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Contact CEH NORA team at
noraceh@ceh.ac.uk

1 **Microclimate in tree cavities and nest-boxes: implications** 2 **for hole-nesting birds**

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4 Marta Maziarz ^a, Richard K. Broughton ^b and Tomasz Wesolowski ^a

5

6 ^a Laboratory of Forest Biology, Wrocław University, Sienkiewicza 21, 50 335 Wrocław,

7 Poland

8 ^b Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford,

9 Wallingford, Oxfordshire, OX10 8BB, UK

10 Corresponding author: Marta Maziarz, email: mart.ann.maz@gmail.com, tel. +4871 322 28

11 17, Laboratory of Forest Biology, Wrocław University, Sienkiewicza 21, 50 335 Wrocław,

12 Poland

13

14 **Abstract**

15 The provision of nest-boxes is widely used as a conservation intervention to increase the

16 availability of cavities for hole-nesting birds, particularly in managed forests, but it is

17 uncertain whether nest-boxes are an appropriate substitute for tree cavities. Tree cavities

18 and nest-boxes may differ in many aspects, including microclimate, but there are few data

19 with which to examine this. We measured the air temperature and relative humidity in vacant

20 tree cavities previously used by breeding marsh tits *Poecile palustris* (a non-excavating

21 forest passerine) and in nest-boxes provided for this species that had similar dimensions to

22 natural nest sites, and we compared values from both with ambient conditions. We examined

23 how tree cavity characteristics influenced microclimate and if similar conditions were

24 replicated in nest-boxes. Tree cavities, particularly those in thicker parts of trees, were more

25 efficient thermal insulators, with temperature extremes dampened to a greater extent relative

26 to ambient values. In contrast, the nest-boxes provided poor insulation with negligible

27 buffering against ambient temperatures. Mean daily relative humidity was high (on average c.
28 90%) in tree cavities, which all had walls of living wood, and this averaged 24% higher than
29 in nest-boxes at comparable ambient conditions (mean humidity 76-78%). These results
30 support previous studies that incorporated various types of tree cavities and nest-boxes,
31 indicating that the environment within nest-boxes differs significantly from that of tree
32 cavities. We conclude that providing nest-boxes may affect microclimatic conditions available
33 for cavity-users, which may have ecological implications for nesting birds.

34

35 Key words: air temperature, relative humidity, *Poecile palustris*, marsh tit, nest-site
36 availability

37

38 **1. Introduction**

39 Tree cavities are used by many forest organisms, and the availability of tree holes is
40 fundamental to maintaining forest biodiversity (Gibbons and Lindenmayer, 2002). Retention
41 of cavity-bearing trees may conflict with forestry management, however, as older or decaying
42 trees are often removed as a standard practice (Newton 1998, Cockle et al., 2010;
43 Wesolowski and Martin, in press). In consequence, cavity resource limitation can be a
44 problem for some species, and non-excavating birds that rely on pre-existing tree holes for
45 nesting seem to be particularly vulnerable in this regard (reviewed in Newton, 1998). Nest-
46 boxes are a popular management tool to increase nest site availability for hole-nesting birds,
47 but their provision may have some negative aspects (McComb and Noble, 1981; Mänd et al.,
48 2005; Wesolowski and Martin, in press). Although increasing the availability of cavities by
49 providing nest-boxes has facilitated the population recovery or increase of several bird
50 species (reviewed in Newton, 1998; Goldingay and Stevens, 2009; and Lindenmayer et al.,
51 2009), there is uncertainty as to whether nest-boxes can be considered an adequate
52 functional substitute for tree holes due to apparent variation in the breeding ecology of birds
53 occupying artificial and natural nest-sites (e.g. Czeszczewik et al., 1999; Mänd et al., 2005;
54 Lambrechts et al., 2010; Wesolowski, 2011). These differences may involve reduced

55 breeding success and survival if predators learn to exploit nest-boxes, or artificially reduced
56 predation risk if extra protection is added (reviewed in Wesolowski, 2011). Nest-boxes may
57 also have the counter-productive effect of providing additional nest sites for potential
58 competitors of the target species (e.g. Mänd et al., 2005; Wesolowski, 2011; Broughton and
59 Hinsley, 2014). Further understanding of the differences between tree cavities and nest-
60 boxes, and the implications for nesting birds, would inform the conservation and
61 management strategies directed at such species in managed forests.

