Forest Ecology and Management 389 (2017) 306–313

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Microclimate in tree cavities and nest-boxes: Implications for hole-nesting birds

Marta Maziarz[a,*], Richard K. Broughton[b], Tomasz Wesołowski[a]

[a] *Laboratory of Forest Biology, Wrocław University, Sienkiewicza 21, 50 335 Wrocław, Poland*
[b] *Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire OX10 8BB, UK*

ARTICLE INFO

*Article history:*
Received 30 October 2016
Received in revised form 31 December 2016
Accepted 2 January 2017
Available online 13 January 2017

*Keywords:*
Air temperature
Relative humidity
*Poecile palustris*
Marsh tit
Nest-site availability

ABSTRACT

The provision of nest-boxes is widely used as a conservation intervention to increase the availability of cavities for hole-nesting birds, particularly in managed forests, but it is uncertain whether nest-boxes are an appropriate substitute for tree cavities. Tree cavities and nest-boxes may differ in many aspects, including microclimate, but there are few data with which to examine this. We measured the air temperature and relative humidity in vacant tree cavities previously used by breeding marsh tits *Poecile palustris* (a non-excavating forest passerine) and in nest-boxes provided for this species that had similar dimensions to natural nest sites, and we compared values from both with ambient conditions. We examined how tree cavity characteristics influenced microclimate and if similar conditions were replicated in nest-boxes. Tree cavities, particularly those in thicker parts of trees, were more efficient thermal insulators, with temperature extremes dampened to a greater extent relative to ambient values. In contrast, the nest-boxes provided poor insulation with negligible buffering against ambient temperatures. Mean daily relative humidity was high (on average c. 90%) in tree cavities, which all had walls of living wood, and this averaged 24% higher than in nest-boxes at comparable ambient conditions (mean humidity 76–78%). These results support previous studies that incorporated various types of tree cavities and nest-boxes, indicating that the environment within nest-boxes differs significantly from that of tree cavities. We conclude that providing nest-boxes may affect microclimatic conditions available for cavity-users, which may have ecological implications for nesting birds.

## 1. Introduction

Tree cavities are used by many forest organisms, and the availability of tree holes is fundamental to maintaining forest biodiversity (Gibbons and Lindenmayer, 2002). Retention of cavity-bearing trees may conflict with forestry management, however, as older or decaying trees are often removed as a standard practice (Newton, 1998; Cockle et al., 2010; Wesołowski and Martin, in press). In consequence, cavity resource limitation can be a problem for some species, and non-excavating birds that rely on pre-existing tree holes for nesting seem to be particularly vulnerable in this regard (reviewed in Newton, 1998). Nest-boxes are a popular management tool to increase nest site availability for hole-nesting birds, but their provision may have some negative aspects (McComb and Noble, 1981; Mänd et al., 2005; Wesołowski and Martin, in press). Although increasing the availability of cavities by providing nest-boxes has facilitated the population recovery or increase of several bird species (reviewed in Newton, 1998; Goldingay and Stevens, 2009; and Lindenmayer et al., 2009), there is uncertainty as to whether nest-boxes can be considered an adequate functional substitute for tree holes due to apparent variation in the breeding ecology of birds occupying artificial and natural nest-sites (e.g. Czeszczewik et al., 1999; Mänd et al., 2005; Lambrechts et al., 2010; Wesołowski, 2011). These differences may involve reduced breeding success and survival if predators learn to exploit nest-boxes, or artificially reduced predation risk if extra protection is added (reviewed in Wesołowski, 2011). Nest-boxes may also have the counter-productive effect of providing additional nest sites for potential competitors of the target species (e.g. Mänd et al., 2005; Wesołowski, 2011; Broughton and Hinsley, 2014). Further understanding of the differences between tree cavities and nest-boxes, and the implications for nesting birds, would inform the conservation and management strategies directed at such species in managed forests.

The insulating function of nest cavities may be particularly important for altricial passerines, whose nestlings are initially incapable of thermoregulation (Hansell, 2000). Poor insulation

---

[*] Corresponding author.
*E-mail address:* mart.ann.maz@gmail.com (M. Maziarz).

http://dx.doi.org/10.1016/j.foreco.2017.01.001
0378-1127/

from ambient temperatures may raise the risk of nestling hypothermia and increase parental costs of warming eggs or nestlings in cool weather (O'Connor, 1975; Haftorn and Reinertsen, 1985), or risk hyperthermia and dehydration in hot environments (Kluijver, 1951; Mertens, 1977; van Balen, 1984; Erbelding-Denk and Trillmich, 1990; Rendell and Verbeek, 1996; Salaberria et al., 2014). Sufficient humidity can also be important, for example in preventing excessive water loss (Mersten-Katz et al., 2012), but heavily saturated air can hinder evaporation and gaseous exchange (Walsberg and Schmidt, 1992). If different thermal and humidity options are available, therefore, birds should seek to occupy cavities that would favour successful reproduction and minimise the parental investment of energy.

As the microclimate of tree holes can vary with location and dimensions (e.g. Wiebe, 2001; Paclík and Weidinger, 2007; Coombs et al., 2010; Maziarz and Wesołowski, 2013), it could be expected that different types of cavity would provide contrasting environments, and so nesting birds would be able to select on the basis of attributes that were most preferable. In forest habitats that are least modified by humans, tree cavities are numerous and diverse (reviewed in Wesołowski and Martin, in press) and so a wide spectrum of microclimatic conditions may be available for hole-nesting birds. There are few data with which to test this assumption, however, as there are limited studies of air temperature and humidity in tree cavities available for nesting birds. The initial cavity microclimate that birds may experience when selecting their nest sites have been investigated in Northern flickers (*Colaptes auratus*; Howe et al., 1987; Wiebe, 2001), South Island saddlebacks (*Philesturnus c. carunculatus*; Rhodes et al., 2009) and great tits (*Parus major*; Maziarz and Wesołowski, 2013). The characteristics of nesting or other tree holes are also seldom reported in the literature; among 19 papers detailing the microclimate of tree cavities only twelve contained information on entrance diameter and ten on the state of cavity walls (living vs. dead), with eight commenting on cavity floor size and five on tree girth at the height of the hole.

The differences in insulation between tree cavities and nest-boxes may affect their use by birds (reviewed in Goldingay and Stevens, 2009), but variation in microclimate between these cavities remains poorly documented. The few studies to date suggest that nest-boxes tend to be less humid than tree cavities, and poorer insulators against ambient temperatures (McComb and Noble, 1981; Isaac et al., 2008a; Grüebler et al., 2014). Additionally, compared to tree cavities, nest-boxes deployed in a given area are usually more uniform in dimensions and location above the ground, and so offer a limited variety of nesting possibilities for non-excavators (reviewed in Lambrechts et al., 2010). Different types of nest-box also seem to provide a rather similar microclimate in general (Goldingay, 2015; Ellis, 2016), which may lessen the opportunity for birds to find optimal thermal and humidity conditions. As such, reducing the number and diversity of cavities, by removing cavity-rich trees and providing nest-boxes, would diminish the cavity microclimate options available to nesting birds. To test this assumption more studies of tree cavities and nest-boxes are needed.

