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Microclimate shifts in nest-boxes and natural cavities throughout reproduction

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Animals breeding in nest-boxes experience nesting environments in which they did not originally evolve. Despite the central importance of nesting microclimate for offspring fitness, little is known about the thermal properties of human-provided nest sites compared to natural ones. In particular, comparisons with offspring in the nest are lacking. Here, we compare microclimate (temperature and absolute humidity) from the onset of breeding, thus starting with nest-site choice and ending with the post-fledging stage, quantified in natural cavities and nest-boxes used by several species of hollow-nesting birds in a temperate deciduous forest. We confirm that across all nesting stages, nest-boxes were thermally unstable when compared to natural cavities, with higher temperature maximums, larger amplitudes and worse insulation from maximum ambient temperatures relative to natural cavities. Surprisingly, as average humidity of natural cavities was previously shown to be higher than in nest-boxes, in the presence of actively thermoregulating young, nest-boxes were more humid than natural cavities. When offspring were in the nest, internal microclimatic shifts were mitigated three times more effectively in natural cavities than in nest-boxes (in terms of mean daily differences from ambient temperature). Artificial cavity microclimate is likely to amplify the adverse effects of projected temperature increases by compromising thermoregulation of developing animals. We stress that conservation efforts should focus on the protection of areas offering natural breeding-hollows to reduce the potential impacts of climate change on breeding animals.

Keywords: absolute humidity, Anthropocene, climate change, natural cavities, nest boxes, temperature

Introduction

Nests provide protection for the developing young and buffer them from external climatic conditions by creating an internal microclimate, i.e. specific temperature and humidity. Both play a vital role for energy and water budgets in endotherms, who have to maintain fixed core temperatures in largely varying thermal environments (Porter

and Kearney 2009). Optimally, the nesting site should assure microclimatic conditions as close as possible to the thermo-neutral zone, i.e. the 'comfort zone' in which the animal does not lose body water for thermoregulation at basal metabolic rate (Porter and Kearney 2009). Animals are able to respond behaviourally to fluctuating temperatures (by hibernating, migrating, seeking protection against rain/wind or resting in shadow, reducing activity at the hottest day time). However, young animals developing in nests have only limited possibilities for such adjustments. Thus the microclimate of the nest environment is the best protection for developing offspring against ambient environment and it needs to be stable across development. The costs of regulating the nest environment can be borne by the parents via behaviours such as incubation, brooding (Ospina et al. 2018, Mueller et al. 2019) or actively altering the nest structure in response to the local environment (Mainwaring et al. 2012, Gwinner et al. 2018, O'Neill et al. 2018, Edwards et al. 2020). Young animals can also actively influence the nesting microclimate, insulation and heat transfer among them (by moving apart or panting), especially during periods of parental inattention (when parents remain outside the nest to forage (Webb and King 1983, Webb 1993)).

Much work has assessed avian far-reaching physiological and behavioural responses to a variable nest environment (Deeming 2011, Bleu et al. 2017, Andreasson et al. 2018) throughout the reproductive season (van der Hoek et al. 2017). Bud burst is one of the most important cues for reproduction onset (Schaper et al. 2011) as it is likely related to future insect abundance and critical during the post-hatch period and the growth and development of nestlings. However, the microclimate of a given nest cavity may be an additional cue in some of the 18% of avian species that breed in cavities (Dhondt and Eyckerman 1979, van der Hoek et al. 2017). Therefore any microclimatic alterations may lead to a mismatch of the temperature cue with photoperiod, bud burst date and food availability assessed at foraging. At pre-hatching stages, during egg laying and incubation, the sole presence of incubating parents and eggs (incubated eggs diffuse water vapour to the nest air through the eggshell pores – a mechanism called eggshell conductance) may influence the nesting cavity microclimate of water vapor conditions (humidity increase above the ambient levels (Deeming 2011)). Several studies have demonstrated how critical incubation temperatures are for further development (Mueller et al. 2019) and survival (Ospina et al. 2018). As the breeding cycle progresses, the nesting microclimate may display additional shifts: post-hatching, it has been shown that the presence of nestlings increased internal temperature in natural cavities by 1.5 to 4.1°C (Maziarz 2019). Such an increase can multiply the effects of abiotic conditions on nestling development (especially in small altricial species, whose nestlings are born with no feathers), with impacts on their growth, thermoregulation, parasite loads and survival (Salaberria et al. 2014, Rodríguez and Barba 2016). Importantly, ambient temperature maxima tolerated by cavity-dependent species may soon be exceeded under current climate change projections, which will be especially marked for climates considered now as temperate (Beck et al. 2018, Strain et al. 2021, United Nations 2021).

Several studies have investigated the extent to which nest cavity microclimate – most often reported in terms of temperature – covaries with avian reproductive success and fitness. For example, heated tree swallow *Tachycineta bicolor* nests fledged a higher number and proportion of offspring, which had larger body mass and longer primary feathers 16 days after hatching (Dawson et al. 2005). The effects of increased temperatures in the nest vary across species: prothonotary warblers *Protonotaria citrea* experienced lower fledging success, whereas Carolina wrens *Thryothorus ludovicianus* had reduced body condition (Mueller et al. 2019). The humidity of a cavity and its effect on its inhabitants (Moyer et al. 2002, Heylen et al. 2013, Maziarz et al. 2017, Schwartz et al. 2020) has previously been approached using relative humidity as a measure. However, relative humidity, unlike absolute humidity, is inaccurate as it does not predict a subject's evaporative water loss (Kurta 2014).

These fundamental conditions for development have rarely been directly compared between natural and artificial, human-provided nesting sites (McComb and Noble 1981, Lei et al. 2014, Maziarz et al. 2017, Strain et al. 2021). All studies pointed to poor insulation of nest-boxes compared to natural nests, which is likely to be driven by the low wall thickness in artificial nests (Strain et al. 2021). Moreover natural hollows have higher humidity than nest-boxes (McComb and Noble 1981, Maziarz et al. 2017, Schwartz et al. 2020, Strain et al. 2021) and ascertain a proper environment for incubation, with internal humidity matching well the water vapor eggshell conductance (Mersten-Katz et al. 2012). Given the fact that hole-nesting birds currently use very different types of nesting cavities – ranging from natural cavities in trees to plywood or woodcrete (a mixture of timber and concrete) nest-boxes – it is important to assess the microclimate of these different breeding cavities to provide a reference benchmark for the reproductive success further recorded in such cavities. For example, it has been demonstrated that woodcrete nest-boxes had higher internal temperatures relative to plywood ones (García-Navas et al. 2010). Consequently, knowledge of the extent to which the different types of breeding cavities provide a homeostatic environment became particularly pressing given the temperature increases recorded recently and those that are projected to occur in the future (Beck et al. 2018, Strain et al. 2021, United Nations 2021).

Here, we report the results of a comparative study on internal nest-site microclimate (temperature and absolute humidity) in two types of nesting cavities: natural cavities and woodcrete nest-boxes at various stages of the nesting cycle: 1) during nest-site choice to examine microclimatic cues for nesting onset, 2) with offspring in the nest to quantify the microenvironment they experience while developing in each type of nesting cavity and 3) in the nesting cavity after all offspring have fledged (post-fledging). Measurements at stage 3 increased the number of replicates allowing to analyse species-specific and cavity attribute-dependent variation

in thermal profiles of natural cavities. Woodcrete nest-boxes are used by several species of small passerines, mainly blue tits *Cyanistes caeruleus* and great tits *Parus major*, thus we included the natural cavities of both these species for comparison. During nest-site choice in early spring (stage (1), but not in the two remaining stages (2) and (3)), we also assessed microclimate in another type of artificial nest-box – plywood nest-boxes, to test if the material used to construct artificial nesting cavity affects our measurements. We predicted that the thermal conditions in nest-boxes of both types (woodcrete and plywood) will be unstable relative to conditions in natural cavities, with larger temperature amplitudes (higher maxima and lower minima) and poorer insulation from ambient conditions. Additionally, woodcrete nest-boxes will generate higher temperatures than plywood ones (García-Navas et al. 2010). In accordance with previous studies (McComb and Noble 1981, Maziarz et al. 2017, Strain et al. 2021), we also predicted that nest-boxes will provide dryer nesting environment across all nesting stages.