62 The insulating function of nest cavities may be particularly important for altricial
63 passerines, whose nestlings are initially incapable of thermoregulation (Hansell, 2000). Poor
64 insulation from ambient temperatures may raise the risk of nestling hypothermia and
65 increase parental costs of warming eggs or nestlings in cool weather (O'Connor, 1975;
66 Haftorn and Reinertsen, 1985), or risk hyperthermia and dehydration in hot environments
67 (Kluijver, 1951; Mertens, 1977; van Balen, 1984; Erbelding-Denk and Trillmich, 1990;
68 Rendell and Verbeek, 1996; Salaberria et al., 2014). Sufficient humidity can also be
69 important, for example in preventing excessive water loss (Mersten-Katz et al., 2012), but
70 heavily saturated air can hinder evaporation and gaseous exchange (Walsberg and Schmidt,
71 1992). If different thermal and humidity options are available, therefore, birds should seek to
72 occupy cavities that would favour successful reproduction and minimise the parental
73 investment of energy.

74 As the microclimate of tree holes can vary with location and dimensions (e.g. Wiebe,
75 2001; Paclík and Weidinger, 2007; Coombs et al., 2010; Maziarz and Wesolowski, 2013), it
76 could be expected that different types of cavity would provide contrasting environments, and
77 so nesting birds would be able to select on the basis of attributes that were most preferable.
78 In forest habitats that are least modified by humans, tree cavities are numerous and diverse
79 (reviewed in Wesolowski and Martin, in press) and so a wide spectrum of microclimatic
80 conditions may be available for hole-nesting birds. There are few data with which to test this
81 assumption, however, as there are limited studies of air temperature and humidity in tree
82 cavities available for nesting birds. The initial cavity microclimate that birds may experience

83 when selecting their nest sites have been investigated in Northern flickers (*Colaptes auratus*;
84 Howe et al., 1987; Wiebe, 2001), South Island saddlebacks (*Philesturnus c. carunculatus*;
85 Rhodes et al., 2009) and great tits (*Parus major*; Maziarz and Wesolowski, 2013). The
86 characteristics of nesting or other tree holes are also seldom reported in the literature;
87 among 19 papers detailing the microclimate of tree cavities only twelve contained information
88 on entrance diameter and ten on the state of cavity walls (living vs. dead), with eight
89 commenting on cavity floor size and five on tree girth at the height of the hole.

90 The differences in insulation between tree cavities and nest-boxes may affect their use
91 by birds (reviewed in Goldingay and Stevens, 2009), but variation in microclimate between
92 these cavities remains poorly documented. The few studies to date suggest that nest-boxes
93 tend to be less humid than tree cavities, and poorer insulators against ambient temperatures
94 (McComb and Noble, 1981; Isaac et al., 2008a; Gruebler et al., 2014). Additionally,
95 compared to tree cavities, nest-boxes deployed in a given area are usually more uniform in
96 dimensions and location above the ground, and so offer a limited variety of nesting
97 possibilities for non-excavators (reviewed in Lambrechts et al., 2010). Different types of nest-
98 box also seem to provide a rather similar microclimate in general (Goldingay, 2015; Ellis,
99 2016), which may lessen the opportunity for birds to find optimal thermal and humidity
100 conditions. As such, reducing the number and diversity of cavities, by removing cavity-rich
101 trees and providing nest-boxes, would diminish the cavity microclimate options available to
102 nesting birds. To test this assumption more studies of tree cavities and nest-boxes are
103 needed.

104 Here, we present the first data on air temperature and humidity in tree cavities and
105 nest-boxes used as nest sites by marsh tits (*Poecile palustris*), a Palaearctic hole-nesting
106 species that relies on pre-existing cavities (Cramp and Perrins, 1993; Wesolowski, 1999).
107 We examine how the tree cavity situation and dimensions influence the initial cavity
108 microclimate that the birds may experience when selecting their nest sites, and check if
109 these conditions are replicated in nest-boxes with dimensions approximating those of tree-
110 cavities. We put these data into a wider context by comparing them with the published

111 measurements of thermal and humidity properties of tree cavities and nest boxes usable for
112 birds and mammals. We draw general conclusions on the microclimatic properties of tree
113 cavities and nest-boxes, and discuss the implications for the ecology and conservation of the
114 cavity-nesting species that use them.