Here, we present the first data on air temperature and humidity in tree cavities and nest-boxes used as nest sites by marsh tits (*Poecile palustris*), a Palaearctic hole-nesting species that relies on pre-existing cavities (Cramp and Perrins, 1993; Wesołowski, 1999). We examine how the tree cavity situation and dimensions influence the initial cavity microclimate that the birds may experience when selecting their nest sites, and check if these conditions are replicated in nest-boxes with dimensions approximating those of tree-cavities. We put these data into a wider context by comparing them with the published measurements of thermal and humidity properties of tree cavities and nest boxes usable for birds and mammals. We draw general conclusions on the microclimatic properties of tree cavities and nest-boxes, and discuss the implications for the ecology and conservation of the cavity-nesting species that use them.

## 2. Materials and methods

### 2.1. Study area

The study capitalised on parallel long-term studies of marsh tits carried out in Białowieża National Park (hereafter 'BNP'; eastern Poland, 52°40′N, 23°50′E) and at Monks Wood National Nature Reserve (eastern England, 52°24′N, 0°14′W). The 47.5 km$^2$ of strictly protected old-growth stands within BNP are a relic of the primeval mixed-deciduous forests which once covered much of lowland Europe (Tomiałojć and Wesołowski, 2004). Monks Wood in the English lowlands is 155 ha of mature, secondary, deciduous woodland that has been largely unmanaged for a century (Broughton et al., 2012).

The microclimate of tree cavities in BNP was measured in 2013–2014 within study plots situated in oak-lime-hornbeam (*Tilio-Carpinetum*) stands (for detailed descriptions see Tomiałojć et al.,1984; Wesołowski, 1996; Wesołowski et al., 2015). Tree holes are superabundant here and birds have a wide array of nesting options, whilst nest-boxes are not provided (Wesołowski, 2007). Instead, nest-boxes with dimensions specifically designed to mimic the natural holes of Marsh Tits were already available during 2015 in Monks Wood, a woodland composed of English oak (*Quercus robur*), common ash (*Fraxinus excelsior*) and field maple (*Acer campestre*; Broughton and Hinsley, 2014). These nest-boxes had been in situ and maintained (to remove old nest material) for at least two years previously, during a population study of marsh tits, and so provided a convenient opportunity to acquire measurements of temperature and humidity to compare with tree cavities used by this species in BNP. In both study areas the data were collected in April-May, during the time corresponding to the incubation period of local marsh tits.

### 2.2. Microclimate measurements

Measurements of air temperature and relative humidity were taken from a respective 24 and 15 tree cavities in BNP, which had been used by marsh tits in previous breeding seasons but were unoccupied during data collection (due to high abundance of tree holes providing alternative nest sites; Wesołowski, 2006, 2007). Eighteen of the cavities were used for breeding by marsh tits one year before the study, and six remaining ones 2–7 years prior to the study, with all considered to be still usable by marsh tits. As nest material in tree cavities disappears between consecutive breeding seasons (Wesołowski, 2000; Hebda et al., 2013), the vacant cavities contained no discernible nest remnants during data collection. The tree cavities were formed by natural decay in living trunks of limes *Tilia cordata* (84%) or hornbeams *Carpinus betulus* (16%), and the median tree girth at breast height was 68 cm. Cavity dimensions were measured using a collapsible ruler and flexible torch (for detailed description and explanation of parameters see Wesołowski, 1996 and Maziarz et al., 2015); the dimensions and other cavity properties are given in Table 1.

Air temperature and humidity were recorded from a respective 18 and 15 empty nest-boxes in Monks Wood, which were constructed from pine planks to dimensions approximating tree cavities used by this species (Broughton and Hinsley, 2014; Table 1). The nest-boxes were in good condition but remained unoccupied in the current year, with either marsh tits or blue tits (*Cyanistes caeruleus*) having used them in a previous breeding season (Broughton and Hinsley, 2014). Joins in the walls and floor were

**Table 1**
The location and dimensions of vacant tree cavities previously used by marsh tits in Białowieża National Park, Poland (n = 22), and nest-boxes targeted at this species in Monks Wood, England (n = 18). For tree cavities the wall thickness was assessed indirectly as half of the difference between tree diameter at hole-height and greatest cavity floor diameter. Shown are medians (and ranges). For detailed description of assessment of cavity characteristics see Wesołowski (1996) and Maziarz et al. (2015).

| Cavity parameters | Tree cavities | Nest-boxes |
|---|---|---|
| Entrance diameter (cm) | | |
| Least | 2.3 (1.7–6.5) | 2.6 (–) |
| Greatest | 6.8 (3.0–10.0) | 2.6 (–) |
| Shape | Ellipse | Circular |
| Floor diameter (cm) | | |
| Least | 7.0 (5–14) | 7.8 (–) |
| Greatest | 9.0 (6–15) | 7.8 (–) |
| Shape | Ellipse | Square |
| Depth (cm) | 18.0 (10–30) | 15.0 (–) |
| Wall thickness (cm) | 6.0 (2.3–19.2) | 2.2 (–) |
| Tree girth at hole height (cm) | 67.0 (38–158) | – |
| Height above ground (m) | 1.5 (0.8–4.5)[a] | 1.7 (1.0–2.4) |
| Entrance orientation (% of nest-sites) | | |
| Northern | 42.9[a] | 36.1 |
| Eastern | 14.3[a] | 27.8 |
| Southern | 17.9[a] | 16.7 |
| Western | 25.0[a] | 19.4 |

[a] Measured for 14 tree cavities.

filled and the external walls were painted with preservative and a marine varnish to seal any cracks. The nest-boxes were attached to trees and located at least 150 m from the woodland edge, under a mature tree canopy (Broughton and Hinsley, 2014). The entrance orientation both of nest-boxes and tree cavities was randomly distributed through the four cardinal directions (respectively $\chi^2 = 1.7$ and 2.7, df = 3, $p > 0.4$; Table 1).

For microclimate measurements we used temperature (DS1922L) and temperature and humidity (DS1923) data loggers (iButtons), tested and calibrated by Dallas Semiconductor/Maxim Inc. (Maxim Integrated Products, 2011a,b). The operating range for DS1922L was −10 °C to +65 °C, and for DS1923 from −20 °C to +85 °C and 0% to 100% relative humidity. Measurement precision for temperature was ±0.5 °C and for humidity ±5%.

The measurements were taken simultaneously by paired data loggers of the same type, positioned inside and outside of each cavity/nest-box, to test the buffering from ambient conditions. The internal data logger was mounted with a thin wire usually 8–11 cm below the entrance hole. The external logger was hung in a radiation shelter (tubular white plastic sleeve of c. 7 cm diameter, open at both sides to permit free air movement and shading of the sensor) and placed in close proximity to the cavity/nest-box, 2–4 m above the ground (above ground frosts) to detect relative differences between ambient air and microclimate of the tree cavity. The mean daily temperatures recorded by the external loggers at tree cavities (on average 15.4 °C, from 9.6 °C to 19.2 °C) closely corresponded to the mean daily values received on the same days from the local weather station at BNP (the Institute of Meteorology and Water Management-National Research Institute in Białowieża; on average 15.3 °C, from 9.7 °C to 19.2 °C; $r_S = 0.98$, $p < 0.001$).

Both data loggers in a set were programmed to simultaneously initiate recording at the expected time of their installation at the cavity/nest-box and continue at five-minute intervals (recording resolution was 0.0625 °C temperature and 0.04% humidity). After a minimum 48 h from installation the loggers were removed and the data were uploaded to a computer using a 1-Wire adapter and Maxim software.

