Microclimate of tree cavities used by Great Tits (Parus major) in a primeval forest

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ABSTRACT

Altricial birds nesting in places with a favourable microclimate would be able to maintain the proper temperature of eggs or nestlings with less effort and thus reproduce more successfully. Tree cavities provide relatively safe nesting sites, but their microclimate is hardly known. Here we present the first data on air temperature and humidity in natural cavities used by Great Tits nesting in a primeval forest in the Białowieża National Park (Eastern Poland). We checked what microclimatic conditions existed in cavities selected by Great Tits, how the construction of a nest changed the microclimate in a cavity and to what extent cavity localisation and cavity dimensions modified the microclimate of the breeding cavities. Great Tits used cavities in the living trees which were characterised by cool but relatively stable temperatures and very high relative humidity. Such conditions appear to be typical for cavities in living trees in general. Cavities with Great Tit broods were warmer and drier that the unused ones. The microclimate did not appear to constitute the major factor determining Great Tit usage of cavities in living trees, but it could exert a modifying effect on the pattern of cavity use by them. By choosing cavities of appropriate dimensions and placing the nest at an appropriate distance from the entrance, Great Tits could modify the cavity microclimate. However, their options were probably constrained by necessity to meet other important requirements, such as nest safety and illumination.

Keywords: air humidity, air temperature, Białowieża National Park, tree cavities, Great Tit, nest site, primeval forest

1. INTRODUCTION

To reproduce successfully birds have to use safe nest sites, which simultaneously provide suitable protection against harmful environmental conditions, such as rain, wind or extreme temperatures (e.g. Nice, 1957; Ricklefs, 1969; Wesołowski, 2002; Radford and Du Plessis, 2003; Amat and Masero, 2004; Wesołowski and Tomiałojć, 2005). The insulating function of a nest is especially important for altricial passerines that produce hatchlings that are small, naked and incapable for self-thermoregulation (Hansell, 2000). Birds occupying places with favourable microclimatic conditions would be able to better maintain a proper temperature of eggs or nestlings with less effort (Ricklefs and Hainsworth, 1969; O’Connor, 1975; Walsberg and King, 1978; Haftorn, 1983; Mertens, 1987). One could expect that these conditions would include moderate, stable air temperatures and humidity.

Tree cavities are found to be the safest among types of nest sites available in forests (Nice, 1957; Wesołowski and Tomiałojć, 2005). Yet, in natural conditions, these safe nest locations frequently remain underutilised. There are usually more nest cavities than birds that could use them (Wesołowski, 2007a). This begs the question: why do not more bird species nest in tree cavities? Although, posed a long time ago (Lack, 1954; Nice, 1957), this question has still not been satisfactorily answered. One could propose the existence of various constraints as a possible explanation. There may be insufficient illumination in cavities (Wesołowski and Maziarz, 2012), but inappropriate microclimatic conditions could be also important. Tree cavities effectively buffer eggs and chicks against ambient conditions, but they sometimes may become too efficient, and to hinder gaseous exchange (e.g. Howe et al., 1987; Ar et al., 2004; Mersten-Katz et al., 2012). This could create dangerous situations. During hot days, large broods may be exposed to extremely high temperatures (Kluijver, 1951; van Balen, 1984) which, along with greater accumulation of harmful gases and lower oxygen content in the air (Howe et al., 1987; Erbelding-Denk and Trillmich, 1990), may endanger the life of nestlings. So far, such situations have been observed only in artificial places – nest boxes. However, striking differences between nest boxes and tree cavities (Wesołowski, 2011) do not permit for generalisations to natural conditions. It is necessary to gather data on microclimate of tree cavities used by birds.