115

116 **2. Materials and Methods**

117 **2.1. Study area**

118 The study capitalised on parallel long-term studies of marsh tits carried out in Białowieża
119 National Park (hereafter 'BNP'; eastern Poland, 52°40'N, 23°50'E) and at Monks Wood
120 National Nature Reserve (eastern England, 52° 24' N, 0° 14' W). The 47.5 km² of strictly
121 protected old-growth stands within BNP are a relic of the primeval mixed-deciduous forests
122 which once covered much of lowland Europe (Tomiałojć and Wesołowski, 2004). Monks
123 Wood in the English lowlands is 155 ha of mature, secondary, deciduous woodland that has
124 been largely unmanaged for a century (Broughton et al., 2012).

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

138

139 2.2. Microclimate measurements

140 Measurements of air temperature and relative humidity were taken from a respective 24 and
141 15 tree cavities in BNP, which had been used by marsh tits in previous breeding seasons but
142 were unoccupied during data collection (due to high abundance of tree holes providing
143 alternative nest sites; Wesolowski 2006, 2007). Eighteen cavities were used for breeding by
144 marsh tits one year before the study, and six remaining ones 2-7 years prior to the study,
145 with all considered to be still usable by marsh tits. As nest material in tree cavities disappears
146 between consecutive breeding seasons (Wesolowski, 2000; Hebda et al., 2013), the vacant
147 cavities contained no discernible nest remnants during data collection. The tree cavities were
148 formed by natural decay in living trunks of limes *Tilia cordata* (84%) or hornbeams *Carpinus*
149 *betulus* (16%), and the median tree girth at breast height was 68 cm. Cavity dimensions were
150 measured using a collapsible ruler and flexible torch (for detailed description and explanation
151 of parameters see Wesolowski, 1996 and Maziarz et al., 2015); the dimensions and other
152 cavity properties are given in Table 1.

153 Air temperature and humidity were recorded from a respective 18 and 15 empty nest-
154 boxes in Monks Wood, which were constructed from pine planks to dimensions
155 approximating tree cavities used by this species (Broughton and Hinsley, 2014; Table 1). The
156 nest-boxes were in good condition but remained unoccupied in the current year, with either
157 marsh tits or blue tits (*Cyanistes caeruleus*) having used them in a previous breeding season
158 (Broughton and Hinsley, 2014). Joins in the walls and floor were filled and the external walls
159 were painted with preservative and a marine varnish to seal any cracks. The nest-boxes
160 were attached to trees and located at least 150 m from the woodland edge, under a mature
161 tree canopy (Broughton and Hinsley, 2014). The entrance orientation both of nest-boxes and
162 tree cavities was randomly distributed through the four cardinal directions (respectively $\chi^2=$
163 1.7 and 2.7, $df = 3$, $p > 0.4$; Table 1).

164 For microclimate measurements we used temperature (DS1922L) and temperature and
165 humidity (DS1923) data loggers (iButtons), tested and calibrated by Dallas
166 Semiconductor/Maxim Inc. (Maxim Integrated Products, 2011a; 2011b). The operating range

167 for DS1922L was -10°C to $+65^{\circ}\text{C}$, and for DS1923 from -20°C to $+85^{\circ}\text{C}$ and 0% to 100%
168 relative humidity. Measurement precision for temperature was $\pm 0.5^{\circ}\text{C}$ and for humidity $\pm 5\%$.

169 The measurements were taken simultaneously by paired data loggers of the same
170 type, positioned inside and outside of each cavity/nest-box, to test the buffering from ambient
171 conditions. The internal data logger was mounted with a thin wire usually 8-11 cm below the
172 entrance hole. The external logger was hung in a radiation shelter (tubular white plastic
173 sleeve of c. 7 cm circumference, open at both sides to permit free air movement and shading
174 of the sensor) and placed in close proximity to the cavity/nest-box, 2-4 m above the ground
175 (above ground frosts) to detect relative differences between ambient air and microclimate of
176 the tree cavity. The mean daily temperatures recorded by the external loggers at tree cavities
177 (on average 15.4°C , from 9.6°C to 19.2°C) closely corresponded to the mean daily values
178 received on the same days from the local weather station at BNP (the Institute of
179 Meteorology and Water Management-National Research Institute in Białowieża; on average
180 15.3°C , from 9.7°C to 19.2°C ; $r_s = 0.98$, $p < 0.001$).

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

186

187 **2.3. Data analysis**

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

195 difference between minimum and maximum hourly mean temperature, and (4) the rate of
196 temperature change($^{\circ}\text{C}\cdot\text{h}^{-1}$), i.e. the quotient of daily amplitude and the duration(hours) from
197 minimum to maximum hourly mean temperature during the day.