### 2.3. Data analysis

Relative air humidity was recorded to a standardised temperature of 25 °C and systematically inflated when humidity exceeded 70% for extended periods. The humidity values were later corrected to the actual temperature and for saturation drift following the manufacturer's equations (Maxim Integrated Products, 2011b; p. 53). From each sample we selected a 24-h sequence of records from 00:01 to 24:00 and calculated hourly means to define: (1) mean, minimum and maximum hourly mean temperature/humidity of a day, (2) the hour of minimum and maximum hourly mean temperature during the day, (3) daily amplitude, i.e. the difference between minimum and maximum hourly mean temperature, and (4) the rate of temperature change (°C h$^{-1}$), i.e. the quotient of daily amplitude and the duration (hours) from minimum to maximum hourly mean temperature during the day.

To compare thermal conditions between tree cavities and nest-boxes we standardised observed internal temperature values to varying ambient conditions by using 'temperature differences' (subtracting mean hourly or mean daily ambient values from the corresponding cavity readings). The relationships between internal and ambient air temperature were assessed using Spearman's rank-order correlation, and similarly the relationship between a cavity's thermal conditions and its structural characteristics. Additionally, a Multiple Linear Regression model was used to examine the capacity of the maximum ambient air temperature and the tree circumference at the hole height (predictor variables) to shape the maximum cavity-internal air temperature (response variable). In this analysis the maximum internal and ambient temperature values were the raw data recorded in 5-min sampling intervals. Mann-Whitney tests were used to compare differences in thermal and humidity conditions between tree holes and nest-boxes, and paired t-tests to compare the conditions inside and outside of tree holes and nest-boxes. Humidity values were logit transformed before statistical analysis. All statistical calculations followed formulae in R version 3.1.2 (The R Core Team, 2014).

## 3. Results

### 3.1. Tree cavities

Mean daily temperature in tree cavities was strongly dependent on mean daily ambient temperature ($r_S = 0.95$, $p < 0.001$, $n = 24$), but the pattern of internal temperature change during a day differed from the ambient (Fig. 1a). The daily minima inside tree cavities averaged 2.0 °C higher and the maxima 2.5 °C lower compared to the ambient values (Table 2), resulting in a lower average daily amplitude of 8.8 °C in the cavity and 13.3 °C outside (paired *t*-test: $t = -7.2$, $p < 0.001$). The rate of temperature change in cavities was approximately half of that recorded outside (Table 2), with daily extremes lagging 1–4 h behind the ambient (Fig. 1a).

The rate of temperature change was significantly lower in those cavities located in thicker parts of trees ($r_S = -0.60$, $p = 0.003$, $n = 22$). In cavities in thicker trees the least entrance diameter was smaller ($r_S = -0.52$, $p = 0.014$, $n = 22$), the greatest floor diameter was larger ($r_S = 0.48$, $p = 0.024$, $n = 22$) and the cavity walls were thicker ($r_S = 0.91$, $p < 0.001$, $n = 22$). Mean daily internal-ambient temperature differences were related neither to the hole-height above the ground nor to the internal cavity dimensions ($r_S < 0.3$, $p > 0.19$, $n = 22$). In consequence, the maximum ambient values and the tree thickness at hole height were good predictors of maximum internal temperatures ($R^2 = 0.82$, residual SE = 1.40, $F_{2,19} = 42.4$, $p < 0.001$; Table 3).

Hourly mean relative humidity in tree cavities was stable throughout the day (Fig. 1b), often exceeding 90%, whereas mean hourly ambient humidity varied during a day and averaged 15% lower in absolute terms than inside cavities (Fig. 1b; Table 2).

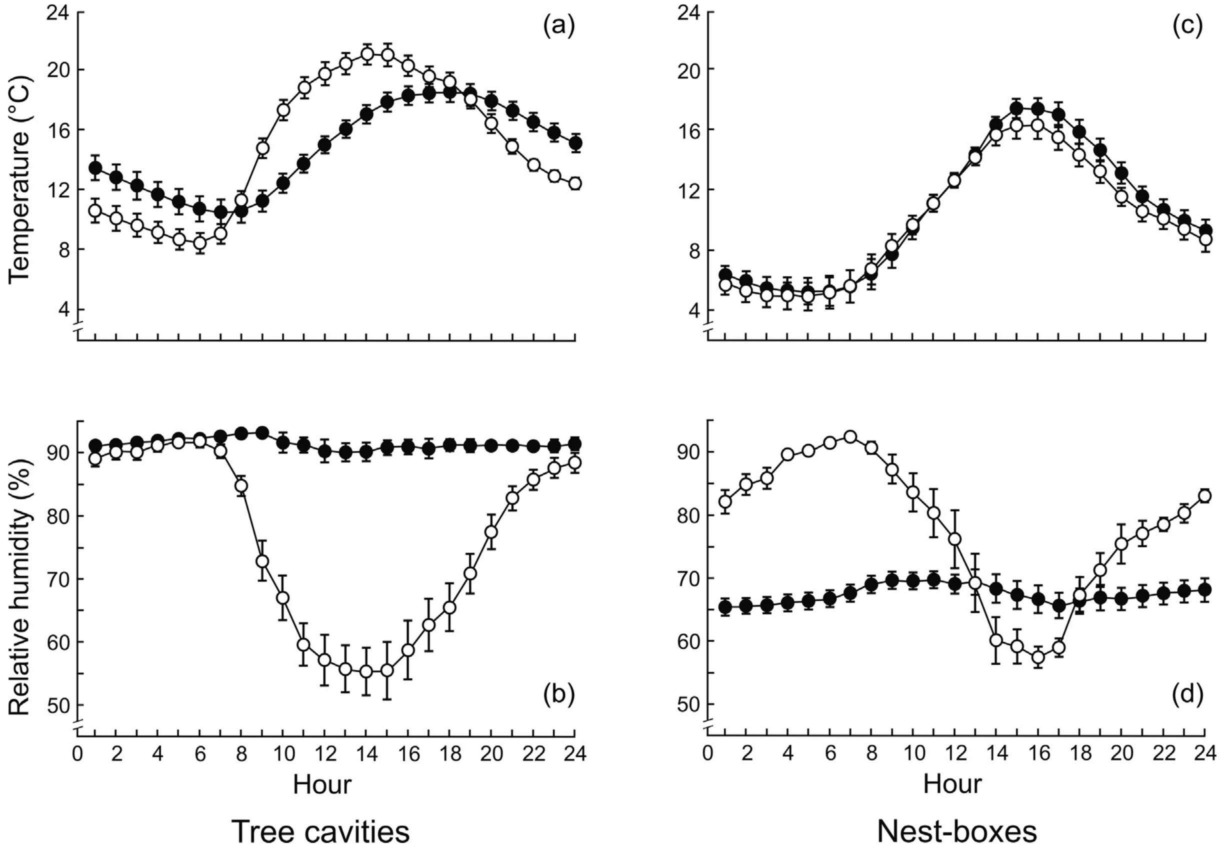

**Fig. 1.** Daily changes in the mean hourly air temperature and relative humidity in vacant tree cavities of marsh tits in Białowieża National Park (Poland), respectively: (a) n = 24, and (b) n = 15 (black dots), and in nest-boxes at Monks Wood (England), respectively: (c) n = 18, and (d) n = 15 (black dots) in relation to ambient conditions (white dots). Shown are means (dots) and SE (whiskers). Measurements in tree cavities were taken in April-May 2013 and 2014, and measurements in nest-boxes in May 2015.