Data on microclimate in tree cavities occupied by breeding birds are rare (Howe et al., 1987; Hooge et al., 1999; Martin and Ghalambor, 1999; Wiebe, 2001; Ar et al., 2004; Rhodes et al., 2009; Mersten-Katz et al., 2012). We presumed that different types of cavities would provide contrasting environments, but there are hardly any data to check this. Available data indicate, though, that air temperatures in cavities may depend on their locality and dimensions (Hooge et al., 1999; Wiebe, 2001; Sedgeley, 2004; Mersten-Katz et al., 2012).
Thus, by selecting cavities with appropriate attributes, the birds would be able to adjust microclimatic conditions in cavities to their requirements, at least to some extent. Whatever the initial conditions, construction of a nest and the presence of an incubating bird, i.e. the bird-nest incubation unit suggested by Deeming (2002), could modify the microclimate in the cavity. During incubation the air is warmed by a single parent while in the late nestling period it is heated by at least a few feathered nestlings. Hence it may be presumed that heat production of the active nest would increase from the incubation to the late nestling period. Yet, this heating effect of an active nest on cavity microclimate has hardly been examined. Howe et al. (1987) found that temperature in a cavity remained essentially unchanged throughout the nestling period of Northern Flicker (Colaptes auratus). Mersten-Katz et al. (2012) recorded that night temperature among nestlings were higher than the temperature among eggs.

The Great Tit is an obligate cavity nester which often uses nest-boxes. Its breeding biology has been very intensively studied, but typically in nest boxes (review in Cramp and Perrins, 1993; Glutz von Blotzheim and Bauer, 1993). As a consequence, natural nest sites of Great Tits are hardly known and factors influencing Great Tits’ decisions on which cavities to use in natural conditions, are largely unknown (Maziarz, 2012). We can only suspect that the cavity microclimate is important and that the birds presumably occupy cavities with suitable thermal and humidity conditions.

Here we present the first data on air temperature and humidity in tree cavities used by Great Tits. We present data on: (1) the microclimatic conditions the birds experience when selecting nest sites; (2) how the presence of an active Great Tit’s nest influences the microclimate in a cavity, and how conditions change between incubation and nestling periods; (3) how the location of a cavity and its dimensions modify the microclimate when breeding birds are present. We discuss the importance of our findings for cavity nesting birds in general.

2. STUDY AREA AND METHODS

The study was carried out in 2009–2010 in the strictly protected part of the Białowieża National Park (Eastern Poland, circa 52°40’N, 23°50’E), within three large permanent study plots. The plots were situated in the deciduous old growth forest of primeval origin (see Wesołowski, 2007b; Wesołowski et al., 2002; 2010; for detailed descriptions and photos). Cavities were superabundant there and the cavity-nesting birds had a wide spectrum of nesting places to choose from (Wesołowski, 2007a).

2.1. Microclimate measurements

We measured air temperature and humidity in two types of cavities: (1) ‘former’ cavities, which had been used by Great Tits in the previous seasons but were unused during the recording year; and (2) breeding cavities, that had been used by Great Tits in the observation year. All the cavities were formed in the process of wood decay. They were placed almost exclusively in living trunks (39/40 and 34/35 respectively), mainly of hornbeams (36/40 and 30/35), with a median girth at the entrance height 135 cm and 119 cm, and median height above ground of circa 4 m. To avoid tree climbing, we selected cavities accessible from the ground or from a ladder, but because there were so few of them, we were forced to include higher ones, up to 7 m above ground.

We took measurements during two periods for each cavity: (1) during incubation, usually 5–6 days after the clutch completion (when incubation behaviour was fully developed and microclimatic conditions should be representative for this period); and (2) in the second part of the nestling period, when young were already feathered (circa 13–14, i.e. at the stage at which measurements could be safely made). At the incubation stage, the data were gathered more or less in parallel in the breeding (median date = 8 May) and in the ‘former’ (median date = 10 May) cavities. At the nestling stage, the recordings in the breeding cavities (median date = 29 May) were made slightly earlier than in the ‘former’ cavities (median date = 4 June). Despite this, the measurements in the ‘former’ cavities overlapped in time with the period in which Great Tit nestlings ≥7 days old were present in nests.