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

213

214 **3. Results**

215 **3.1. Tree cavities**

216 Mean daily temperature in tree cavities was strongly dependent on mean daily ambient
217 temperature ($r_s = 0.95$, $p < 0.001$, $n = 24$), but the pattern of internal temperature change
218 during a day differed from the ambient (Fig. 1a). The daily minima inside tree cavities
219 averaged 2.0°C higher and the maxima 2.5°C lower compared to the ambient values (Table
220 2), resulting in a lower average daily amplitude of 8.8°C in the cavity and 13.3°C outside
221 (paired t-test: $t = -7.2$, $p < 0.001$). The rate of temperature change in cavities was

222 approximately half of that recorded outside (Table 2), with daily extremes lagging 1-4 hours
223 behind the ambient (Fig. 1a).

224 The rate of temperature change was significantly lower in those cavities located in
225 thicker parts of trees ($r_S = -0.60$, $p = 0.003$, $n = 22$). In cavities in thicker trees the least
226 entrance diameter was smaller ($r_S = -0.52$, $p = 0.014$, $n = 22$), the greatest floor diameter was
227 larger ($r_S = 0.48$, $p = 0.024$, $n = 22$) and the cavity walls were thicker ($r_S = 0.91$, $p < 0.001$, $n =$
228 22). Mean daily internal-ambient temperature differences were related neither to the hole-
229 height above the ground nor to the internal cavity dimensions ($r_S < 0.3$, $p > 0.19$, $n = 22$). In
230 consequence, the maximum ambient values and the tree thickness at hole height were good
231 predictors of maximum internal temperatures ($R^2 = 0.82$, residual SE = 1.40, $F_{2,19} = 42.4$, $p <$
232 0.001; Table 3).

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

236

237 **3.2. Nest-boxes**

238 Mean daily internal and ambient temperatures of nest-boxes were strongly correlated ($r_S =$
239 0.95, $p < 0.001$, $n = 18$), and the pattern of temperature change throughout the day inside
240 nest-boxes closely followed that of outside (Fig. 1c). Internal daily minimum and maximum
241 temperatures were both higher than the ambient by respective averages of 0.3°C and 1.1°C,
242 and these extremes typically lagged up to 1 hour behind the ambient temperature extremes
243 (Fig.1c). The average daily amplitude of 13.4°C inside nest-boxes was significantly greater
244 than the mean 12.5°C outside (paired t -test, $t = 3.3$, $df = 17$, $p = 0.004$), but the internal and
245 ambient temperatures changed at the same rate (mean 1.3 °C·h⁻¹; Table 2).

246 The nest-boxes were comparatively warmer than the tree cavities, relative to ambient
247 conditions. The mean daily internal-ambient temperature differences for nest-boxes (on
248 average 0.6°C) were significantly greater than those for tree cavities (on average -0.2°C;
249 Mann-Whitney test, $W = 367$, $p < 0.001$). The hourly mean temperatures inside nest-boxes

250 slightly exceeded the respective ambient values for most of the day and, as such, hourly
251 mean internal-ambient temperature differences remained stable, at just above zero
252 throughout the day (Fig. 2). In contrast to nest-boxes, the hourly mean internal-ambient
253 temperature differences in tree cavities fluctuated greatly during the 24 hours (Fig. 2).

254 Hourly mean relative humidity inside nest-boxes was comparatively stable throughout
255 the day, with a mean daily amplitude of 10% compared to the 39% variation recorded outside
256 (Table 2, Fig. 1d). The average mean daily humidity of 67% was some 11% lower than the
257 ambient value (Table 2). The nest-boxes were substantially less humid than tree cavities
258 despite similar ambient conditions (Table 2); mean daily humidity inside nest boxes was 24%
259 lower than in tree cavities, which was a highly significant difference (Mann-Whitney test, $W =$
260 0 , $p < 0.001$).

261

262 **4. Discussion**

263 **4.1. Microclimate of tree cavities**

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

272 The mean daily temperature amplitude of c. 9°C in tree holes used by marsh tits was
273 one of the highest recorded in tree cavities so far; it ranged between 1°C and 16°C in other
274 studies (Table 4). The temperature amplitude of marsh tit cavities was surprisingly large for
275 holes in living wood, where the amplitude is typically 2-3°C (Table 4). Instead, the high
276 temperature amplitude in tree cavities of marsh tits was more typical of cavities with walls of
277 dead wood (Wiebe, 2001; Maziarz and Wesolowski, 2013), which is supposed to have lesser

278 heat capacity and, thus, insulate less efficiently than live wood (e.g. McComb and Noble,
279 1981; Hooge et al., 1999; Wiebe, 2001). As the amplitude of temperature variation inside
280 marsh tit cavities was also comparatively high (a ratio of 0.7 between the mean internal and
281 ambient amplitudes; Table 4) this suggests that the greater temperature variation was due to
282 lower thermal buffering of the marsh tit cavities rather than more variable ambient conditions.