**Table 2**
Comparison of internal and ambient daily air temperatures and relative humidity of vacant tree cavities previously used by marsh tits in Białowieża National Park (Poland) and nest-boxes targeted at this species in Monks Wood (England). The values shown refer to hourly means.

| Variable | Tree-cavities | | | | | | Nest-boxes | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Internal | | Ambient | | Paired *t*-test | | Internal | | Ambient | | Paired *t*-test | |
| | Mean (SD) | Range | Mean (SD) | Range | *t* | p | Mean (SD) | Range | Mean (SD) | Range | *t* | p |
| Daily temperature (°C) | n = 24 cavities | | | | | | n = 18 boxes | | | | | |
| Mean | 14.8 (3.0) | 9–19 | 15.0 (2.9) | 9–19 | −1.6 | 0.117 | 10.6 (3.0) | 7–14 | 10.1 (3.3) | 7–14 | 6.7 | <0.001 |
| Minimum | 10.4 (4.2) | 0–16 | 8.4 (3.9) | −1 to 13 | 8.3 | < 0.001 | 4.6 (4.1) | 0–9 | 4.3 (4.3) | −1 to 9 | 3.9 | 0.001 |
| Maximum | 19.2 (3.1) | 15–25 | 21.7 (3.8) | 16–27 | −5.9 | < 0.001 | 18.0 (3.1) | 13–23 | 16.9 (3.7) | 13–21 | 4.1 | <0.001 |
| Rate of change (°C $h^{-1}$) | 0.8 (0.4) | 0–2 | 1.5 (0.6) | 0–3 | −6.5 | < 0.001 | 1.3 (0.5) | 1–2 | 1.3 (0.5) | 1–2 | −0.2 | 0.863 |
| Daily relative humidity (%) | n = 15 cavities | | | | | | n = 15 boxes | | | | | |
| Mean | 91.4 (3.1) | 86–96 | 75.9 (8.3) | 62–87 | 9.5 | < 0.001 | 67.4 (6.0) | 58–77 | 78.0 (5.5) | 72–84 | −6.6 | <0.001 |
| Minimum | 86.3 (6.9) | 68–95 | 52.1 (14.8) | 29–72 | 12.1 | < 0.001 | 62.9 (7.2) | 50–75 | 54.9 (9.3) | 42–65 | 3.3 | 0.005 |
| Maximum | 94.4 (2.1) | 91–97 | 92.7 (3.0) | 88–97 | 2.3 | 0.040 | 73.1 (5.6) | 63–81 | 93.8 (1.3) | 92–97 | −17.0 | <0.001 |

**Table 3**
The results of the Multiple Linear Regression model to predict the maximum daily air temperature in marsh tit tree cavities. The response variable was the maximum internal temperature recorded during 5-min sampling intervals, and predictor variables were corresponding maximum ambient temperature and the tree circumference at hole height.

| Parameter | Estimate | SD error | *t* | p |
|---|---|---|---|---|
| Intercept | 7.78 | 1.94 | 4.02 | 0.0007 |
| Maximum ambient temperature | 0.65 | 0.08 | 8.45 | <0.0001 |
| Tree circumference | −0.05 | 0.01 | −4.04 | 0.0007 |

### 3.2. Nest-boxes

Mean daily internal and ambient temperatures of nest-boxes were strongly correlated ($r_S = 0.95$, $p < 0.001$, $n = 18$), and the pattern of temperature change throughout the day inside nest-boxes closely followed that of outside (Fig. 1c). Internal daily minimum and maximum temperatures were both higher than the ambient by respective averages of 0.3 °C and 1.1 °C, and these extremes typically lagged up to 1 h behind the ambient temperature extremes (Fig. 1c). The average daily amplitude of 13.4 °C inside nest-boxes was significantly greater than the mean 12.5 °C outside (paired *t*-test, $t = 3.3$, df = 17, $p = 0.004$), but the internal and ambient temperatures changed at the same rate (mean 1.3 °C h$^{-1}$; Table 2).

The nest-boxes were comparatively warmer than the tree cavities, relative to ambient conditions. The mean daily internal-ambient temperature differences for nest-boxes (on average 0.6 °C) were significantly greater than those for tree cavities (on average −0.2 °C; Mann-Whitney test, $W = 367$, $p < 0.001$). The hourly mean temperatures inside nest-boxes slightly exceeded the respective ambient values for most of the day and, as such, hourly mean internal-ambient temperature differences remained stable, at just above zero throughout the day (Fig. 2). In contrast to nest-boxes, the hourly mean internal-ambient temperature differences in tree cavities fluctuated greatly during the 24 h (Fig. 2).

Hourly mean relative humidity inside nest-boxes was comparatively stable throughout the day, with a mean daily amplitude of 10% compared to the 39% variation recorded outside (Table 2, Fig. 1d). The average mean daily humidity of 67% was some 11% lower than the ambient value (Table 2). The nest-boxes were substantially less humid than tree cavities despite similar ambient conditions (Table 2); mean daily humidity inside nest boxes was 24% lower than in tree cavities, which was a highly significant difference (Mann-Whitney test, $W = 0$, $p < 0.001$).

## 4. Discussion

### 4.1. Microclimate of tree cavities

Tree cavities used by marsh tits offered a microclimate that was significantly buffered from outside conditions. Although air temperatures inside the cavities were strongly affected by ambient temperatures, the internal daily temperature extremes were reduced and typically lagged several hours behind the ambient. Consequently, the internal temperatures changed at a lower rate than outside. A thorough literature review revealed a similar buffering effect in almost all studies incorporating various empty tree cavities (Table 4), indicating that dampening of the daily temperature fluctuations constitutes an inherent feature of most tree cavities.

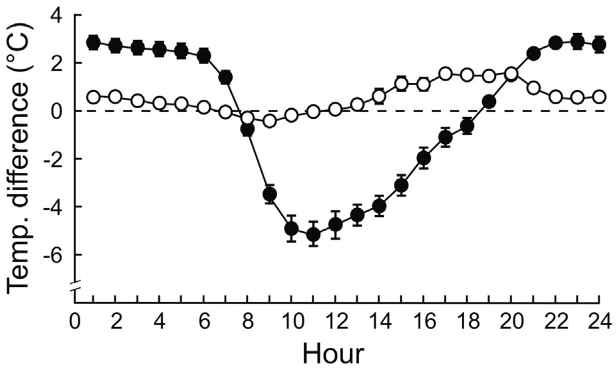

**Fig. 2.** Daily changes of mean hourly internal-ambient temperature differences in vacant tree cavities of marsh tits in Białowieża National Park (Poland) (black dots; n = 24) and in nest-boxes at Monks Wood (England) (white dots; n = 18). Shown are means (dots) and SE (whiskers). "0" level occurs when internal and ambient temperatures are equal. Measurements in tree cavities were taken in April-May 2013 and 2014, and measurements in nest-boxes in May 2015.

The mean daily temperature amplitude of c. 9 °C in tree holes used by marsh tits was one of the highest recorded in tree cavities so far; it ranged between 1 °C and 16 °C in other studies (Table 4). The temperature amplitude of marsh tit cavities was surprisingly large for holes in living wood, where the amplitude is typically 2–3 °C (Table 4). Instead, the high temperature amplitude in tree cavities of marsh tits was more typical of cavities with walls of dead wood (Wiebe, 2001; Maziarz and Wesołowski, 2013), which is supposed to have lesser heat capacity and, thus, insulate less efficiently than live wood (e.g. McComb and Noble, 1981; Hooge et al., 1999; Wiebe, 2001). As the amplitude of temperature variation inside marsh tit cavities was also comparatively high (a ratio of 0.7 between the mean internal and ambient amplitudes; Table 4) this suggests that the greater temperature variation was due to lower thermal buffering of the marsh tit cavities rather than more variable ambient conditions.