We used 18 temperature (DS1922L) and six humidity and temperature (DS1923) data loggers (iButtons) on a rotational basis in different cavities and on different plots. Their size (diameter of 17 mm, thickness of 6 mm) allowed us to place them easily in cavities even with the narrowest entrances. All data loggers were tested and calibrated by Dallas Semiconductor/Maxim Inc. (Maxim Integrated Products, 2011a; 2011b). Their operating range was for DS1922L from -10°C to +65°C, and for DS1923 from -20°C to +85°C; from 0% to 100% relative humidity. Measurements precision given by the producer was for temperature ±0.5°C, and for humidity ±5% (see also below). To make sure that all loggers were properly calibrated, we put all of them side by side on a table, and compared their recordings over 24 hours. In room conditions, the values recorded by all loggers were sufficiently comparable; the differences between the recorded values did not exceed 1°C temperature and 3% humidity.

We installed a set of two data loggers at each cavity: (1) one hung on a thin wire inside the cavity; and (2) the second was placed on the same height, about 2 m above ground (out of the range of ground frosts), in a cover.
minimising direct solar radiation. In breeding cavities, the loggers were hung right above the nest (usually 11–14 cm below the lower edge of cavity entrance), but not touching it, near to the frontal wall so as not to disturb the birds entering and leaving the nest. The loggers were usually ignored by birds, except for two pairs which used cavities with small openings. These birds partially pulled out the device, but that did not disrupt breeding (both cases excluded from analyses). In ‘former’ cavities, loggers were mounted just above the cavity bottom, up to circa 40 cm (median 22–24 cm) below the lower edge of cavity entrance. They were switched on before mounting, but all recordings made before the installation time were discounted. The loggers in the set recorded temperature (or temperature and humidity) within 2 minutes of each other, every 5 minutes continuously for circa 48 hours (recording’s resolution was 0.0625°C temperature and 0.04% humidity). We noted additional information: (1) the time of the beginning and the end of each session when the loggers were mounted and removed; (2) coordinates of cavities; and (3) individual number of each loggers’ set (see above) written on the cover of the external logger (this helped us to avoid swapping the sets put into different cavities). After the measurements, the loggers were removed from the forest and the data were transferred to a computer using a 1-Wire adapter and software (Maxim).

2.2. Analyses

All readings of relative humidity were taken if the temperature was 25°C (Maxim Integrated Products, 2011a; p. 53). We corrected those values to actual temperature measured by the same logger, using an equation given by the producer (Maxim Integrated Products, 2011a; p. 53). As humidity sensors were exposed to a high-humidity environment (about 70% or higher) for extended time periods, they systematically inflated humidity values. We compensated those errors using an equation given by Maxim Integrated Products (2011a; p.53).

From each sampling period, we selected a 24 hour series of records (from 00:01 to 24:00). We calculated hourly means which were used to define: (1) mean, minimum and maximum hourly mean temperature/humidity of a day; (2) the time when the minimum and maximum hourly mean temperatures occurred (hour of the day); (3) daily amplitude, i.e. the difference between minimum and maximum mean hourly temperature; and (4) the rate of heating (°C·h⁻¹), which was the quotient of daily amplitude and the number of hours passing from an hour of minimum to an hour of maximum hourly mean temperature. The threshold ambient temperature, below which incubating female expends more energy to keep eggs warm, is circa 15°C for tits (Haftorn and Reinertsen, 1985; Mertens, 1987). To evaluate (indirectly) a female’s incubation effort, we calculated the percentage of time when the air temperature records in cavity that was below 15°C by expressing the number of 5-minute recordings with a temperature below 15°C as a percentage of the 288 recordings gathered during the 24 hours observation period.

We standardised temperature values observed in cavities to varying ambient conditions by calculating the “temperature difference” by subtracting the mean daily external temperature from the mean daily temperature recorded in the cavity during the same series of measurements.

All statistical analyses followed formulae in STATISTICA 9.1 (StatSoft, 2010). To check if the temperature changed between two nesting stages in the ‘former’ cavities, we applied non-parametric Wilcoxon matched pair tests. Repeated measures MANOVA (within effects) was used to test simultaneously: mean, minimum and maximum internal temperature and humidity differences between two cavity types. In similar comparisons, to include the effect of the day, we used ANCOVA (GRM). All regression analyses were checked with non-parametric Spearman correlations tests. For the remaining comparisons we used one-way ANOVA.