Methods

All nesting cavities (natural cavities and nest-boxes) were located in the same study area: Bielany Forest in the capital city of Warsaw, Poland. The site is characterised by hornbeam-oak stands with > 100 years succession. Microclimate, that is variation of temperature and humidity, was measured inside nesting cavities at three nesting stages: 1) early in spring during nest-site choice (measured across three types of cavities: natural cavities, woodcrete nest-boxes and plywood nest-boxes), 2) during nesting with offspring in the nest (measured for natural cavities and woodcrete nest-boxes) and 3) post-fledging (measured for natural cavities and woodcrete nest-boxes). For nesting stage (1), a set consisting of a standard plywood nest-box and a woodcrete nest-box was temporarily mounted during nest-site choice in 2019, next to random natural cavities occupied in 2018, for the purpose of comparative measurements between all three types of cavities (Supporting information). For nesting stages (2) and (3), the measurements took place in 2018–2019 in a subset of randomly chosen natural cavities (mainly located in hornbeams and oaks) and woodcrete nest-boxes (Schwegler 1b) used for active breeding in two plots within the forest – one with only natural cavities (30 ha core area) and one with nest-boxes (15 ha with 65 nest-boxes). The measurements lasted for the entire nesting period. Throughout that time, we specifically focused on comparisons between two types of cavities: natural cavities and woodcrete nest-boxes. For details on fieldwork and study site, please refer to Sudyka et al. (2022a). Briefly, we performed intensive nest searches at the natural cavity plot and weekly nest-box rounds to record all relevant phenological and reproductive success-related parameters (e.g. lay date, clutch size, fledging success). We measured nest cavitiy dimensions using a measuring tape (precision 0.1 cm, according to the methodology in Wesołowski and Rowiński (2012) and Maziarz et al. (2016)). We also recorded cavity

orientation (entrance facing one of the eight cardinal and intercardinal directions, that is relevant for the amount of received solar radiation (Griffiths et al. 2017)). Microclimatic measurements were taken automatically every hour by means of i-Buttons: temperature data loggers (maxim integrated DS1921G, range: −40°C to +85°C; precision ± 1°C; resolution: 0.5°C) and temperature and humidity loggers (maxim integrated DS1923-F5, range: −20 to +85 °C; 0–100% RH; precision: ± 0.5°C, ± 5% RH, resolution: 0.5°C, 0.6% RH). The measurements were taken simultaneously by paired data loggers of the same type, positioned inside and outside of each natural cavity/nest-box, to precisely test the buffering against ambient conditions at the nest level. The internal data logger was mounted with a thin transparent wire at the level of the nest cup. The nesting space offers various microclimates in a way that the temperature inside the nest cup may vary from the microclimate in the interior of nest cavity (Mersten-Katz et al. 2012). Our study quantified the immediate microclimate of the nesting cavity space, rather than the microclimate within the nest cup. The external logger was hung in a protective white plastic tube to shade it from direct sunlight and precipitation (double layer of plastic cups cut open at both sides to permit free air movement, Supporting information) and placed at the same height and orientation as the cavity/nest-box entrance, between 10 and 20 cm from the nest opening. In early spring during nest-site choice (stage (1), below), the measuring set included three loggers, each in: a natural cavity, a woodcrete nest-box, a plywood nest-box and a fourth external i-Button to measure ambient conditions at the same height above ground for all nesting cavities (Supporting information). During nesting and after fledging (stages (2) and (3), below), the set included an i-Button inside a natural cavity/woodcrete nest-box and an external i-Button to measure ambient conditions at the same height above the ground as the nest was located (Supporting information). Since the number of i-Buttons was not sufficient to cover all locations at once for the measurement stages (1) and (3), we moved the loggers across locations. We excluded the first measurement made at each location to allow the ambient conditions to settle (thus the first measurement considered in the analyses was taken between 61 and 119 min after installation). Importantly, temperature and humidity i-Button data loggers record relative humidity, a measure with limited biological relevance (Kurta 2014). Under conditions of constant relative humidity, evaporative water loss can vary by more than 100%, depending on ambient temperature and it has been demonstrated that changes in relative humidity do not matter for body temperature, metabolic rate or thermal conductance (Eto et al. 2017). Consequently, there is no effect of relative humidity on thermoregulation. This may be relevant not only for nestlings, but also for incubating adults due to their differential ambient condition-dependent thermoregulation. In this context, the limited reporting of the role of absolute humidity in the avian literature is puzzling given its crucial role across reproductive stages (Mersten-Katz et al. 2012) and its alterations related to anthropogenic actions (Lambrechts et al. 2017, James Reynolds et al. 2019).

Relative humidity (RH) is the partial pressure of water vapor that actually exists in the air (*Ea*), relative to the saturated vapor pressure (*Es*), which is the maximum pressure possible by water vapor at a given temperature (Eq. 1; Kurta 2014):

$$RH = Ea \, / \, Es \times 100 \qquad (1)$$

There are standard meteorological equations allowing to transform recorded temperature and relative humidity into absolute humidity. To do so, we first calculated saturated vapor pressure (after Alduchov and Eskridge 1996, Eq. 2):

$$Es(t) = 6.11 \times e^{(17.625 \times t)/(243.04+t)} \qquad (2)$$

t: temperature measured by i-Button in °C.

We then calculated the actual vapor pressure (*Ea*), which is a measure of absolute humidity of our interest, by transforming the basic formula (Eq. 1) to Eq. 3:

$$Ea = Es \times RH \, / \, 100 \qquad (3)$$

RH: relative humidity measured by i-Button in %.

We quantified dimensions of nesting cavities in natural cavities and nest-boxes used for measuring microclimate during the three nesting stages based on the methodology of Wesołowski and Rowiński (2012) and Maziarz et al. (2016), see all cavities dimensions in Table 1.

Microclimate during nest-site choice in early spring – a comparison of natural cavities, woodcrete and plywood nest-boxes

To quantify internal microclimate conditions at the stage of nest-site choice (1), we placed i-Buttons measuring temperature and humidity in natural cavities occupied in the previous, 2018 breeding season by blue tits and great tits (some of them were reused in the 2019 season). We further mounted one woodcrete and one plywood nest-box at similar height and orientation as the natural cavity during the time of measurements (Supporting information), creating a comparative measurement set. Such a set was installed and moved among 10 different locations of random natural cavities occupied in the preceding breeding season from 7 March to 17 April 2019; in total, 30 natural and artificial cavities were analysed, with 2904 temperature reads and 2904 humidity reads.

Microclimate during nesting

We placed i-Buttons in natural cavities and woodcrete nest-boxes during incubation in May 2018 and May–early June 2019; the measurements lasted for the entire nesting period. The internal data logger was always placed outside of the nest cup, so it never came in direct contact with avian bodies (nestlings or adults), which would distort the microclimate

readings. We evaluated nest microclimate in the phase of active nesting (with birds present), starting from the final days of incubation (median days of incubation 3.3, range 0.3–8.4), hatching day (day 0), up to 16 days of nestling presence in the nest (to keep the maximum number of nests in this analysis, as the earliest fledging in our subset was at 17 days and we excluded the fledging day). Clutch size did not vary between the different cavity types in the subset of nests measured at this stage (mean ± SD: 10 ± 2.1 in natural cavities versus 10 ± 3.2 in woodcrete nest-boxes; species were pooled as we did not differentiate for species in this analysis due to the low number of nests). In nine nests we analysed 3906 temperature reads and in five nests 1968 humidity reads.

Microclimate in active nests measured soon after fledging

There were limited opportunities to evaluate microclimate variables in natural cavities during nesting because of the difficulty of positioning a logger due to small entrances and internal cavity layout (narrow corridors, ledges, crevices and protuberances in the bark causing the transparent wire holding the loggers to disturb birds entering the nest), resulting in a high risk of abandonment. We therefore placed loggers in natural cavities and woodcrete nest-boxes soon after fledging in both 2018 and 2019 breeding seasons. This allowed us to measure species-specific natural cavity microclimate variation (in cavities whose dimensions are known to differ between blue tits and great tits, Sudyka et al. 2022a) and woodcrete nest-box microclimate variation in a larger number of replicates whilst accounting for natural variation of nest parameters (e.g. height above the ground and orientation). To control for phenology and seasonal changes in environmental variables (as ambient temperatures were higher post-fledging than during nesting; $F_{1,6948} = 811.317$, p < 0.0001, Supporting information), nests of the same species in woodcrete nest-boxes and natural cavities with similar lay date (± 1 day) and clutch size (± 1 egg) were matched in pairs and were simultaneously measured with the same type of logger. Thus, the microclimate was measured at a similar time after fledging for each nest – consequently the temperature rise in time should be correlated in both types of nesting cavities measured. Additionally, for nests with later phenology (lay and hatch dates) the period when nestlings remain in the nest overlapped with the post-fledging period of earlier nests. For example, when first nests in each season fledged, nestlings in the remaining ca 30% nests were 10 days old or younger. At the population level nesting stage with young in the nest (2) and post-fledging stage (3) were not disconnected temporally and ambient temperatures overlapped between the two stages in most of their ranges (Supporting information). 90 nests (43 blue tit and 47 great tit) yielded 4198 temperature reads and 45 nests (20 blue tit and 25 great tit) yielded 2102 humidity reads.