The temperature in tree cavities used by marsh tits changed by an average 0.8 °C h$^{-1}$, which was three to four times faster than in tree cavities used by great tits in BNP (average 0.2–0.3 °C h$^{-1}$; Maziarz and Wesołowski, 2013). The great tit cavities had a floor area twice as large as those of marsh tits, and were situated in parts of trees that were twice as thick (reviewed in Maziarz et al., 2015). Similarly, those marsh tit cavities in thicker parts of trees, which also tended to have a greater floor diameter and thicker walls, were more efficient insulators with a lower rate of temperature change. Such an effect has also been found in other studies (e.g. Calder et al., 1983 in Gibbons and Lindenmayer, 2002; Wiebe, 2001; Isaac et al., 2008b; Rhodes et al., 2009; Coombs et al., 2010; Maziarz and Wesołowski, 2013; Otto et al., 2016), showing that cavities situated in trees of various size may create a wide spectrum of insulation options for their users.

The mean daily relative humidity in marsh tit tree cavities was high (mean 91%) and stable throughout the day, in contrast to a much lower (mean 76%) and fluctuating ambient humidity. A stable humidity throughout the day that averaged c. 90% was also found in other unoccupied cavities (Sedgeley, 2001; Maziarz and Wesołowski, 2013). Yet, Clement and Castleberry (2013) reported a daily air humidity fluctuating between 80% and 90% inside tree cavities, at ambient humidity of 70–95%. McComb and Noble (1981) recorded values as low as 74% in tree cavities, and O'Connell and Keppel (2016) between 37% and 56%, but this was still usually above the ambient humidity. As studies of humidity are mostly from cavities in living trees, where the air is constantly saturated with water from the surrounding growing walls, they should not be generalised to cavities in dead wood without further study. It could be surmised that cavities in living and decaying substrates could exhibit a range of humidity values, some of which could be relatively dry.

### 4.2. Microclimate in nest-boxes compared to tree cavities

The microclimate in empty nest-boxes designed for marsh tits differed significantly from that inside the tree cavities used by this species. Compared to the tree holes, the nest-boxes were warmer and offered negligible buffering against ambient temperatures; indeed, the daily minima and maxima were both slightly higher than the ambient values. The pattern of temperature change inside nest-boxes used in this study was generally similar to that found in all other studies incorporating small to large-sized nest-boxes (3.2–15 cm entrance diameter, 121–1800 cm$^2$ floor area), whether constructed of wood or sawdust and concrete; the maximum inter-

**Table 4**
A review of relationships between daily thermal conditions inside (in) and outside (out) of vacant tree cavities. Time lag is the number of hours after which the internal daily minimum and maximum temperatures followed the ambient extremes; n = sample size.

| Former occupants | n | State of walls | Daily temp. (°C) | | Temp. amplitude (°C) | | | Time lag (h) | Source |
|---|---|---|---|---|---|---|---|---|---|
| | | | Min | Max | In | Out | In/out | | |
| None | 2 | Living | In > out | In < out | 7 | 10 | 0.7 | 1–2 | McComb and Noble (1981) |
| None | 2 | –[a] | In > out | In > out | 8 | 9 | 0.9 | 1–2 | Calder et al. (1983) in Gibbons and Lindenmayer (2002) |
| None | 24 | Living | In > out | In < out | 2 | 9 | 0.3 | 2–3 | Sedgeley (2001); knot-holes |
| None | 11 | Living | In > out | In < out | 5 | 10 | 0.5 | 2–3 | Sedgeley (2001); trunk holes |
| None | 12 | – | In > out | In < out | 4 | 12 | 0.4 | 2–4 | Ruczyński (2006) |
| None | 70 | Dead[b] | In > out | – | – | – | – | – | Paclík and Weidinger (2007) |
| None | 14 | Living | In = out | In > out | 9 | 7 | 1.3 | 0–1 | Isaac et al. (2008b)[d] |
| None | 34 | Living[c] | In > out | In < out | 2 | 4 | 0.5 | – | Rhodes et al. (2009)[d] |
| None | 104 | – | In > out | In < out | 11 | 43 | 0.3 | 2–6 | Coombs et al. (2010) |
| None | 45 | – | In > out | In < out | 3 | 8 | 0.4 | 1–2 | Clement and Castleberry (2013) |
| None | 21 | Living | In > out | In < out | 3 | 5 | 0.6 | 1–2 | Grüebler et al. (2014) |
| None | 1 | – | In > out | In < out | 16 | 23 | 0.7 | 1–2 | O'Connell and Keppel (2016)[d] |
| Birds | | | | | | | | | |
| *Aegotheles cristatus* | 11 | – | In > out | In < out | 12 | 15 | 0.8 | – | Doucette et al. (2011) |
| *Colaptes auratus* | 1 | – | In > out | In > out | 13 | 14 | 0.9 | −6 to 2 | Howe et al. (1987) |
| *Colaptes auratus* | 86 | Dead[b] | In > out | In < out | 11 | 26 | 0.4 | 2–5 | Wiebe (2001) |
| *Philesturnus c. carunculatus* | 34 | Living[c] | In > out | In < out | 1 | 4 | 0.4 | – | Rhodes et al. (2009)[d] |
| *Parus major* | 35 | Living | In > out | In < out | 3 | 9 | 0.3 | 3–6 | Maziarz and Wesołowski (2013) |
| *Poecile palustris* | 24 | Living | In > out | In < out | 9 | 13 | 0.7 | 2–3 | This study |
| Mammals | | | | | | | | | |
| *Trichosurus vulpecula* | 10 | Living | In > out | In ⩾ out | 7 | 7 | 1.0 | 0–1 | Isaac et al. (2008b)[d] |
| *Eptesicus fuscus* | 19 | – | In > out | In < out | 8 | 12 | 0.7 | 2–4 | Willis and Brigham (2007) |
| *Nyctalus noctula/leisleri* | 12 | – | In > out | In < out | 4 | 12 | 0.4 | 4–5 | Ruczyński (2006) |
| *Plecotus auritus* | 6 | – | In > out | In < out | 3 | 7 | 0.5 | 2–6 | Otto et al. (2016)[d] |
| *Chalinolobus tuberculatus* | 24 | Living | In > out | In < out | 2 | 9 | 0.2 | 4–5 | Sedgeley (2001); knot-holes |
| *Ch. tuberculatus* | 11 | Living | In > out | In < out | 3 | 10 | 0.3 | 5 | Sedgeley (2001); trunk holes |
| *Myotis bechsteinii* | 6 | – | In > out | In < out | 2 | 7 | 0.2 | 4–7 | Otto et al. (2016)[d] |
| *M. nattereri* | 6 | – | In > out | In < out | 2 | 7 | 0.3 | 3–8 | Otto et al. (2016)[d] |
| *M. nattereri* | 3 | Living | In > out | In < out | 2 | 10 | 0.2 | 2–3 | Smith and Racey (2005) |
| *Procyon lotor* | 2 | Living | In > out | In < out | 2 | 10 | 0.2 | 2–5 | Stains (1961) |

[a] Data unavailable.
[b] c. 50% of cavities in dead trees.
[c] 20% of cavities in dead trees.
[d] Mean values calculated from reported data.