3. RESULTS

3.1. ‘Former’ cavities

Mean daily temperature in the ‘former’ cavities was 13°C on average during the time corresponding to the incubation and 14°C during the time corresponding to the nestling period (Table 1). Changes in the mean daily temperatures followed variation in the ambient temperatures (incubation: \(t = 0.66, P < 0.001, df = 33\); nestling period: \(t = 0.88, P < 0.001, df = 31\)). Temperatures in the cavities and outside them were lower (by 2–5°C on average) in 2009 than in 2010, but differences between mean daily internal and ambient temperatures stayed the same in both years (ANOVA, incubation: \(F_{1,33} = 0.0, P = 0.99\); nestling period: \(F_{1,31} = 1.5, P = 0.23\)). The differences remained similar also in the two nesting stages within each year (Wilcoxon test, in 2009: \(Z = 0.3; P = 0.80\); in 2010: \(Z = 1.3, P = 0.19\)). The temperature in cavities was below 15°C for 73% (SD = 31.0, n = 35) of a day on average during the period corresponding to the incubation and for 61% (SD = 45.1, n = 33) of a day in time corresponding to the nestling period.

The daily pattern of temperature change in cavities differed from that recorded outside them at the same time (Figure 1A). The minimum temperatures in cavities were much higher and the maximum much lower than outside (Table 1). The mean daily internal amplitudes were circa 2°C, about four times smaller than ambient ones (Figure 1A), both during the incubation and the nestling period.
Also, extreme hourly means ranged less in the cavities than outside during the whole nesting period (6.1–20.9°C vs. 0.5–25.8°C respectively, Table 1). The mean rate of temperature change in cavities was from three to five times lower than outside (Table 1). As a result, the minima and maxima in cavities occurred with a few hours lag (Figure 1A). During colder days, the temperature in cavities was often higher, but during warmer days, lower than outside (Figure 2).

Mean daily air humidity in the ‘former’ cavities often exceeded 90% and did not vary during a day, whereas the ambient humidity strongly fluctuated and generally was lower than in cavities (Figure 1B).

3.2 Breeding cavities

Internal temperatures at two nesting stages strongly depended on ambient temperatures (incubation: \( r_S = 0.71, \ P < 0.001, \ df = 38 \)); nestling period: \( r_S = 0.59, \ P = 0.002, \ df = 22 \), but changed a much lower extent than outside (Table 1). Mean hourly internal temperatures ranged from 1.9°C to 24.6°C (Table 1). These do not include the very high close to 30°C maxima recorded in two cavities. As they were well above the highest temperatures recorded outside, they were probably due to measurement errors.

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Table 1 Comparison of internal and ambient air temperatures in the ‘former’ and the breeding cavities of Great Tits during the incubation and the nestling periods. The temperatures shown refer to the hourly mean values. Mean, minimum and maximum internal temperatures were similar in both types of cavities during the incubation period (repeated measures MANOVA, within effects, \( F_{1,73} = 0.3, \ P = 0.60 \)), but significantly higher in the breeding cavities in the nestling period (repeated measures MANOVA, within effects, \( F_{1,55} = 11.6, \ P = 0.001 \))