Table 1. Microclimate variables for the different types of nesting cavities taken at three nesting stages – (1) before, (2) during and (3) after breeding. Each stage was analysed separately (see Table 2–3, Supporting information for results). Linear dimensions of each type of nesting cavity in cm on the graphs below; for natural cavities, collective median values and (and ranges) shown (for details on nest dimensions at each stage see Supporting information). TEMP: temperature in °C and HUM: absolute humidity as vapor pressure in hPa.

Nesting stage	Variable	Natural cavity		Woodcrete box		Plywood box		Ambient	
		TEMP	HUM	TEMP	HUM	TEMP	HUM	TEMP	HUM
(1) Nest-site choice	Mean ± SD	7.2 ± 3.06	10.7 ± 2.28	7.6 ± 4.55	6.9 ± 1.82	7.7 ± 4.54	6.5 ± 2.06	7.4 ± 4.43	7.0 ± 1.71
	Minimum	−1.0	5.5	−1.9	3.4	−1.5	2.9	−2.0	3.5
	Maximum	16.6	17.4	21.1	12.7	21.6	13.1	19.6	11.7
	Mean difference with ambient ± SD (min–max)	−0.21 ± 3.549 (−11.0 to 8.6)	3.73 ± 2.502 (−2.2 to 10.7)	0.20 ± 0.845 (−6.5 to 4.1)	−0.07 ± 1.170 (−3.4 to 3.6)	0.27 ± 1.051 (−7.0 to 4.5)	−0.45 ± 1.623 (−5.1 to 4.4)	.	.
(2) Young in nest	Mean ± SD	16.5 ± 3.76	19.7 ± 4.62	20.3 ± 5.02	22.3 ± 6.45	.	.	15.0 ± 4.57	13.2 ± 4.16
	Minimum	5.5	9.2	3.0	7.7	.	.	1.0	4.6
	Maximum	29.8	36.6	33.5	40.1	.	.	26.9	23.4
	Mean difference with ambient ± SD (min–max)	1.72 ± 4.127 (−9.5 to 11.2)	7.07 ± 2.877 (−0.7 to 20.0)	5.20 ± 3.218 (−2.5 to 19.5)	8.17 ± 5.247 (−2.7 to 25.7)	.	.	.	.
(3) Post-fledging	Mean ± SD	19.4 ± 3.28	25.2 ± 5.85	20.5 ± 4.61	21.9 ± 6.36	.	.	20.5 ± 4.86	17.1 ± 4.11
	Minimum	11.5	13.8	8.0	9.8	.	.	7.0	5.2
	Maximum	27.8	42.8	31.6	41.6	.	.	33.8	28.5
	Mean difference with ambient ± SD (min–max)	−1.01 ± 3.582 (−12.0 to 8.3)	8.16 ± 4.603 (−3.2 to 24.6)	−0.08 ± 1.591 (−3.5 to 16.5)	4.83 ± 5.248 (−4.6 to 22.0)	.	.	.	.

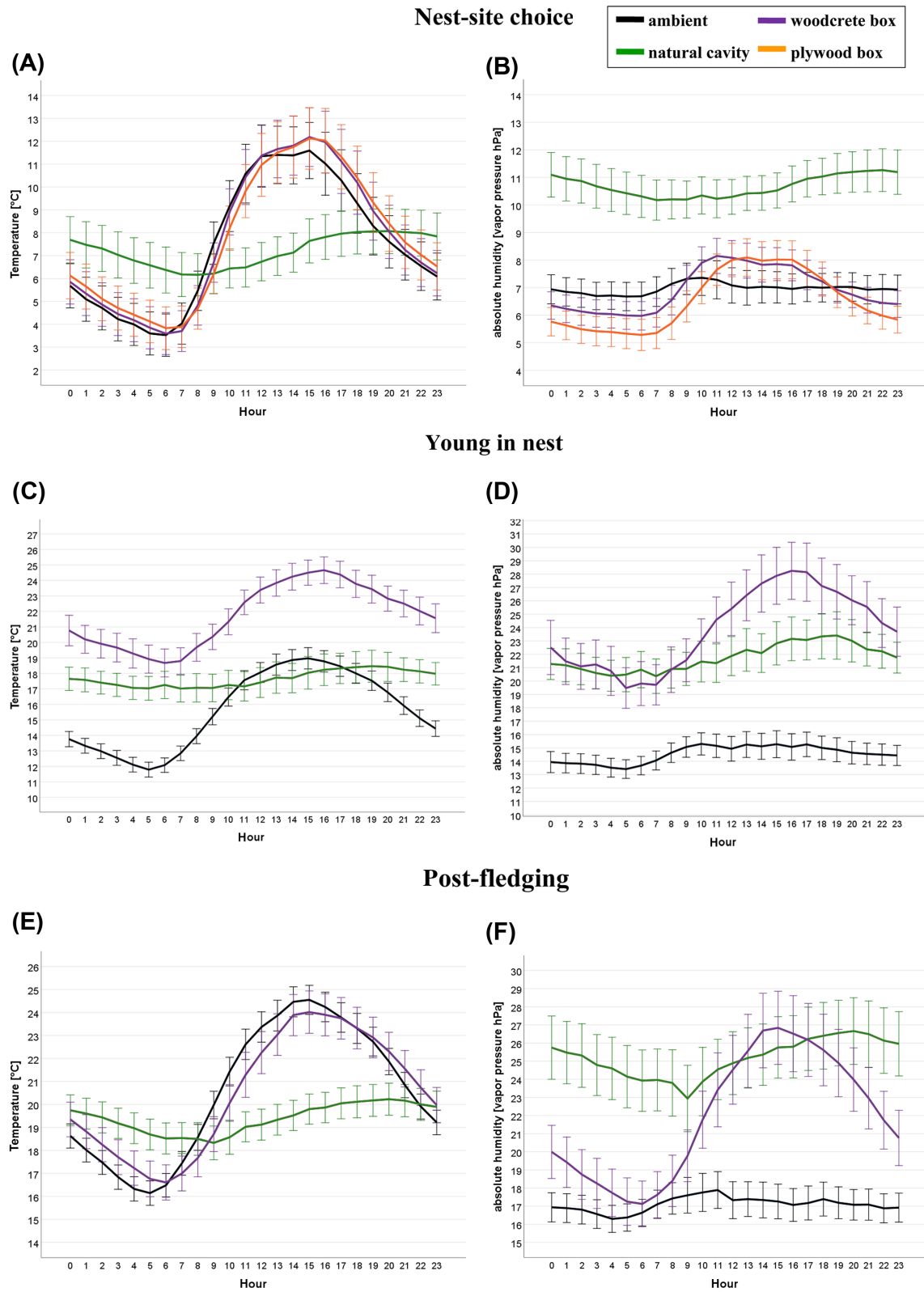Figure 1. Daily changes in hourly mean temperature (A, C, E) and absolute humidity (B, D, F) across three nesting stages: at nest-site choice (A, B), in the presence of young in the nest (C, D) and post-fledging (E, F). Raw data, mean ± 95% CI are shown, sample sizes for all graphs see Supporting information. These data were used to calculate daily mean, maximum, minimum, amplitude and insulation.

Statistical analysis

We modelled five response variables for both temperature (T) and absolute humidity (H) inside the nesting cavity, calculated from values recorded each day (24 hourly measurements see Fig. 1): mean daily (Tmean, Hmean), minimum daily (Tmin, Hmin), maximum daily (Tmax, Hmax), difference between daily maximum and minimum (amplitude: Tmax–Tmin, Hmax–Hmin) and insulation, that is the minimum difference between conditions inside the cavity and outside of it (minimum daily difference for Tinside–Toutside and Hinside–Houtside calculated each hour). Analyses on insulation inform about the degree of protection against maximum values of ambient conditions which each type of nesting cavity provides (i.e. how much lower are the values inside the nest relative to outside values at the hottest/most humid daytime).