283 The temperature in tree cavities used by marsh tits changed by an average $0.8^{\circ}\text{C}\cdot\text{h}^{-1}$,
284 which was three to four times faster than in tree cavities used by great tits in BNP (average
285 $0.2\text{-}0.3^{\circ}\text{C}\cdot\text{h}^{-1}$; Maziarz and Wesolowski, 2013). The great tit cavities had a floor area twice as
286 large as those of marsh tits, and were situated in parts of trees that were twice as thick
287 (reviewed in Maziarz et al., 2015). Similarly, those marsh tit cavities in thicker parts of trees,
288 which also tended to have a greater floor diameter and thicker walls, were more efficient
289 insulators with a lower daily rate of temperature change. Such an effect has also been found
290 in other studies (e.g. Calder et al., 1983 in Gibbons and Lindenmayer, 2002; Wiebe, 2001;
291 Isaac et al., 2008b; Rhodes et al., 2009; Coombs et al., 2010; Maziarz and Wesolowski,
292 2013; Otto et al., 2016), showing that cavities situated in trees of various size may create a
293 wide spectrum of insulation options for their users.

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

306

307 **4.2. Microclimate in nest-boxes compared to tree cavities**

308 The microclimate in empty nest-boxes designed for marsh tits differed significantly from that
309 inside the tree cavities used by this species. Compared to the tree holes, the nest-boxes
310 were warmer and offered negligible buffering against ambient temperatures; indeed, the daily
311 minima and maxima were both slightly higher than the ambient values. The pattern of
312 temperature change inside nest-boxes used in this study was generally similar to that found
313 in all other studies incorporating small to large-sized nest-boxes (3.2-15 cm entrance
314 diameter, 121-1800 cm² floor area), whether constructed of wood or sawdust and concrete;
315 the maximum internal temperatures almost always exceeded the ambient ones, but the
316 minima were usually slightly lower than outside (Table 5).

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

327 At an average 67%, the mean daily humidity in the marsh tit nest-boxes was a mean
328 24% lower than in the tree cavities, despite similar ambient conditions. This difference
329 between nest-boxes and tree cavities in the current study was remarkable and much greater
330 than the 1% disparity reported by McComb and Noble (1981) in other nest-boxes. The 64%
331 mean relative humidity in wooden nest-boxes measured by Amat-Valero et al. (2014) was
332 close to that found in the marsh tit nest-boxes, but Erbelding-Denk and Trillmich (1990)
333 recorded much lower values of 49% and 59% in two empty nest-boxes at midday. Olszewski

334 (1971) reported a higher humidity than the current study, averaging 84-85% in sawdust and
335 concrete nest-boxes despite a similar ambient mean of 79%. Ellis (2016) gave average
336 values of 86-99% humidity in plywood nest boxes of various dimensions, which was
337 exceptionally high and comparable to tree cavities, but was still lower than the ambient
338 humidity. The majority of reported humidity values in nest-boxes, however, fall well below
339 those recorded in tree holes, demonstrating that nest-boxes are generally much drier places
340 than tree cavities for nesting birds, with the air in the latter constantly saturated with water
341 from living walls.

342

343 **4.3. Implications of microclimate differences between tree cavities and nest-boxes**

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

349 Effective insulation against harsh ambient conditions is important for endothermic
350 animals to conserve energy during various stages of reproduction, and the buffering
351 properties of cavities are potentially important in environments where temperatures fluctuate
352 greatly within and between days and seasons (O'Connor, 1975; Haftorn and Reinertsen,
353 1985; Hansell, 2000; Goldingay and Stevens, 2009). Installing poorly-insulating nest-boxes in
354 such areas may expose their users to greater extremes of temperature than they would
355 otherwise experience in tree cavities (Isaac et al., 2008a). For example, mortality of
356 passerine chicks due to hyperthermia has only been reported from nest-boxes (e.g. Kluijver,
357 1951; Mertens, 1977; van Balen, 1984; Erbeling-Denk and Trillmich, 1990; Rendell and
358 Verbeek, 1996), indicating a greater potential for overheating than in generally cooler tree
359 cavities. This risk could be reduced by placing nest-boxes with improved insulation in shaded
360 sites (Isaac et al., 2008a; Goldingay, 2015), but hyperthermia and dehydration may still be
361 difficult to avoid in hot climates (Goldingay and Stevens, 2009, Salaberria et al., 2014).