<table>
<thead>
<tr>
<th>Daily temperature (°C)</th>
<th>‘Former’ cavities</th>
<th>Breeding cavities</th>
<th>ANOVA</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Internal</td>
<td>Ambient</td>
<td></td>
<td>Internal</td>
</tr>
<tr>
<td></td>
<td>Mean (SD)</td>
<td>Range</td>
<td></td>
<td>Mean (SD)</td>
</tr>
<tr>
<td>Incubation period</td>
<td></td>
<td></td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Mean</td>
<td>13.2 (2.1)</td>
<td>8.9–16.8</td>
<td>12.8 (2.4)</td>
<td>8.0–16.4</td>
</tr>
<tr>
<td>Minimum</td>
<td>11.8 (2.2)</td>
<td>6.8–16.0</td>
<td>8.5 (3.1)</td>
<td>0.5–13.5</td>
</tr>
<tr>
<td>Maximum</td>
<td>14.7 (2.2)</td>
<td>10.1–18.0</td>
<td>17.3 (3.4)</td>
<td>10.2–22.1</td>
</tr>
<tr>
<td>Rate of change (°C·h⁻¹)</td>
<td>0.3 (0.2)</td>
<td>0.1–0.7</td>
<td>0.9 (0.5)</td>
<td>0.2–2.5</td>
</tr>
<tr>
<td>Nestling period</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>14.2 (3.3)</td>
<td>8.4–19.0</td>
<td>14.3 (3.5)</td>
<td>7.9–19.2</td>
</tr>
<tr>
<td>Minimum</td>
<td>12.8 (3.4)</td>
<td>6.1–18.1</td>
<td>9.4 (3.5)</td>
<td>3.8–15.2</td>
</tr>
<tr>
<td>Maximum</td>
<td>15.7 (3.4)</td>
<td>9.2–20.9</td>
<td>19.2 (3.9)</td>
<td>10.7–25.8</td>
</tr>
<tr>
<td>Rate of change (°C·h⁻¹)</td>
<td>0.2 (0.2)</td>
<td>0.1–0.8</td>
<td>1.0 (0.3)</td>
<td>0.5–1.7</td>
</tr>
</tbody>
</table>

* The number of cavities containing nestlings was smaller due to nest losses.
The mean daily internal amplitudes reached almost 3°C, three times less than ambient ones (Figure 3A and 4A). The temperature in the breeding cavities changed least, at twice the lower rate than outside them (Table 1). The daily maxima usually occurred with a few hours lag (Figure 3A and 4A).

Mean daily temperatures in the breeding cavities increased in the nesting cycle (Table 1). The differences between mean internal and ambient temperatures increased from on average circa 1°C during incubation to 3-4°C in the nestling period (Table 1, ANOVA, F_{1,62} = 21.8, P < 0.001). Temperature remained below 15°C for 74% (SD = 29.9, n = 40) of a day during the incubation and for 26% (SD = 31.5, n = 24) of a day in the nestling period.

Internal ambient temperature differences increased with hole height above the ground (0.4°C m^{-1}) both during the incubation (r_s = -0.5; P = 0.002, df = 33) and the nestling period (r_s = -0.4, P = 0.026, df = 38) and the nestling period (r_s = -0.5, P = 0.016, df = 22). The line indicates regression trend.

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Internal ambient temperature differences increased with hole height above the ground (0.4°C m^{-1}) both during the incubation (r_s = -0.5; P = 0.002, df = 33) and the nestling period (r_s = -0.4; P = 0.032, df = 36) and the nestling period (r_s = -0.5, P = 0.016, df = 22). The line indicates regression trend.
Breeding cavities placed in thicker parts of trees had thicker walls ($r_s = 0.79$, $P < 0.001$, $df = 30$). The differences increased with the cavity depth ($r_s = 0.45$, $P = 0.007$, $df = 32$). The line indicates regression trend.

The internal ambient temperature differences were slightly higher in the breeding cavities during the incubation and much higher in the nestling period than in the ‘former’ cavities in corresponding periods (Figure 8). Although thermal patterns found in the breeding cavities were still similar to those in the ‘former’ ones (Figure 1A, 3A and 4A).
Table 2 Comparison of internal and ambient air humidity in the ‘former’ and the breeding cavities of Great Tits during the incubation and the nestling periods. The values shown refer to the hourly mean values. Mean, minimum and maximum internal humidity were similar in both types of cavities during the incubation period (repeated measures MANOVA, within effects, $F_{1,25} = 0.7, P = 0.42$), but significantly lower in the breeding cavities in the nestling period (repeated measures MANOVA, within effects, $F_{1,12} = 12.4, P = 0.004$).