We used linear mixed models to explain variation of the abovementioned components of temperature and absolute humidity measured in natural and artificial cavities at three nesting stages: 1) during nest-site choice, 2) with young in the nest and 3) post-fledging. We introduced nesting cavity type (as cavity type) as a categorical response variable and fitted the following ambient values as covariates: i) mean ambient temperature and humidity in the models explaining Tmean and Hmean respectively, ii) minimum ambient temperature and humidity in the models explaining Tmin and Hmin respectively, iii) maximum ambient temperature and humidity in the models explaining Tmax and temperature insulation and Hmax and humidity insulation respectively, iv) ambient temperature and humidity amplitudes in the models explaining Tmax–Tmin and Hmax–Hmin respectively. To directly compare the two types of artificial cavities at the nest-site choice stage (1), we used nest-box type (woodcrete versus plywood) as a categorical response variable and the covariates (i–iv) for each of the five modelled variables respectively.

In models explaining microclimate variation during nesting (2), we additionally introduced a categorical factor – nestling age – to account for variation in nesting microclimate experienced before the young start to thermoregulate on their own (≤ 6 days of age) and after (> 6 days) (active thermoregulation starts in tits between 4 and 6 days of age; Mertens 1977). In models explaining microclimate variation at the post-fledging stage (3), we additionally accounted for the species that occupied the cavity (blue tit or great tit), cavity orientation (one of eight cardinal and intercardinal directions cavity entrance was facing) and entrance height (above ground level), though these were retained only if significant as main factors or in interactions.

Additional tests were performed across the three nesting stages pooled together, to quantify stage-specific differences in overall buffering abilities of two different cavity types (natural cavities and woodcrete nest-boxes), inferred in terms of mean daily differences with ambient temperature and humidity in two separate models. It is important to note that the buffering variable is different than the abovementioned insulation, which we describe as protection against daily temperature maxima. As response variables, we fitted mean daily difference for Tinside–Toutside and Hinside–Houtside calculated hourly. We fitted nesting stage and cavity type alongside their interaction as fixed factors.

In all models, we controlled for location (nest ID) and date of sampling as random factors (thus, if a nest was used in both years, we retained the same nest ID for both years; this was the case of 2 cavities and 8 nest-boxes in models on post-fledging stage). We log-transformed absolute humidity values in all analyses where it was fitted as response variable to ensure normality of residuals. We checked all interactions of main factors in all models and removed non-significant interactions (p > 0.05). We checked all models for overdispersion and multicollinearity (VIF scores in all models never exceed 4) and performed Z-score scaling of all continuous variables for clarity of parameter estimates. Differences in basic nesting cavity dimensions of natural cavities and nest-boxes at each nesting stage (Supporting information) and for blue tit and great tit nests in natural cavities during post-fledging stage (Supporting information) were investigated with Kruskal–Wallis tests. All analyses were performed in R (ver. 4.0.4; www.r-project.org). Details of sample sizes for each analysis are shown in the Supporting information.

Results

Nesting cavity type (natural cavity versus woodcrete nest-box) was found to have a nesting stage-specific effect on the internal temperature and humidity of nests (Table 1–3, Fig. 2–3, Supporting information).

1) Microclimate in early spring during nest-site choice. We detected considerable differences both in absolute humidity and temperature between natural cavities and artificial nests, regardless of the material they were made from (Table 2.1, 3.1, Fig. 1A, B, Supporting information). Temperature values of Tmean, Tmax and insulation were higher in nest-boxes of both types relative to natural cavities (Fig. 2A, Supporting information). In contrast, humidity values inferred as Hmean, Hmin, Hmax and insulation and also Tmin were lower in both types of nest-boxes in relation to natural cavities (Fig. 2B, Supporting information). Consequently, daily amplitudes of temperature and humidity were higher in nest-boxes (Table 3.1), and nest-box temperature and humidity responded more strongly to changing ambient conditions than natural cavities (significant cavity type × ambient conditions interaction; Table 2.1, 3.1, Fig. 2A, B, 3A, Supporting information, with the exception of humidity amplitude and insulation). The direct comparison of the two artificial cavities (Supporting information) showed that woodcrete and plywood nest-boxes had statistically identical temperature profiles (Fig. 1A, except minimum temperature, which was higher in plywood than in woodcrete nest-boxes resulting in lower amplitudes in plywood nest-boxes). In terms of humidity, Hmean and Hmin were

Table 2. Linear mixed models examining variation of daily maximum temperature and absolute humidity measured in natural and artificial nests across three nesting stages: (1) nest-site choice, (2) with young in the nest and (3) post-fledging. During nest-site choice (1) two types of artificial nests-boxes were considered: woodcrete and plywood. When young stayed in the nest (2) nestling age was considered and post-fledging (3) we additionally accounted for species, nest exposure and height. Natural cavities, nestling age less than 6 days and blue tit were used as a reference for parameter estimates and all estimates are shown after Z-score scaling of continuous variables. We present the final models with non-significant main factors and interactions removed (apart from the focal cavity type). Sample sizes for each analysis are shown in the Supporting information. Significant differences (p < 0.05) are indicated in bold.

			Temperature				Humidity			
			χ^2	df	Pr(> χ^2)	Estimate ± SE	χ^2	df	Pr(> χ^2)	Estimate ± SE
Nesting stage	Predictor	Effect			Variance for random effects				Variance for random effects	
1) Nest-site choice	Cavity type		**218.244**	**2,102**	**< 0.0001**		**187.793**	**2,109**	**< 0.0001**	
		Woodcrete box				0.778 ± 0.060				−1.157 ± 0.101
		Plywood box				0.752 ± 0.060				−1.240 ± 0.101
	Ambient		**289.626**	**1,56**	**< 0.0001**		**43.843**	**1,55**	**< 0.0001**	
		Maximum ambient				0.472 ± 0.056				0.124 ± 0.086
	Cavity type × ambient		**62.635**	**2,102**	**< 0.0001**		**24.879**	**2,109**	**< 0.0001**	
		Woodcrete × ambient				0.403 ± 0.060				0.417 ± 0.101
		Plywood × ambient				0.419 ± 0.060				0.457 ± 0.089
	Random effect	*Date*			*0.030*				*0.046*	
		Location			*0.052*				*0.154*	
		Residual			*0.091*				*0.261*	
2) Young in nest	Cavity type		**21.454**	**1,7**	**< 0.0001**		**4.099**	**1,3**	**0.043**	
		Nest-box				1.055 ± 0.254				−0.073 ± 0.192
	Ambient		**231.530**	**1,54**	**< 0.0001**		**71.456**	**1,43**	**< 0.0001**	
		Maximum ambient				0.512 ± 0.052				0.604 ± 0.135
	Nestling age		**183.767**	**1,93**	**< 0.0001**		**46.138**	**1,59**	**< 0.0001**	
		>6 days				0.699 ± 0.079				0.335 ± 0.193
	Cavity type × ambient		**19.822**	**1,111**	**< 0.0001**		0.185	1,45	0.667	
		Nest-box × ambient				0.286 ± 0.064				0.148 ± 0.155
	Ambient × nestling age		**4.166**	**1,113**	**0.041**		**7.069**	**1,57**	**0.008**	
		Ambient × >6 days				−0.130 ± 0.063				−0.073 ± 0.214
	Type × nestling age		**5.554**	**1,125**	**0.018**		**18.727**	**1,45**	**< 0.0001**	
		Nest-box × >6 days				0.253 ± 0.107				1.141 ± 0.245
	Type × ambient × nestling age						**5.105**	**1,56**	**0.024**	
		Nest-box × ambient × >6 days									−0.647 ± 0.286
	Random effect	*Date*			*0.020*				*0.059*	
		Location			*0.132*				*0.014*	
		Residual			*0.108*				*0.171*	

(Continued)

Table 2. Continued.