**Table 5**
A review of the relationship between daily thermal conditions inside (in) and outside (out) of vacant nest-boxes. Time lag is the number of hours after which the internal daily minimum and maximum temperatures followed the ambient extremes; values below "0" indicate that internal extremes preceded the ambient ones; n = sample size.

| Studied occupants | n | Entrance diameter (cm) | Floor diameter (cm) | Material | Daily temp. (°C) | | Temp. amplitude (°C) | | | Time lag (h) | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Min | Max | In | Out | In/out | | |
| None | 2 | 13 × 13 | 30 × 60 | Wood | In = out | In > out | 10 | 9 | 1.1 | 0–1 | McComb and Noble (1981) |
| None | 1 | 3.3 × 3.3 | 11 × 11 | Wood | In ⩽ out | In > out | 17 | 12 | 1.4 | −1 to 0 | Olszewski (1971) |
| None | 1 | 4.7 × 4.7 | 13 × 13 | Wood | In ⩽ out | In < out | 10 | 12 | 0.8 | −1 to 0 | Olszewski (1971) |
| None | 1 | 4.7 × 4.7 | 13 × 13 | Sawdust concrete | In ⩽ out | In > out | 15 | 12 | 1.3 | 0–1 | Olszewski (1971) |
| None | 4 | 10 × 10 | 26 × 25 | Plywood | In ⩽ out | In > out | 20 | 16 | 1.3 | 0 | Ellis (2016)[a] |
| None | 4 | 10 × 10 | 25 × 25 | Plywood | In ⩽ out | In > out | 20 | 16 | 1.3 | 0 | Ellis (2016)[a] |
| None | 4 | 6 × 6 | 20 × 25 | Plywood | In ⩽ out | In > out | 20 | 16 | 1.3 | 0 | Ellis (2016)[a] |
| None | 4 | 8 × 8 | 25 × 25 | Plywood | In ⩽ out | In > out | 20 | 16 | 1.3 | 0 | Ellis (2016)[a] |
| None | 4 | 15 × 10 | 26 × 25 | Plywood | In ⩽ out | In > out | 20 | 16 | 1.3 | 0 | Ellis (2016)[a] |
| None | 4 | 5 × 5 | 31 × 15 | Plywood | In ⩽ out | In > out | 20 | 16 | 1.3 | 0 | Ellis (2016)[a] |
| *Athene noctua* | 18 | 6.5 × 6.5 | 18 × 83 | Wood | In ⩽ out | In > out | 6 | 5 | 1.2 | 0–1 | Grüebler et al. (2014) |
| *Poecile palustris* | 18 | 2.6 × 2.6 | 8 × 8 | Wood | In > out | In > out | 13 | 13 | 1.1 | 0–1 | This study |
| *Passer montanus* | 3 | 3.2 × 3.2 | 11 × 11 | Woodcrete | – | – | 18 | – | – | – | García-Navas et al. (2010) |
| *P. montanus* | 3 | 3.2 × 3.2 | 12 × 12 | Wood | – | – | 15 | – | – | – | García-Navas et al. (2010) |

[a] Mean values calculated from reported data.

nal temperatures almost always exceeded the ambient ones, but the minima were usually slightly lower than outside (Table 5).

As in our study, the temperature amplitudes in other nest-boxes were high, varying between 6 °C and 20 °C across studies (c. 13 °C in this study), and also had large internal-ambient amplitude ratios ranging from 0.8 to 1.4 (1.1 in marsh tit nest-boxes; Table 5). This shows that the thermal properties of the marsh tit nest-boxes appear typical of such devices in general. The low thermal buffering found in nest-box studies is in stark contrast to that of tree cavities, and appears to override other factors such as situation or internal dimensions. This may be due to the generally much thinner walls, floors and roofs of nest-boxes, which are typically constructed of sheets of wood or a moulded sawdust-concrete mix, whereas tree cavities are encased within a solid tree stem that usually extends many metres above and below the cavity itself.

At an average 67%, the mean daily humidity in the marsh tit nest-boxes was a mean 24% lower than in the tree cavities, despite similar ambient conditions. This difference between nest-boxes and tree cavities in the current study was remarkable and much greater than the 1% disparity reported by McComb and Noble (1981) in other nest-boxes. The 64% mean relative humidity in wooden nest-boxes measured by Amat-Valero et al. (2014) was close to that found in the marsh tit nest-boxes, but Erbelding-Denk and Trillmich (1990) recorded much lower values of 49% and 59% in two empty nest-boxes at midday. Olszewski (1971) reported a higher humidity than the current study, averaging 84–85% in sawdust and concrete nest-boxes despite a similar ambient mean of 79%. Ellis (2016) gave average values of 86–99% humidity in plywood nest boxes of various dimensions, which was exceptionally high and comparable to tree cavities, but was still lower than the ambient humidity. The majority of reported humidity values in nest-boxes, however, fall well below those recorded in tree holes, demonstrating that nest-boxes are generally much drier places than tree cavities for nesting birds, with the air in the latter constantly saturated with water from living walls.

### 4.3. Implications of microclimate differences between tree cavities and nest-boxes

The current results provide evidence that nest-boxes differ from tree cavities; they are drier and less well insulated, which has further implications for cavity-nesting birds. Thus, providing nest-boxes in areas where the diversity of the tree cavity resource has been reduced in the course of forest management may change the character of thermal and humidity options available for nesting birds, and cause further complications.

Effective insulation against harsh ambient conditions is important for endothermic animals to conserve energy during various stages of reproduction, and the buffering properties of cavities are potentially important in environments where temperatures fluctuate greatly within and between days and seasons (O'Connor, 1975; Haftorn and Reinertsen, 1985; Hansell, 2000; Goldingay and Stevens, 2009). Installing poorly-insulating nest-boxes in such areas may expose their users to greater extremes of temperature than they would otherwise experience in tree cavities (Isaac et al., 2008a). For example, mortality of passerine chicks due to hyperthermia has only been reported from nest-boxes (e.g. Kluijver, 1951; Mertens, 1977; van Balen, 1984; Erbelding-Denk and Trillmich, 1990; Rendell and Verbeek, 1996), indicating a greater potential for overheating than in generally cooler tree cavities. This risk could be reduced by placing nest-boxes with improved insulation in shaded sites (Isaac et al., 2008a; Goldingay, 2015), but hyperthermia and dehydration may still be difficult to avoid in hot climates (Goldingay and Stevens, 2009; Salaberria et al., 2014).

Nest-boxes that are drier than tree cavities could have some advantages for breeding birds, such as a lower risk of nest-soaking (reviewed in Wesołowski, 2011; Wesołowski and Martin, in press), though a low humidity could also carry risks. The relatively dry and warm environment in nest-boxes can be attractive to nesting Aculeata bees and wasps, which may be significant competitors of birds that are capable of deterring or usurping nesting passerines from nest-boxes, but they are rarely found in tree cavities (Broughton et al., 2015). Similarly, the drier and warmer environment of nest-boxes may foster the occurrence and development of flea larvae in bird nests (Eeva et al., 1994; Heeb et al., 2000), facilitating flea infestations in nest-boxes but explaining the low occurrence of these ectoparasites in tree cavities (Wesołowski and Stańska, 2001; Hebda and Wesołowski, 2012). Abundant fleas in nests can lead to reduced growth of nestlings and increased mortality, or abandonment by adult birds (reviewed in Mazgajski, 2007). As such, provisioning nest-boxes can lead to increased ectoparasite loads and competition between nesting birds and social bees and wasps, both of which can reduce the breeding success of birds.