<table>
<thead>
<tr>
<th>Daily Relative Humidity (%)</th>
<th>‘Former’ Cavities</th>
<th>Breeding Cavities</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Internal</td>
<td>Ambient</td>
</tr>
<tr>
<td></td>
<td>Median</td>
<td>Range</td>
</tr>
<tr>
<td>Incubation period</td>
<td>$n = 12$ cavities</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>93.0</td>
<td>77.6–96.6</td>
</tr>
<tr>
<td>Minimum</td>
<td>92.1</td>
<td>69.1–96.3</td>
</tr>
<tr>
<td>Maximum</td>
<td>93.5</td>
<td>82.5–97.2</td>
</tr>
<tr>
<td>Nestling period</td>
<td>$n = 6$ cavities</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>96.6</td>
<td>95.0–97.6</td>
</tr>
<tr>
<td>Minimum</td>
<td>96.2</td>
<td>94.2–97.5</td>
</tr>
<tr>
<td>Maximum</td>
<td>97.0</td>
<td>95.4–97.7</td>
</tr>
</tbody>
</table>

Mean daily air humidity in the breeding cavities remained usually slightly below 90% (Table 2). It was stable during a day despite highly variable ambient conditions (Figure 3B and 4B). Daily maxima and minima differed by from 0.5% to 2% on average in cavities, whereas by from 25% to 38% outside (Table 2). Mean daily humidity in breeding cavities was similar to that one in the ‘former’ cavities during the incubation period, but almost 10% lower in the nestling period (Table 2).

4. DISCUSSION

The mean daily temperatures in the ‘former’ Great Tit cavities were quite low (on average 13–14°C) and did not differ from the ambient ones. An analogous pattern was found in other unused cavities in living trees (McComb and Noble, 1981; Sedgeley, 2001; Ruczyński, 2006; Rhodes et al., 2009), although they differed from values measured in cavities with dead walls. Martin and Ghalambor (1999) found that daily temperature amplitude in cavities of North American Pygmy Nuthatch (Sitta pygmaea) located in dead substrates (McEllin, 1979; Hay and Güntert, 1983), amounted to circa 10°C. Similar daily amplitudes were recorded by Wiebe (2001) in excavated mainly dead wood cavities used previously by Northern Flicker (Colaptes auratus). These results suggest that cavities in living wood would provide better buffered thermal conditions than the cavities in dead substrates.

The mean daily relative humidity in the ‘former’ Great Tits cavities exceeded 90%, it was about 10% higher than the ambient one. These values were consistent with those recorded by Sedgeley (2001) in cavities in living Southern Beeches (Nothofagus; mean 93%). The mean hourly humidity given by McComb and Noble (1981) for unused cavities with living walls (74%) was much lower, but ambient humidity (mean 69%) measured in this study was also lower.

The majority of the Eurasian non-excavators breed in cavities located in living trees (Bai et al., 2005; Walankiewicz et al., 2007; Wesołowski, 2007a). Strong walls of such cavities are known to provide mechanical protection against predators (Alatalo et al., 1990; Albano, 1992; Christman and Dhondt, 1997; Wesołowski, 2002). However, predation avoidance is not the only problem the birds have to solve. Adequate nest illumination is another issue that birds have to take into account to successfully breed in cavities (Wesołowski and Maziarz, 2012). The cavity microclimate could constitute yet another problem.

The consequence of using cavities in living trees by the birds is the exposure to microclimatic conditions not found in the outside world. Cavities in such places are relatively stable thermally, but they are quite cool and very humid (air is almost saturated with water vapour). For example the birds may conserve heat on cold nights and avoid overheating on hot days. The microclimate might hinder
the development of flea larvae (Siphonaptera; Hebda and Wesołowski, 2012). Humid conditions may also prevent harmful excessive water loss (Deeming, 2011, Mersten-Katz et al., 2012) but there are also some costs. On the other hand, coping with a cool and humid cavity might require an increase in the energy expenditures of the breeding birds (O’Connor, 1975; Haftorn, 1983; Haftorn and Reinertsen, 1985; Mertens, 1987). Construction of the nest insulating the eggs or young may decrease the costs to some extent (e.g. O’Connor, 1975; Winkler, 1993; Deeming, 2002). Although at temperatures below 15°C persisting for three quarters of a day in Great Tit cavities (shown here), incubating or brooding females probably still have to expend energy for heating eggs or small young almost all of the time (Haftorn and Reinertsen, 1985; Mertens, 1987). A very humid environment may cause problems with too little evaporation, as well (see Walsberg and Schmidt, 1992).