Nesting stage	Predictor	Effect	Temperature				Humidity			
			χ^2	df	Pr(> χ^2)	Estimate ± SE	χ^2	df	Pr(> χ^2)	Estimate ± SE
			Variance for random effects				Variance for random effects			
3) Post-fledging	Cavity type		**40.261**	**1,64**	**< 0.0001**		**5.345**	**1,20**	**0.021**	
		Nest-box				0.510 ± 0.128				−0.271 ± 0.116
	Ambient		**1020.804**	**1,116**	**< 0.0001**		**53.843**	**1,72**	**< 0.0001**	
		Maximum ambient				0.336 ± 0.039				0.508 ± 0.096
	Height		**16.910**	**1,68**	**< 0.0001**		**13.800**	**1,32**	**0.0002**	
		Height				0.198 ± 0.048				0.222 ± 0.060
	Species		1.167	1,103	0.280					
		Great tit				−0.206 ± 0.136				
	Cavity type × ambient		**456.940**	**1,177**	**< 0.0001**		3.497	1,49	0.061[a]	
		Nest-box × ambient				0.622 ± 0.049				0.190 ± 0.102
	Type × species		1.187	1,96	0.276					
		Nest-box × great tit				0.170 ± 0.156				
	Ambient × species		0.034	1,196	0.855					
		Ambient × great tit				−0.130 ± 0.054				
	Cavity type × ambient × species		**10.921**	**1,176**	**0.001**					
		Nest-box × ambient × great tit				0.232 ± 0.070				
	Random effect	*Date*				*0.011*				*0.224*
		Location				*0.174*				*0.071*
		Residual				*0.044*				*0.215*

[a]We retained the interaction as it was close to significance, and the removal of this interaction did not change the model outcome for the remaining main factors: cavity type: $\chi^2 = 5.456$, p = 0.019; ambient maximum humidity: $\chi^2 = 54.487$, p < 0.0001 and height: $\chi^2 = 14.8719$, p = 0.0001.

lower in plywood nest-boxes when compared to woodcrete ones, leading to larger amplitudes and better insulation against maximum ambient humidity in plywood nest-boxes (Fig. 1B, Supporting information).

2) Microclimate during nesting – from incubation to fledging. At this nesting stage, microclimate patterns changed relative to measurements made in nest-boxes without offspring in the cavity (Fig. 1C, D). Most importantly, nestling age (broods younger or older than 6 days) influenced all temperature and humidity variables, with older broods experiencing higher temperature and humidity in the nesting cavity (Table 2.2, 3.2, Supporting information). The significant interactions between nesting cavity type and nestling age showed that the increase in temperature and humidity values in woodcrete nest-boxes when nestlings were older than 6 days was higher than the increase in natural cavities (with the exception of temperature amplitude and insulation). This resulted in higher values for all temperature variables as well as Hmean and Hmax after day 6 in nest-boxes relative to natural cavities (Fig. 4, Supporting information). Moreover, we found no overall differences (regardless of nestling age) between nesting cavity types in Hmean and humidity insulation (Supporting information) and also Tmin (Supporting information). As in all other nesting stages, temperatures (specifically Tmean, Tmax and insulation) were overall higher in nest-boxes relative to natural cavities (Table 2.2, Supporting information). However, in the case of Hmin and Hmax, the overall values (regardless of nestling age) were only

slightly (yet significantly) lower in woodcrete nest-boxes relative to natural cavities (Table 2.2, Supporting information). Consequently, nest-boxes exhibited higher daily amplitudes in temperature and humidity compared to natural cavities (Table 3.2). Importantly, nest-box temperatures responded more strongly to changing ambient conditions than natural cavities (significant cavity type × ambient temperatures interactions; Table 2.2, 3.2, Fig. 2C, 3C, Supporting information, with the exception of Tmin). In terms of humidity, this response did not vary between cavity types (there was a non-significant cavity type × ambient humidities interaction for all humidity values; Table 2.2, 3.2, Supporting information).

3) Microclimate in occupied nests measured soon after fledging. Variation in absolute humidity and temperature between natural cavities and woodcrete nest-boxes detected at this stage was largely consistent with differences observed early in the season, during nest-site choice (stage (a), when birds were not constantly present in nests; Table 2.3, 3.3, Fig. 1E, F, 3E, F, Supporting information). Since at this stage (3) we analysed microclimate variation in cavities occupied by the two species of tits in the same breeding season, we were able to additionally detect species-specific differences for natural cavity thermal profiles in terms of temperature (Tmean, Tmax and temperature amplitude) and humidity amplitude. Thus, great tit cavities had greater buffering abilities than blue tit cavities: the internal temperature grew less in response to increasing ambient temperatures (significant interaction cavity

Table 3. Linear mixed models examining variation of daily amplitudes of temperature and absolute humidity measured in natural and artificial nests across three nesting stages: (1) nest-site choice, (2) with young in the nest and (3) post-fledging. During nest-site choice (1) two types of artificial nests-boxes were considered: woodcrete and plywood. When young stayed in the nest (2) nestling age was considered and post-fledging (3) we accounted for species, nest orientation and height. Natural cavities, nestling age less than 6 days and blue tit were used as a reference for parameter estimates and all estimates are shown after Z-score scaling of continuous variables. We present the final models with non-significant main factors and interactions removed (apart from the focal cavity type). Sample sizes for each analysis are shown in Supporting information. Significant differences (p < 0.05) are indicated in bold.

Nesting stage	Predictor	Effect	Temperature				Humidity			
			χ^2	df	Pr(> χ^2)	Estimate ± SE	χ^2	df	Pr(> χ^2)	Estimate ± SE
					Variance for random effects				Variance for random effects	
1) Nest-site choice	Cavity type		**625.410**	**2,101**	**< 0.0001**		**39.614**	**2,103**	**< 0.0001**	
		Woodcrete box				1.128± 0.058				0.581 ± 0.131
		Plywood box				1.215 ± 0.058				0.797 ± 0.131
	Ambient		**257.440**	**1,64**	**< 0.0001**		3.595	1,70	0.058	
		Ambient amplitude				0.135 ± 0.050				0.159 ± 0.084
	Cavity type × ambient		**180.320**	**2,101**	**< 0.0001**					
		Woodcrete × ambient				0.674 ± 0.058				
		Plywood × ambient				0.676 ± 0.058				
	Random effect	*Date*			*0.022*				*0.236*	
		Location			*0.028*				*0.166*	
		Residual			*0.085*				*0.438*	
2) Young in nest	Cavity type		**24.488**	**1,7**	**< 0.0001**		3.611	1,3	0.057	
		Nest-box				1.369 ± 0.277				0.682 ± 0.520
	Ambient		**169.182**	**1,60**	**< 0.0001**		**8.684**	**1,52**	**0.003**	
		Ambient amplitude				0.248 ± 0.055				0.229 ± 0.078
	Nestling age		**6.134**	**1,95**	**0.013**		**12.294**	**1,79**	**0.0005**	
		> 6 days				0.149 ± 0.071				0.241 ± 0.200
	Cavity type × ambient		**83.480**	**1,132**	**< 0.0001**					
		Nest-box × ambient				0.635 ± 0.070				
	Ambient × nestling age		**6.503**	**1,89**	**0.011**					
		Ambient × > 6 days				−0.191 ± 0.075				
	Type × nestling age						**5.316**	**1,78**	**0.021**	
		Nest-box × > 6 days								0.695 ± 0.302
	Random effect	*Date*			*0.002*				*0.039*	
		Location			*0.160*				*0.282*	
		Residual			*0.177*				*0.397*	
3) Post-fledging	Cavity type		**338.239**	**1,61**	**< 0.0001**		**61.160**	**1,25**	**< 0.0001**	
		Nest-box				1.123 ± 0.099				0.684 ± 0.209
	Ambient		**295.211**	**1,96**	**< 0.0001**		**25.454**	**1,107**	**< 0.0001**	
		Ambient amplitude				0.299 ± 0.051				0.180 ± 0.076
	Height		**7.650**	**1,72**	**0.006**		**9.144**	**1,36**	**0.002**	
		Height				0.099 ± 0.036				0.223 ± 0.074
	Species		0.552	1,102	0.457		0.523	1,49	0.470	
		Great tit				−0.186 ± 0.099				−0.466 ± 0.217
	Type × ambient		**318.127**	**1,161**	**<0.0001**		**10.448**	**1,68**	**0.001**	
		Nest-box × ambient				0.625 ± 0.068				0.295 ± 0.091
	Type × species		3.095	1,94	0.079		**5.433**	**1,31**	**0.020**	
		Nest-box × great tit				0.239 ± 0.129				0.645 ± 0.277
	Ambient × species		3.351	1,218	0.067					
		Ambient × great tit				−0.193 ± 0.063				
	Type × ambient × species		**7.050**	**1,163**	**0.008**					
		Nest-box × ambient × great tit				0.232 ± 0.087				
	Random effect	*Date*			*0.035*				*0.202*	
		Location			*0.064*				*0.115*	
		Residual			*0.100*				*0.230*	

type × ambient temperature × species; Table 2.3, 3.3, Supporting information). Furthermore, the cavity type × species interaction for humidity amplitude denotes that the increase of amplitude in nest-boxes was lower for great tits than for blue tits, pointing to more stable humidity conditions in great tit cavities (Table 3.3). The height at which the entrance of the nest was located was always positively correlated with temperature and absolute humidity of nests (Table 2.3, 3.3, Supporting information), but nest orientation did not show any effect on microclimate variables (for orientation in all models p > 0.15).