Accumulation of nest material between breeding seasons is another frequent phenomenon of nest-boxes that is rarely observed in tree cavities, most probably due to humid conditions in the latter promoting decomposition of nests over winter (Wesołowski, 2000; Hebda et al., 2013). The accumulation of nesting material in nest-boxes may induce infestations by overwintering fleas, and also reduce the functional depth of the cavity for birds, which reduces nest-site safety (Rendell and Verbeek, 1996; reviewed in Mazgajski, 2007). Regular cleaning of nest-boxes is necessary to alleviate these problems, but such maintenance is labour intensive (Møller, 1989; Rendell and Verbeek, 1996; Wesołowski, 2011).

All of these practical and ecological differences between tree holes and nest-boxes have implications for nest-box studies of cavity-nesting birds, which are the basis of much of our understanding of their breeding ecology. Such limitations should, therefore, be considered if attempting to extrapolate results from nest-boxes to a wider population of birds breeding in tree holes, as the conclusions reached could be misleading (Lambrechts et al., 2010; Wesołowski, 2011).

In summary, nest-boxes generally appear to provide a relatively warm and dry microclimate which is distinct from cool and humid tree cavities. The contrasting microclimate of nest-boxes and tree cavities is one of several important, often inter-linked, distinctions that have direct ecological impacts on their use by cavity-nesting species. Providing nest-boxes should therefore be undertaken with consideration of their limitations and potential influences. For species conservation, the provision of nest-boxes should be regarded as a targeted and temporary intervention rather than routine practice. In the long term, the retention of cavity-bearing trees is a more sustainable, cost-effective and less disruptive measure (Goldingay and Stevens, 2009; Lindenmayer et al., 2009; Cockle et al., 2010; Wesołowski and Martin, in press).

## Acknowledgements

The authors are very grateful to M. Cholewa, M. Czuchra, G. Hebda, and P. Rowiński for participation in fieldwork, including nest finding and checking. We also thank M. Wojciechowski and S. Freeman for technical and statistical advice, the administration of Białowieża National Park for kind cooperation, Natural England for access to Monks Wood NNR, and Prof. K. Migała for advice on weather data. R. Goldingay and an anonymous reviewer provided valuable comments for improvements to an earlier draft of the manuscript. The work was supported by an internal grant from the Faculty of Biological Sciences, Wrocław University (MM, TW), and studies at Monks Wood were funded by the Natural Environment Research Council.

## References

Amat-Valero, M., Calero-Torralbo, M.A., Václav, R., Valera, F., 2014. Cavity types and microclimate: implications for ecological, evolutionary, and conservation studies. Int. J. Biometeorol. 58, 1983–1994.

van Balen, J.H., 1984. The relationship between nest-box size, occupation and breeding parameters of the Great Tit *Parus major* and some other hole-nesting species. Ardea 72, 163–175.

Broughton, R.K., Hebda, G., Maziarz, M., Smith, K.W., Smith, L., Hinsley, S.A., 2015. Nest-site competition between bumblebees (Bombidae), social wasps (Vespidae) and cavity-nesting birds in Britain and the Western Palearctic. Bird Study 62, 427–437.

Broughton, R.K., Hill, R.A., Freeman, S.N., Bellamy, P.E., Hinsley, S.A., 2012. Describing habitat occupation by woodland birds with territory mapping and remotely sensed data: an example using the marsh tit (*Poecile palustris*). Condor 114, 812–822.

Broughton, R.K., Hinsley, S.A., 2014. A nestbox trial for British marsh tits *Poecile palustris*. Ringing Migration 29, 77–80.

Calder, T.G., Golding, B.G., Manderson, A.D., 1983. Management for Arboreal Species in the Wombat State Forest. Environmental Report No. 16. Graduate School of Environmental Science, Monash University. Unpublished, Melbourne.

Clement, M.J., Castleberry, S.B., 2013. Tree structure and cavity microclimate: implications for bats and birds. Int. J. Biometeorol. 57, 437–450.

Cockle, K., Martin, K., Drever, M.C., 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biol. Conserv. 143, 2851–2857.

Coombs, A.B., Bowman, J., Garroway, C.J., 2010. Thermal properties of tree-cavities during winter in a northern hardwood forest. J. Wildlife Manage. 74, 1875–1881.

Cramp, S., Perrins, C.M. (Eds.), 1993. The Birds of the Western Palearctic, Vol. VII: Flycatchers to Shrikes. Oxford University Press, Oxford.

Czeszczewik, D., Walankiewicz, W., Mitrus, C., Nowakowski, W., 1999. Nest-box data of Pied Flycatcher *Ficedula hypoleuca* may lead to erroneous generalizations. Vogelwelt 120, 361–365.

Doucette, L.I., Brigham, R.M., Pavey, C.R., Geiser, F., 2011. Roost type influences torpor use by Australian owlet-nightjars. Naturwissenschaften 98, 845–854.

Eeva, T., Lehikoinen, E., Nurmi, J., 1994. Effects of ectoparasites on breeding success of Great Tits (*Parus major*) and Pied Flycatchers (*Ficedula hypoleuca*) in an air pollution gradient. Can. J. Zool. 72, 624–635.

Ellis, M.V., 2016. Influence of design on the microclimate in nest boxes exposed to direct sunshine. Australian Zoologist 38, 95–101.

Erbelding-Denk, C., Trillmich, F., 1990. Nestbox climate and its effects on Starling (Sturnus vulgaris) nestlings. J. Ornithol. 131, 73–84 [in German, English summary].

García-Navas, V., Arroyo, L., Sanz, J.J., 2010. Woodcrete nestboxes: are they adequate for multi brooded species? Ardeola 57, 159–166.

Gibbons, P., Lindenmayer, D., 2002. Tree Hollows and Wildlife Conservation in Australia. CSIRO Publishing, Collingwood.

Goldingay, R.L., 2015. Temperature variation in nest boxes in eastern Australia. Australian Mammol. 37, 225–233.

Goldingay, R.L., Stevens, J.R., 2009. Use of artificial tree hollows by Australian birds and bats. Wildlife Res. 36, 81–97.

Grüebler, M.U., Widmer, S., Korner-Nievergelt, F., Naef-Daenzer, B., 2014. Temperature characteristics of winter roost-sites for birds and mammals: tree cavities and anthropogenic alternatives. Int. J. Biometeorol. 58, 629–637.

Haftorn, S., Reinertsen, R.E., 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit (*Parus caeruleus*). Auk 102, 470–478.

Hansell, M.H., 2000. Bird Nests and Construction Behaviour. Cambridge University Press, Cambridge.

Hebda, G., Pochrząst, K., Mitrus, S., Wesołowski, T., 2013. Disappearance rates of old nest material from tree cavities: an experimental study. Scand. J. Forest Res. 28, 445–450.

Hebda, G., Wesołowski, T., 2012. Low flea loads in birds' nests in tree cavities. Ornis Fennica 89, 139–144.

Heeb, P., Kölliker, M., Richner, H., 2000. Bird-ectoparasite interactions, nest humidity and ectoparasite community structure. Ecology 81, 958–968.

Hooge, P.N., Stanback, M.T., Koenig, W.D., 1999. Nest-site selection in the Acorn Woodpecker. Auk 116, 45–54.