Taken together, the birds occupying cavities in living trees have greater chance to avoid predation (see above), although at a cost of investing more energy in brood rearing. One could expect that the birds breeding in such conditions would try to minimise these extra costs and exhibit some cost-reducing behaviour. By selecting warm cavities with a stable and warmer microclimate the birds could lower energetic expenditures for heating eggs and the young (Haftorn, 1983; Haftorn and Reinertsen, 1985; Mertens, 1987) and increase growth rate and body mass of nestlings (Dawson et al., 2005; Nilsson et al., 2008; Ardia et al., 2010). Our observations indicate that, indeed, Great Tits could modify the microclimatic conditions by occupying cavities with different dimensions or by adjusting the nest distance from the cavity opening.

By using cavities placed in thicker parts of trees (so with thicker walls) Great Tits ensured more stable conditions in the incubation period; much warmer during cold days and colder during hot days (Figure 7). Next, by building smaller or larger nests, the birds could modify the cavity depth on which thermal conditions during incubation depended (Figure 5). Also, by selecting cavities of smaller or larger entrances the birds could control the air warmth inside cavities; the internal-ambient temperature differences decreased in cavities with larger entrances (Figure 6), probably due to heat convection and improved gas exchange through openings (Howe and Kilgore, 1987; Rhodes et al., 2009).

Incubating Great Tit females only slightly warmed the air in the cavity. So, during incubation they had to rely solely on insulating attributes of the cavity they had selected and modified. The substantial temperature increase in cavities at the nestling stage was most probably just a consequence of presence of a brood in a cavity (see also Mersten-Katz et al., 2012).

Mertens (1977) claimed that hypothermia naturally never occurred in Great Tits broods, but hyperthermia may sometimes be a real danger. High nestling mortality was often found in nest-boxes exposed to direct sun operation, in which the internal temperature reached 40°C and was maintained at that level for several hours (Kluijver, 1951). However, higher nestling mortality in temperatures 21–31°C occurred only in abnormal conditions — in narrow nest-boxes containing exceptionally large broods (van Balen, 1984). The highest temperatures in Great Tits’ cavities recorded in this study, did not exceed 24°C. So, in the natural conditions, the broods did not seem to face the risk of hyperthermia. The maximum temperatures exceeding 30°C, which could lead to hyperthermia, were recorded only in tree cavities placed in dead wood (Howe et al., 1987; Martin and Ghalambor, 1999; Wiebe, 2001). Thus the conditions in nest-boxes used by Great Tits could resemble more closely the situation found in the dead wood cavities than to one detected by us in the living trees. Our results lend no support for hyperthermia to be important for birds using cavities in the living trees.

**CONCLUSIONS**

Cavities in living trees used by Great Tits were characterised by relatively cool, stable temperatures and very high relative humidity. As data from other studies largely confirm this pattern, it can be tentatively proposed that cavities in the living trees would offer the birds roughly similar microclimatic conditions. This suggestion has to be tested in the future studies. The microclimate appears to be a modifying factor beyond Great Tit and other cavity nesters’ usage of cavities in the living trees. By choosing cavities of appropriate dimensions and placing nest at an appropriate distance from the entrance, Great Tits could adjust the cavity microclimate to some extent. Their options were probably constrained by other important requirements such as nest safety and illumination. It remains to be seen how Great Tits reconcile these different needs. To best of our knowledge, this is the first study where the microclimate of the previously and the currently used natural cavities was compared and contrasted with the ambient condition.

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