362 Nest-boxes that are drier than tree cavities could have some advantages for breeding
363 birds, such as a lower risk of nest-soaking (reviewed in Wesolowski, 2011; Wesolowski and
364 Martin, in press), though a low humidity could also carry risks. The relatively dry and warm
365 environment in nest-boxes can be attractive to nesting Aculeata bees and wasps, which may
366 be significant competitors of birds that are capable of deterring or usurping nesting
367 passerines from nest-boxes, but they are rarely found in tree cavities (Broughton et al.,
368 2015). Similarly, the drier and warmer environment of nest-boxes may foster the occurrence
369 and development of flea larvae in bird nests (Eeva et al., 1994; Heeb et al., 2000), facilitating
370 flea infestations in nest-boxes but explaining the low occurrence of these ectoparasites in
371 tree cavities (Wesolowski and Stańska, 2001; Hebda and Wesolowski, 2012). Abundant fleas
372 in nests can lead to reduced growth of nestlings and increased mortality, or abandonment by
373 adult birds (reviewed in Mazgajski, 2007). As such, provisioning nest-boxes can lead to
374 increased ectoparasite loads and competition between nesting birds and social bees and
375 wasps, both of which can reduce the breeding success of birds.

376 Accumulation of nest material between breeding seasons is another frequent
377 phenomenon of nest-boxes that is rarely observed in tree cavities, most probably due to
378 humid conditions in the latter promoting decomposition of nests over winter (Wesolowski,
379 2000; Hebda et al., 2013). The accumulation of nesting material in nest-boxes may induce
380 infestations by overwintering fleas, and also reduce the functional depth of the cavity for
381 birds, which reduces nest-site safety (Rendell and Verbeek, 1996; reviewed in Mazgajski,
382 2007). Regular cleaning of nest-boxes is necessary to alleviate these problems, but such
383 maintenance is labour intensive (Møller, 1989; Rendell and Verbeek, 1996; Wesolowski,
384 2011).

385 All of these practical and ecological differences between tree holes and nest-boxes
386 have implications for nest-box studies of cavity-nesting birds, which are the basis of much of
387 our understanding of their breeding ecology. Such limitations should, therefore, be
388 considered if attempting to extrapolate results from nest-boxes to a wider population of birds

389 breeding in tree holes, as the conclusions reached could be misleading (Lambrechts et al.,
390 2010; Wesolowski, 2011).

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

401

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411

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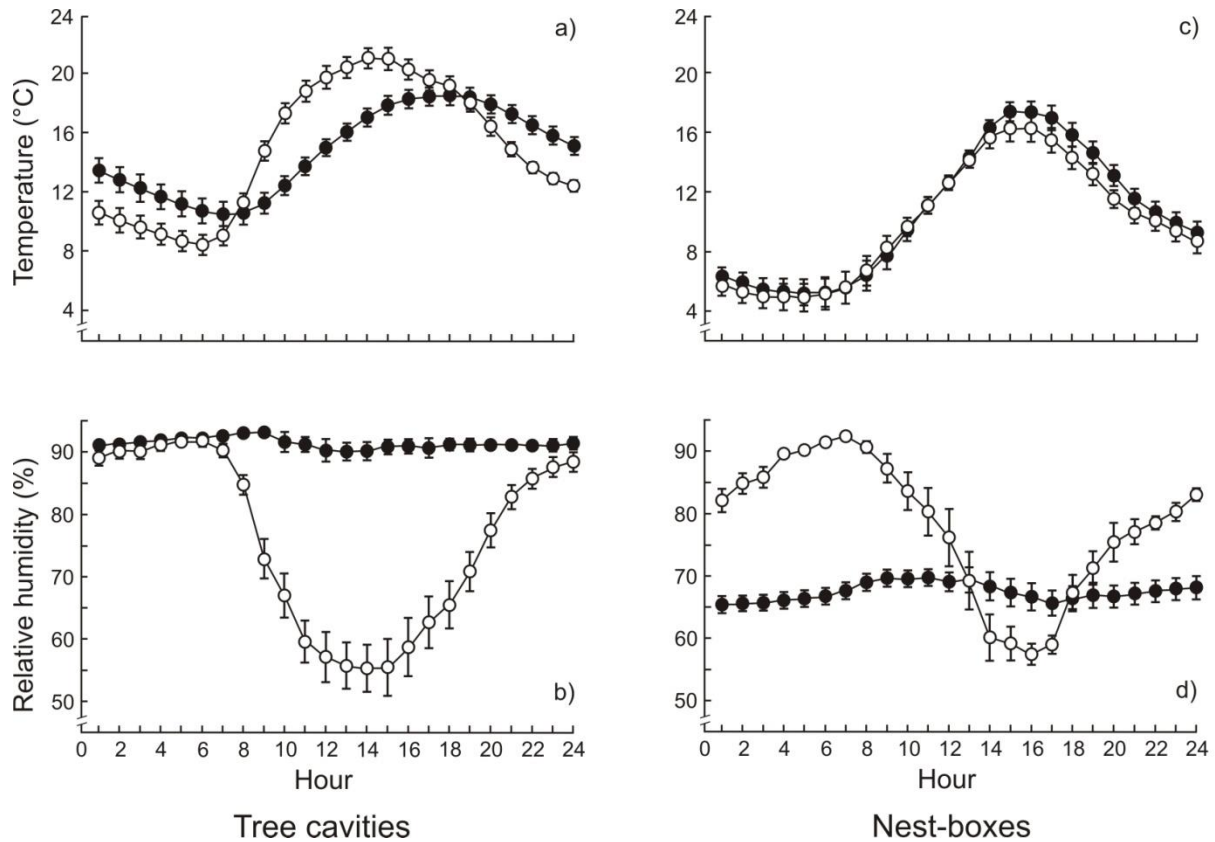
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580 **Figures**