Differences with mean daily ambient conditions across the three nesting stages

There were marked differences across nesting stages and cavity types in both temperature and humidity (Fig. 5, Supporting information). The mean daily difference from ambient temperature was higher in woodcrete nest-boxes than in natural cavities, in particular when young remained in the nest, as shown by the significant cavity type × nesting stage interaction (Fig. 5A, Supporting information). Absolute humidity difference was on average lower in woodcrete nest-boxes than in natural cavities across all stages. However, when young remained in the nest, the increase in the difference from ambient humidity relative to other nesting stages was higher in woodcrete nest-boxes than in natural cavities (significant cavity type × nesting stage, Fig. 5B, Supporting information).

Discussion

For the first time in the context of natural versus artificial cavity comparisons, we report on internal microclimate conditions accounting for stages of nestling development, and in terms of absolute humidity. Importantly, we show that active nest-boxes were not only invariably warmer but, after young start to thermoregulate, were also more humid than natural cavities in terms of average and maximum humidity.

Our results confirm previous findings showing that nest-boxes (woodcrete and plywood) were thermally unstable (yielding larger daily variations) (McComb and Noble 1981, Maziarz et al. 2017, Strain et al. 2021) and provided lower buffering from ambient temperatures (Schwartz et al. 2020) relative to natural cavities. Higher nest-box temperature maximums (Table 2), larger amplitudes (Table 3) and worse insulation from maximum ambient temperatures (Supporting information) in comparison to natural cavities were observed across all nesting stages (in woodcrete nest-boxes; plywood nest-boxes were only tested at nest-site choice). Microclimate buffering against ambient conditions was dependent on cavity type: nest-box temperatures responded more strongly to variation in ambient weather conditions than natural cavities across all nesting stages (Table 2, 3, Fig. 2, 3, Supporting information). When nestlings were not present in the nest (irrespectively of whether measurements were made during nest-site choice (stage 1) or post-fledging (stage 3)), the

thermal profile of the nest-box interior closely followed the hourly variation of ambient temperature (Fig. 1A, B, E, F). During nest-site choice, when we measured microclimate in two types of nest-boxes (woodcrete and plywood), the same pattern was observed in both, implying that the material used for construction did not affect insulating qualities. While temperature profiles of woodcrete and plywood nest-boxes were highly similar (but note slightly higher minima and lower amplitudes in plywood nest-boxes; Supporting information), mean and minimum humidities were lower in plywood nest-boxes, leading to larger humidity amplitudes when compared to woodcrete ones. Nevertheless, the microclimatic variation between the two types of artificial cavities (woodcrete versus plywood) was orders of magnitude lower when each type of artificial cavity were compared to natural cavities (Supporting information to compare with Table 2.1, 3.1, Supporting information).

When nestlings were present in the nest, the temperature profile of woodcrete nest-boxes, whilst still mirroring ambient temperature variation (Fig. 1C), increased on average by over 5°C relatively to outside temperatures (Table 1, Fig. 5A). Strikingly, when nestlings started to thermoregulate (broods older than 6 days), the maximum daily temperature inside the nesting space was on average 7.4°C higher in nest-boxes relative to outside temperatures, and only 1.0°C higher in natural cavities relative to outside temperatures (average daily maximum ± SD: 26.7 ± 3.15°C in nest-boxes and 20.6 ± 3.94°C in natural cavities).