Howe, S., Kilgore, D.L., Colby, C., 1987. Respiratory gas concentrations and temperatures within nest cavities of the northern flicker (*Colaptes auratus*). Can. J. Zool. 65, 1541–1547.

Isaac, J.L., de Gabriel, J.L., Goodman, B.A., 2008b. Microclimate of daytime den sites in a tropical possum: implications for the conservation of tropical arboreal marsupials. Anim. Conserv. 11, 281–287.

Isaac, J.L., Parsons, M., Goodman, B.A., 2008a. How hot do nest boxes get in the tropics? A study of nest boxes for the endangered mahogany glider. Wildlife Res. 35, 441–445.

Kluijver, H.N., 1951. The population ecology of the Great Tit, *Parus m. major* L. Ardea 39, 1–135.

Lambrechts, M.M., Adriaensen, F., Ardia, D.R., et al., 2010. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. Acta Ornithol. 45, 1–26.

Lindenmayer, D.B., Welsh, A., Donnelly, C., Crane, M., Michael, D., Macgregor, C., McBurney, L., Montague-Drake, R., Gibbons, P., 2009. Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. Biol. Conserv. 142, 33–42.

Mänd, R., Tilgar, V., Lõhmus, A., Leivits, A., 2005. Providing nest boxes for hole-nesting birds - does habitat matter? Biodiversity Conserv. 14, 1823–1840.

Maxim Integrated Products Inc, 2011. DS1922L/ DS1922T: Temperature Logger iButton with 8KB Data-Log Memory. 19–4990, Rev 10.

Maxim Integrated Products Inc, 2011. DS1923: Hygrochron Temperature/Humidity Logger iButton with 8KB Data-Log Memory. 19–4991, Rev 4.

Mazgajski, T.D., 2007. Effect of old nest material on nest site selection and breeding parameters in secondary hole nesters - a review. Acta Ornithol. 42, 1–14.

Maziarz, M., Wesołowski, T., 2013. Microclimate of tree cavities used by Great Tits (*Parus major*) in a primeval forest. Avian Biol. Res. 6, 47–56.

Maziarz, M., Wesołowski, T., Hebda, G., Cholewa, M., 2015. Natural nest-sites of Great Tits (*Parus major*) in a primeval temperate forest (Białowieża National Park, Poland). J. Ornithol. 156, 613–623.

McComb, W.C., Noble, R.E., 1981. Microclimates of nest boxes and natural cavities in bottomland hardwoods. J. Wildlife Manage. 45, 284–289.

Mersten-Katz, C., Barnea, A., Yom-Tov, Y., Ar, A., 2012. The woodpecker's cavity microenvironment: advantageous or restricting? Avian Biol. Res. 5, 227–237.

Mertens, J.A.L., 1977. Thermal conditions for successful breeding in great tits (*Parus major* L.). I. Relation of growth and development of temperature regulation in nestling Great Tits. Oecologia 28, 1–29.

Møller, A.P., 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? Oikos 56, 421–423.

Newton, I., 1998. Population Limitation in Birds. Academic Press, San Diego.

O'Connell, C., Keppel, G., 2016. Deep tree hollows: important refuges from extreme temperatures. Wildlife Biol. 22, 305–310.

O'Connor, R.J., 1975. The influence of brood size upon metabolic rate and body temperature in nestling blue tits *Parus caeruleus* and house sparrows *Passer domesticus*. J. Zool. 175, 391–403.

Olszewski, J.L., 1971. Comparison of the microclimate of nesting boxes. Wiad. Ekol. 17, 164–169 (In Polish, English summary).

Otto, M.S., Becker, N.I., Encarnação, J.A., 2016. Roost characteristics as indicators for heterothermic behavior of forest-dwelling bats. Ecol. Res. 31, 385–391.

Paclík, M., Weidinger, K., 2007. Microclimate of tree-cavities during winter nights - implications for roost site selection in birds. Int. J. Biometeorol. 51, 287–293.

Core Team, R., 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Rendell, W.B., Verbeek, N.A.M., 1996. Are avian ectoparasites more numerous in nest boxes with old nest material? Can. J. Zool. 74, 1819–1825.

Rhodes, B., O'Donnell, C., Jamieson, I., 2009. Microclimate of natural cavity nests and its implications for a threatened secondary-cavity-nesting passerine of New Zealand, the South Island Saddleback. Condor 111, 462–469.

Ruczyński, I., 2006. Influence of temperature on maternity roost selection by noctule bats (*Nyctalus noctula*) and Leisler's bats (*N. leisleri*) in Białowieża Primeval Forest, Poland. Can. J. Zool. 84, 900–907.

Salaberria, C., Celis, P., López-Rull, I., Gil, D., 2014. Effects of temperature and nest heat exposure on nestling growth, dehydration and survival in a Mediterranean hole-nesting passerine. Ibis 156, 265–275.

Sedgeley, J.A., 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. J. Appl. Ecol. 38, 425–438.

Smith, P.G., Racey, P.A., 2005. The itinerant Natterer: physical and thermal characteristics of summer roosts of *Myotis nattereri* (Mammalia: Chiroptera). J. Zool. Lond. 266, 171–180.

Stains, H.J., 1961. Comparisons of temperatures inside and outside two tree dens used by racoons. Ecology 42, 410–413.

Tomiałojć, L., Wesołowski, T., 2004. Diversity of the Białowieża Forest avifauna in space and time. J. Ornithol. 145, 81–92.

Tomiałojć, L., Wesołowski, T., Walankiewicz, W., 1984. Breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland). Acta Ornithol. 20, 241–310.

Walsberg, G.E., Schmidt, C.A., 1992. Effects of variable humidity on embryonic development and hatching success of mourning doves. Auk 109, 309–314.

Wesołowski, T., 1996. Natural nest sites of marsh tit (*Parus palustris*) in a primaeval forest (Białowieża National Park, Poland). Vogelwarte 38, 235–249.

Wesołowski, T., 1999. Marsh tits (*Parus palustris*) are not excavators. Ibis 141, 149.

Wesołowski, T., 2000. What happens to old nests in natural cavities? Auk 117, 498–500.

Wesołowski, T., 2006. Nest-site re-use: Marsh Tit *Poecile palustris* decisions in a primeval forest. Bird Study 53, 199–204.

Wesołowski, T., 2007. Lessons from long-term hole-nester studies in a primeval temperate forest. J. Ornithol. 148 (Suppl. 2), S395–S405.

Wesołowski, T., 2011. Reports from nestbox studies: a review of inadequacies. Acta Ornithol. 46, 13–17.

Wesołowski, T., Czeszczewik, D., Hebda, G., Maziarz, M., Mitrus, C., Rowiński, P., 2015. 40 years of breeding bird community dynamics in a primeval temperate forest (Białowieża National Park, Poland). Acta Ornithol. 50, 95–120.

Wesołowski, T., Martin, K., in press. Tree holes and hole nesting birds in European and North American forests. In: Mikusiński, G., Roberge, J.-M., Fuller, R.J. (Eds.), Ecology and Conservation of European Forest Birds. Cambridge University Press, Cambridge (In press).

Wesołowski, T., Stańska, M., 2001. High ectoparasite loads in hole nesting birds - a nest box bias? J. Avian Biol. 32, 281–285.

Wiebe, K.L., 2001. Microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? Auk 118, 412–421.

Willis, C.K.R., Brigham, R.M., 2007. Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. Behav. Ecol. Sociobiol. 62, 97–108.