581



582

Tree cavities

Nest-boxes

583 Fig. 1. Daily changes in the mean hourly air temperature and relative humidity in vacant tree

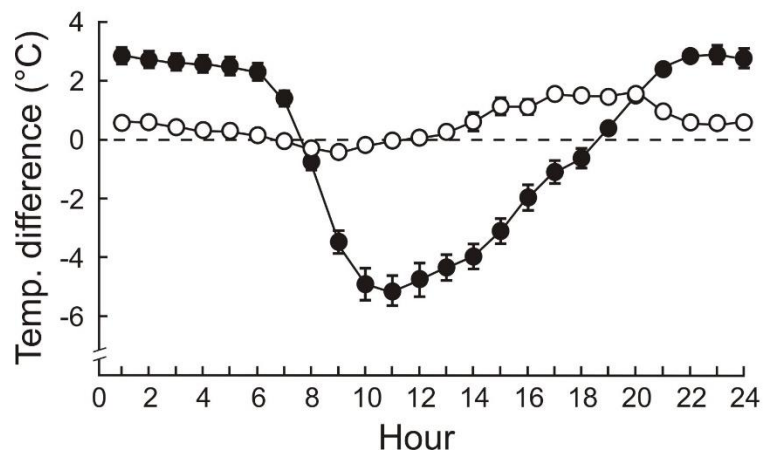
584 cavities of marsh tits in Białowieża National Park (Poland), respectively: a) $n = 24$, and b) $n =$ 585 15 (black dots), and in nest-boxes at Monks Wood (England), respectively: c) $n = 18$, and d)586 $n = 15$ (black dots) in relation to ambient conditions (white dots). Shown are means (dots)

587 and SE (whiskers). Measurements in tree cavities were taken in April-May 2013 and 2014,

588 and measurements in nest-boxes in May 2015.

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591

592 Fig. 2. Daily changes of mean hourly internal-ambient temperature differences in vacant tree

593 cavities of marsh tits in Białowieża National Park (Poland) (black dots; $n = 24$) and in nest-

594 boxes at Monks Wood (England) (white dots; $n = 18$). Shown are means (dots) and SE

595 (whiskers). "0" level occurs when internal and ambient temperatures are equal.

596 Measurements in tree cavities were taken in April-May 2013 and 2014, and measurements in

597 nest-boxes in May 2015.

598

599

600 **Figure legends**

601 Fig. 1. Daily changes in the mean hourly air temperature and relative humidity in vacant tree
602 cavities of marsh tits in Białowieża National Park (Poland), respectively: a) $n = 24$, and b) $n =$
603 15 (black dots), and in nest-boxes at Monks Wood (England), respectively: c) $n = 18$, and d)
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605 and SE (whiskers). Measurements in tree cavities were taken in April-May 2013 and 2014,
606 and measurements in nest-boxes in May 2015.

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610 cavities of marsh tits in Białowieża National Park(Poland) (black dots; $n = 24$) and in nest-
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612 (whiskers). "0" level occurs when internal and ambient temperatures are equal.
613 Measurements in tree cavities were taken in April-May 2013 and 2014, and measurements in
614 nest-boxes in May 2015.

