland passerines. –Bird Study 55(2): 222–232. DOI: 10.1080/00063650809461526

Hewson, C. M., Amar, A., Lindsell, J. A., Thewlis, R. M., Butler, S., Smith, K. & Fuller, R. J. 2007. Recent changes in bird populations in British broadleaved woodland. – Ibis 149(s2): 14–28. DOI: 10.1111/j.1474-919X.2007.00745.x

Lambrechts, M. M., Adriaensen, F., Ardia, D. R., Artemyev, A. V., Atiénzar, F., Bańbura, J., Barba, E., Bouvier, J-C., Camproden, J., Cooper, C. B., Dawson, R. D., Eens, M., Eeva, T., Faivre, B., Garamszegi, L. Z., Goodenough, A. E., Gosler, A. G., Grégoire, A., Griffith, S. C., Gustafsson, L., Johnson, L. S., Kania, W., Keišs, O., Llambias, P. E., Mainwaring, M. C., Mänd, R., Massa, B., Mazgajski, T. D., Møller, A. P., Moreno, J., Naef-Daenzer, B., Nilsson, J-Å., Norte, A. C., Orell, M., Otter, K. A., Park, C. R., Perrins, C. M., Pinowski, J., Porkert, J., Potti, J., Remes, V., Richner, H., Rytkönen, S., Shiao, M-T., Silverin, B., Slagsvold, T., Smith,

H. G., Sorace, A., Stenning, M. J., Stewart, I., Thompson, C. F., Tryjanowski, P., Török, J., van Noordwijk, A. J., Winkler, D. W. & Ziane, N. 2010. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. – Acta Ornithologica 45(1): 1–26. DOI: 10.3161/000164510X516047

Lambrechts, M. M., Caizergues, A. E., Perrier, C., Charmantier, A. & Caro, S. P. 2020. Surface temperatures of non-incubated eggs in Great Tits *(Parus major)* are strongly associated with ambient temperature. – International Journal of Biometeorology 64(10): 1767–1775. DOI: 10.1007/s00484-020-01958-1

Le Roux, D. S., Ikin, K., Lindenmayer, D. B., Bistricer, G., Manning, A. D. & Gibbons, P. 2016. Effects of entrance size, tree size and landscape context on nest box occupancy: Considerations for management and biodiversity offsets. – Forest Ecology and Management 366(1): 135–142. DOI: 10.1016/j.foreco.2016.02.017

Lumsden, H. G. 1986. Choice of nestboxes by Tree Swallows, *Tachycineta bicolor*, House Wrens, *Troglodytes aedon*, Eastern Bluebirds, *Sialia sialis*, and European Starlings, *Sturnus vulgaris*. – Canadian Field-Naturalist 100(3): 43–49.

Lundberg, A. & Alatalo, R. V. 1992. The Pied Flycatcher. – T & AD Poyser, London

Mainwaring, M. C. & Hartley, I. R. 2012. Causes and consequences of differential growth in birds: a behavioral perspective. – Advances in the Study of Behavior 44: 22–277. DOI: 10.1016/B978-0-12-394288-3.00006-X

Mainwaring, M. C. & Hartley, I. R. 2016. Local weather conditions have complex effects on the growth of Blue Tit nestlings. – Journal of Thermal Biology 60(1): 12–19. DOI: 10.1016/j.jtherbio.2016.05.005

Mainwaring, M. C., Reynolds, S. J. & Weidinger, K. 2015. The influence of predation on the location and design of nests. – In: Deeming, D. C. & Reynolds, S. J. (eds.) Nests, eggs, and incubation: new ideas about avian reproduction. – Oxford University Press, Oxford, pp. 50–64.

Mazgajski, T. D. 2007. Nest hole age decreases nest site attractiveness for the European Starling *Sturnus vulgaris*. – Ornis Fennica 84(1): 32–38.

Maziarz, M., Broughton, R. K. & Wesołowski, T. 2017. Microclimate in tree cavities and nest-boxes: Implications for hole-nesting birds. – Forest Ecology and Management 389(1): 306–313. DOI: 10.1016/j.foreco.2017.01.001

Mennill, D. J. & Ratcliffe, L. M. 2004. Nest cavity orientation in Black-capped Chickadees *Poecile atricapillus*: do the acoustic properties of cavities influence sound reception in the nest and extra-pair matings? – Journal of Avian Biology 35(6): 477–482. DOI: 10.1111/j.0908-8857.2004.03351.x

Miller, K. E. 2010. Nest-site limitation of secondary cavity-nesting birds in even-aged southern pine forests. – Wilson Journal of Ornithology 122(1): 126–134. DOI: 10.1676/07-130.1

Mitchell, A. 1974. A Field Guide to the Trees of Britain and Northern Europe. – Collins, London