Absolute humidity was consistently higher at nest-site choice and post-fledging in natural cavities (Table 1, 2.1, 2.3, 3.1, 3.3, Fig. 1B, F, Supporting information). Surprisingly, humidity increased dramatically in woodcrete nest-boxes during nesting (Fig. 1D, 5B), in particular after the nestlings started to thermoregulate on their own (Fig. 4B, Supporting information). In this period the maximum daily humidity inside the nesting space was on average 15.1 hPa higher in woodcrete nest-boxes relative to outside conditions, and 8.1 hPa higher in natural cavities relative to outside conditions (average daily maximum ± SD: 32.3 ± 4.41 hPa in nest-boxes and 26.4 ± 4.86 hPa in natural cavities). The higher absolute humidity of nest-boxes relative to natural cavities with active nests contrasts with a study that investigated relative humidity and did not differentiate for nestling development stages (Schwartz et al. 2020). This increase is likely a consequence of the increased evaporative water loss from nestlings and parents due to the higher temperatures occurring in nest-boxes. It has to be noted that the apparent temperature perceived by nesting birds was higher than the one measured within the cavity space (as loggers never came to contact with bird bodies) because of the additional heat produced and transferred by thermoregulating siblings (Webb and King 1983). Such a raise in both temperature and humidity, while still below critical thresholds (McKechnie and Wolf 2010), can possibly increase costs of thermoregulation and thus entail biological consequences for nestling development and fitness (Janas et al. 2022). Additional energetic resources might be necessary to facilitate the increased evaporative cooling in nest-box-reared
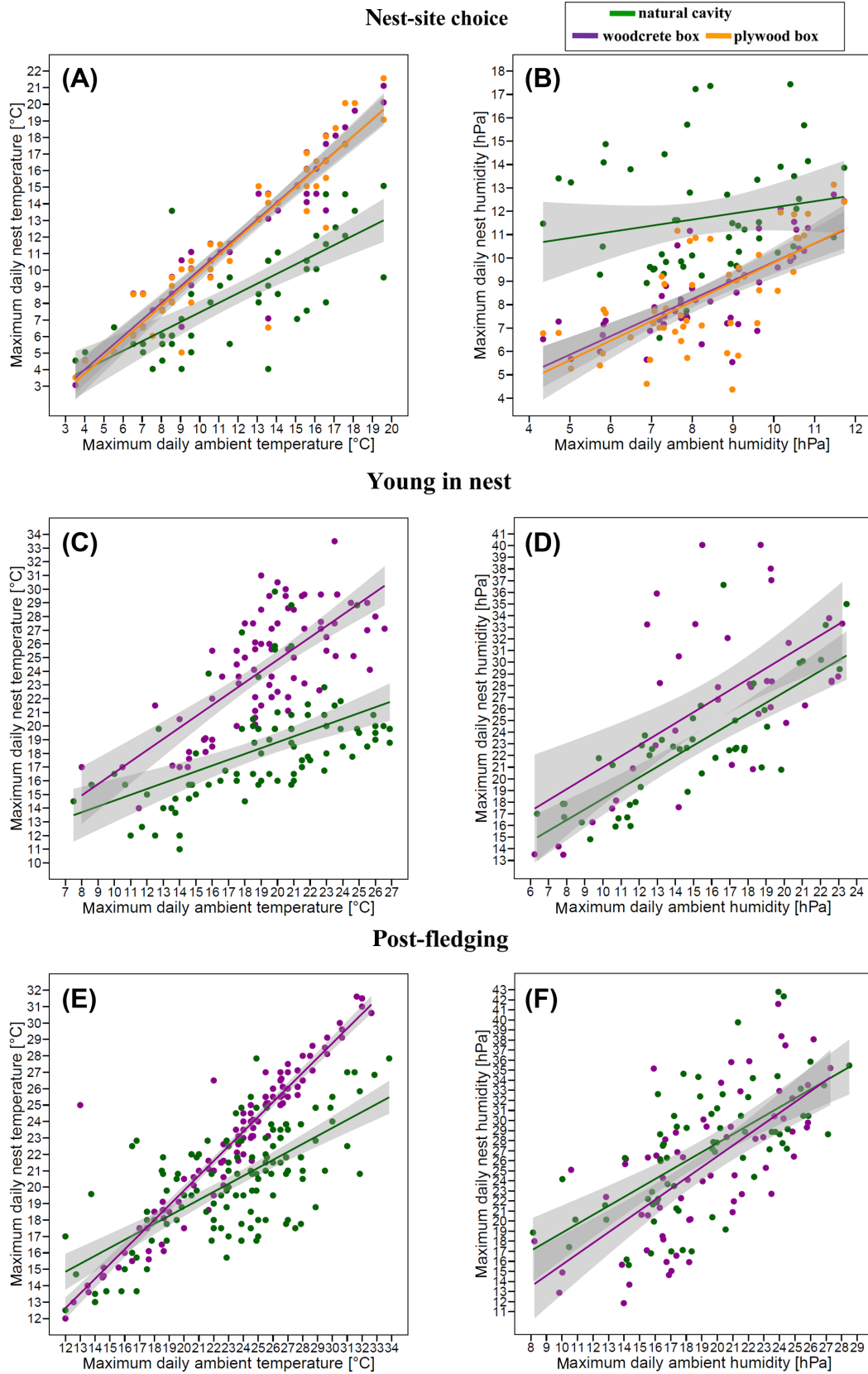
Figure 2. Variation in maximum daily nest temperature (A, C, E) and absolute humidity as vapor pressure (B, D, F) across three nesting stages: at nest-site choice (A, B), in the presence of young in the nest (C, D) and post-fledging (E, F). Raw data points with regression lines ± 95% CI (shaded in grey) are shown. For statistical results see Table 2 and for sample sizes Supporting information. In (D) the interaction of cavity type with maximum ambient humidity was non-significant, but we show it for the consistency of data presentation.
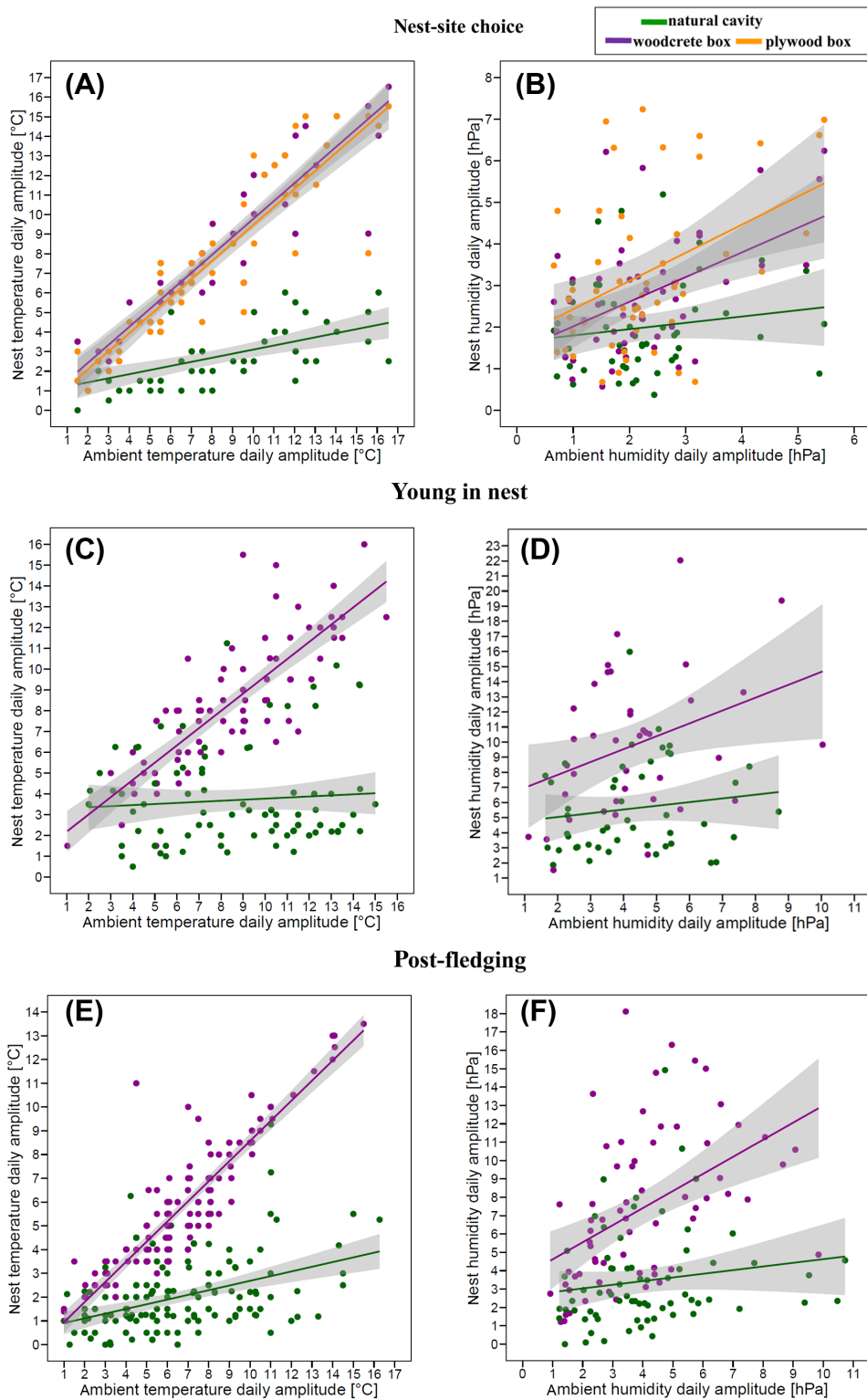
Figure 3. Variation in daily amplitudes of nest temperature (A, C, E) and absolute humidity (B, D, F) across three nesting stages: at nest-site choice (A, B), in the presence of young in the nest (C, D) and post-fledging (E, F). Raw data points with regression lines ± 95% CI (shaded in grey) are shown. For statistical results see Table 3 and for sample sizes Supporting information. In (D) the interaction of cavity type with ambient humidity amplitude was non-significant, but we show it for the consistency of data presentation.
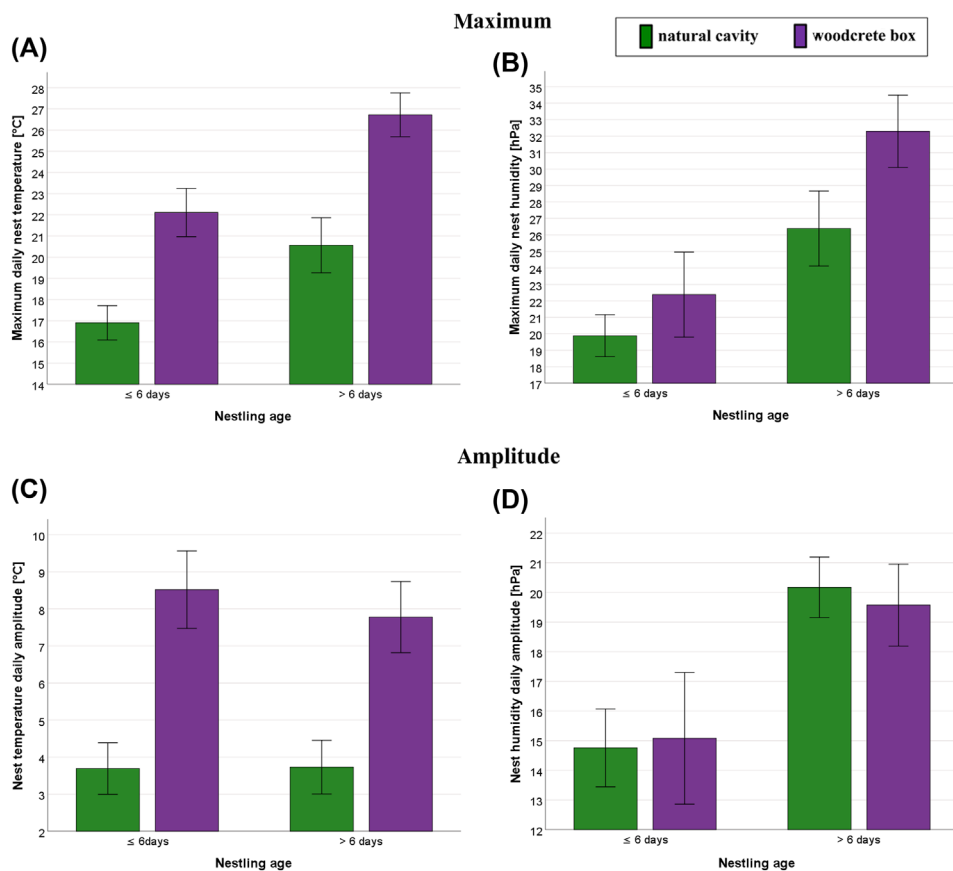
Maximum