Møller, A. P., Adriaensen, F., Artemyev, A., Bańbura, J., Barba, E., Biard, C., Blondel, J., Bouslama, Z., Bouvier, J-C., Camprodon, J., Cecere, F., Chaine, A., Charmantier, A., Charter, M., Cichoń, M., Cusimano, C., Czeszewik, D., Doligez, B., Doutrelant, C., Dubiec, A., Eens, M., Eeva, T., Faivre, B., Ferns, P. N., Forsman, J. T., García-del-Ray, E., Goldshtein, A., Goodenough, A. E., Gosler, A. G., Góźdź, I., Grégoire, A., Gustafsson, L., Hartley, I. R., Heeb, P., Hinsley, S. A., Isenmann, P., Jacob, S., Järvinen, A., Juškaitis, R., Kania, W., Korpimäki, E., Krams, I., Laaksonen, T., Leclercq, B., Lehikoinen, E., Loukola, O., Lundberg, A., Mainwaring, M. C., Mänd, R., Massa, B., Mazgajski, T. D., Merino, S., Mitrus, C., Mönkkönen, M., Morales-Fernaz, J., Moreno, J., Morin, X., Nager, R. G., Nilsson, J-Å., Nilsson, S. G., Norte, A. C., Orell, M., Perret, P., Perrins, C. M., Pimentel, C. S., Pinxten, R., Priedniece, I., Quidoz, M-C., Remeš, V., Richner, H., Robles Díez, H., Russell, A., Rytkönen, S., Senar, J. C., Seppänen, J. T., Pascoal da Silva, L., Slagsvold, T., Solonen, T., Sorace, A., Stenning, M. J., Török, J., Tryjanowski, P., van Noordwijk, A. J., von Numers, M., Walankiewicz, W. & Lambrechts, M. M. 2014. Clutch size variation in Western Palearctic secondary hole-nesting passerine birds in relation to nestbox design. – Methods in Ecology and Evolution 5(4): 353–362. DOI: 10.1111/2041-210X.12160

Monti, F., Nelli, L., Catoni, C. & Dell'Omo, G. 2019. Nest box selection and reproduction of European Rollers in Central Italy: a 7-year study. – Avian Research 10(1): 13. DOI: 10.1186/s40657-019-0150-0

Mueller, A. J., Twedt, D. J. & Bowers, E. K. 2019. Rapid adoption of nest boxes by Prothonotary Warblers *(Protonotaria citrea)* in mesic deciduous forest. – Canadian Journal of Zoology 97(12): 1109–1115. DOI: 10.1139/cjz-2019-0059

Navara, K. J. & Anderson, E. M. 2011. Eastern Bluebirds choose nestboxes based on box orientation. – Southeast Naturalist 10(4): 713–720. DOI: 10.1656/058.010.0410

O'Connor, R. J. 1984. The Growth and Development of Birds. – John Wiley and Sons, London

Rodwell, J. S. 1991. British Plant Communities, Volume 1: Woodlands and Scrub. – Cambridge University Press, Cambridge

Rohrbaugh, R. W. Jr. & Yahner, R. H. 1997. Effects of macrohabitat and microhabitat on nest box use and nesting success of American Kestrels. – Wilson Bulletin 109(1): 410–423.

Sacilotto, K. A. & Anderson, J. T. 2005. Avian nest box use on islands in the Ohio River. – Northeastern Naturalist 12(4): 403–410. DOI: 10.1656/1092-6194(2005)012[0403:ANBUOI]2.0.CO;2

Salaberria, C., Celis, P., López-Rull, I. & Gill, D. 2014. Effects of temperature and nest heat exposure on nestling growth, dehydration and survival in a Mediterranean hole-nesting passerine. – Ibis 156(2): 265–275. DOI: 10.1111/ibi.12121

Samplonius, J. M. & Both, C. 2019. Climate change may affect fatal competition between two bird species. – Current Biology 29(2): 327–331. DOI: 10.1016/j.cub.2018.11.063

Smith, K. W., Smith, L., Charman, E., Briggs, K., Burgess, M., Dennis, C., Harding, M., Isherwood, C., Isherwood, I. & Mallord, J. 2011. Large-scale variation in the temporal patterns of the frass fall of defoliating caterpillars in oak woodlands in Britain: implications for nesting woodland birds. – Bird Study 58(4): 506–511. DOI: 10.1080/00063657.2011.616186

Stanback, M. T., Niemasik, E., Millican, D. & McGovern, P. 2019. Pairing nest boxes does not promote coexistence of Eastern Bluebirds *(Sialia sialis)* and subordinate cavity nesters. – Wilson Journal of Ornithology 131(2): 422–427. DOI: 10.1676/18-93

Wachob, D. G. 1996. A microclimate analysis of nest-site selection by Mountain Chickadees. – Journal of Field Ornithology 67(4): 525–533.

Wilkin, T. A., King, L. E. & Sheldon, B. C. 2009. Habitat quality, nestling diet, and provisioning behaviour in Great Tits *Parus major*. – Journal of Avian Biology 40(2): 135–145. DOI: 10.1111/j.1600-048X.2009.04362.x

Wilson, J. 2015. A nest-box and colour-ringing study of Bearded Tits *Panurus biarmicus* at Leighton Moss, Lancashire. – Ringing and Migration 30(2): 75–80. DOI: 10.1080/03078698.2015.1128247