Figure 4. Maximum daily nest temperature (A) and absolute humidity (B) and daily amplitudes of nest temperature (C) and absolute humidity (D) with young in nest stage in natural cavities (green) and in woodcrete nest-boxes (dark magenta). The graphs show cavity-type-wise differences according to nestling age: before 6 days of age when nestlings are not yet able to thermoregulate on their own and after 6 days of age when this mechanism is activated. Raw data ± 95% CI are shown. For statistical results see Table 2.2 and 3.2 and for sample sizes Supporting information. In (C) the interaction of cavity type with nestling age was non-significant, but we show it for the consistency of data presentation.
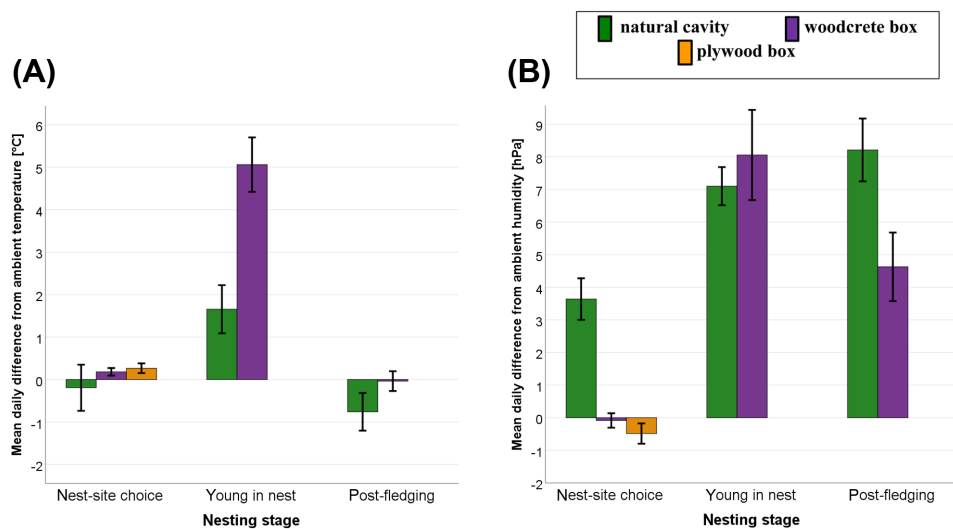
Figure 5. Mean daily difference from ambient temperature (A) and absolute humidity (B) at three nesting stages. Raw data, mean ± 95% CI are shown. Results of the comparison (with plywood boxes excluded) in the Supporting information.

young that could otherwise be devoted to growth (Boyles et al. 2011, Nord and Nilsson 2019, van de Ven et al. 2020), and survival (Cunningham et al. 2013, Bourne et al. 2020).

While during nesting the differences between cavity types were mainly driven by maximum values of temperature and humidity, the minimum values remained largely unaffected by cavity type (no overall differences in Tmin, Hmin was only slightly lower in woodcrete nest-boxes relative to natural cavities; Table 2.2, Supporting information) and all lie within the thermoneutral zone for developing young. Due to the modest number of nests measured during the breeding stage (2) when nestlings were present inside the nests (nine nests assessed for temperature and five for humidity, Supporting information), the variation of microclimates in natural cavities during active nesting may not have been entirely captured in our study. Nevertheless, the daily microclimatic patterns we noted were largely coherent within nesting cavity types and the differences between the cavity types were clear (e.g. $p < 0.0001$ for higher temperature maximum, amplitude, worse insulation from high ambient temperatures in woodcrete nest-boxes than in natural cavities and $p < 0.0001$ for the interactions testing the increase of maximum and mean humidity in nest-boxes relative to natural cavities when nestlings were thermoregulating; Table 2, 3, Supporting information). As such the unmeasured variation may quantitatively influence the results, but it is not likely that the outcome would be qualitatively affected if more nests were included.

Internal nest-site microclimate is important primarily due to varying metabolic and evaporative water requirements not only for young and adults, but also for eggs during incubation. The microclimate associated with incubation is largely controlled by nest quality and parental care (Grant 1982) but this can be facilitated, or hampered, by the microclimate within the breeding cavity space. Consequently, birds can be affected at all nesting stages, but at each stage the impact on fitness can act differently. Pre-hatching, at nest building and incubation, high relative temperatures during the day and low at night may provide erroneous cues for animals, resulting in shifts of breeding phenology (Dhondt and Eyckerman 1979, Purcell et al. 1997, Czeszczewik 2004). Indeed, as reported elsewhere on our study site, blue tits and great tits using nest-boxes started incubating earlier than in natural cavities, even before clutch completion (Sudyka et al. 2022a). This can lead to increased hatching asynchrony with possible consequences on survival of the late hatched nestlings (Stenning 1996).

The internal microclimates of artificial cavities can also have developmental and even fitness consequences in species with lower tolerance to hyperthermia and lower ability to passively dissipate heat i.e. smaller body size (McKechnie and Wolf 2010). Thus, the fitness consequences of nest-box provisioning can be species-specific. In accordance with this, we have recently reported in the same study period a negative impact of nest-boxes in blue tits, which were found to have a lower hatching and fledging success in nest-boxes relative to those breeding in natural cavities and in consequence fewer young fledged, but no apparent effects in the larger great tits (Sudyka et al. 2022a). Additionally, great tit cavities

displayed better buffering qualities than the ones occupied by blue tits (Supporting information), particularly when ambient temperatures were rising. The differences likely stem from the fact that great tit cavities were located lower above the ground (thus less exposed to insolation, Supporting information), and in general have larger volumes than blue tits cavities (Sudyka et al. 2022a, Supporting information).

Conclusion and outlook

Internal microclimatic shifts were mitigated three times more effectively in natural cavities than in nest-boxes (in terms of the mean daily difference from ambient temperature, Table 1, Fig. 5A). With projected increase in ambient temperatures of between 4 and 5°C (Beck et al. 2018, United Nations 2021), microclimatic conditions in nesting-hollows may soon exceed levels enforcing rapid evaporative water loss (i.e. approaching body temperature). Importantly, the shift towards hot summers can be further exacerbated in the urban space due to the heat-island effect (Oke 1982); worldwide the majority of urbanized areas, and consequently many populations using nest-boxes, occur in such climates. We expect that this is likely to enhance non-selective mortality risks resulting in reproductive failure of entire nest-box breeding populations, phenomena that have already been observed (Charmantier, unpubl.). As these mortality risks driven by temperature are highly dependent on humidity variation, more data on absolute humidity in breeding cavities is needed alongside measurements of core and body surface temperatures of nestlings to quantify their water requirements (Kurta 2014).

Our results provide ground data of fundamental importance for the need to re-evaluate the use of nest-boxes as a default conservation tool in the face of climate change, also in the climates now considered as temperate. At the bare minimum, a design of nest-boxes that mitigates acute heat stress and dehydration is required (Watchorn et al. 2022), which entails large internal volumes, thicker walls (Maziarz 2019, Strain et al. 2021), avoiding direct sunlight, avoiding orientations, which receive the greatest amount of solar radiation during the hottest time of the day (Griffiths et al. 2017) and choosing high surface reflectance – painting boxes to light colours (Griffiths et al. 2017, Rueegger 2019) (yet it has to be considered that the colour might influence box occupancy (Browne 2006)). While it is not sufficient to manipulate nest-box size and shape, because these parameters might have no detectable influence on the internal temperature fluctuations (Ellis 2016), constructing nest-boxes of boles of aspen replicated the microclimate of natural cavities more closely and appeared to have slightly better insulating properties than traditional plywood nest-boxes (Griebel et al. 2020). Nevertheless, such a well-thought design will require investment and careful planning, and the best nest-box will not provide the nesting climate offered by a natural hollow. Thus, a much simpler and cost-efficient solution is to protect ecosystems that provide natural nesting-hollows and old-growth tree stands, which are likely to be more effective in the long-run.

Author contributions

Irene Di Lecce and **Marta Szulkin** contributed equally to this publication. **Joanna Sudyka**: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Supervision (lead); Writing – original draft (lead); Writing – review and editing (equal). **Irene Di Lecce**: Conceptualization (supporting); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Marta Szulkin**: Funding acquisition (lead); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mw6m9060v (Sudyka et al. 2022b).

Supporting information

The Supporting information associated with this article is available with the online version.

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