615

616

617 **Tables**

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

| Cavity parameters | Tree cavities | Nest-boxes |
|---|----------------------------|---------------|
| Entrance diameter (cm): | | |
| least | 2.3 (2-7) | 2.6 (–) |
| greatest | 6.8 (3-10) | 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 | 1.8 (1.5-2.0) |
| 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 |

624

^a measured for 14 tree cavities

625 Table 2. Comparison of internal and ambient daily air temperatures and relative humidity of vacant tree cavities previously used by marsh tits in
 626 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) | -1-13 | 8.3 | <0.001 | 4.6 (4.1) | 0-9 | 4.3 (4.3) | -1-9 | 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 |

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

| Parameter | Estimate | SD error | <i>t</i> | 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 |

632
633

634 Table 4. A review of relationships between daily thermal conditions inside (in) and outside (out) of vacant tree cavities. Time lag is the number
 635 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 (hours) | 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 (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) |
| None | 34 | living ^c | in > out | in < out | 2 | 4 | 0.5 | — | Rhodes et al. (2009) |
| 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) |
| Birds | | | | | | | | | |
| <i>Aegotheles cristatus</i> | 11 | — | in > out | in < out | 12 | 15 | 0.8 | — | Doucette et al. (2011) |
| <i>Colaptes auratus</i> | 1 | — | in > out | in > out | 13 | 14 | 0.9 | -6-2 | Howe et al. (1987) |
| <i>Colaptes auratus</i> | 86 | dead ^b | in > out | in < out | 11 | 26 | 0.4 | 2-5 | Wiebe (2001) |
| <i>Philesturnus c. carunculatus</i> | 34 | living ^c | in > out | in < out | 1 | 4 | 0.4 | — | Rhodes et al. (2009) |

| | | | | | | | | | |
|----------------------------------|----|--------|----------|----------|---|----|-----|-----|-------------------------------|
| <i>Parus major</i> | 35 | living | in > out | in < out | 3 | 9 | 0.3 | 3-6 | Maziarz and Wesołowski (2013) |
| <i>Poecile palustris</i> | 24 | living | in > out | in < out | 9 | 13 | 0.7 | 2-3 | this study |
| Mammals | | | | | | | | | |
| <i>Trichosurus vulpecula</i> | 10 | living | in > out | in ≥ out | 7 | 7 | 1.0 | 0-1 | Isaac et al. (2008b) |
| <i>Eptesicus fuscus</i> | 19 | – | in > out | in < out | 8 | 12 | 0.7 | 2-4 | Willis and Brigham (2007) |
| <i>Nyctalus noctula/leisleri</i> | 12 | – | in > out | in < out | 4 | 12 | 0.4 | 4-5 | Ruczyński (2006) |
| <i>Plecotus auritus</i> | 6 | – | in > out | in < out | 3 | 7 | 0.5 | 2-6 | Otto et al. (2016) |
| <i>Chalinolobus tuberculatus</i> | 24 | living | in > out | in < out | 2 | 9 | 0.2 | 4-5 | Sedgeley (2001); knot-holes |
| <i>Ch. tuberculatus</i> | 11 | living | in > out | in < out | 3 | 10 | 0.3 | 5 | Sedgeley (2001); trunk holes |
| <i>Myotis bechsteinii</i> | 6 | – | in > out | in < out | 2 | 7 | 0.2 | 4-7 | Otto et al. (2016) |
| <i>M. nattereri</i> | 6 | – | in > out | in < out | 2 | 7 | 0.3 | 3-8 | Otto et al. (2016) |
| <i>M. nattereri</i> | 3 | living | in > out | in < out | 2 | 10 | 0.2 | 2-3 | Smith and Racey (2005) |
| <i>Procyon lotor</i> | 2 | living | in > out | in < out | 2 | 10 | 0.2 | 2-5 | Stains (1961) |

636 ^a data unavailable; ^b c. 50% of cavities in dead trees; ^c 20% of cavities in dead trees

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638 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
 639 of hours after which the internal daily minimum and maximum temperatures followed the ambient extremes; values below “0” indicate that
 640 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 (hours) | Source |
|--------------------------|----|------------------------|---------------------|------------------|------------------|----------|----------------------|-----|--------|------------------|----------------------------|
| | | | | | min | max | in | out | in/out | | |
| None | 2 | 13 x 13 | 30 x 60 | wood | in = out | in > out | 10 | 9 | 1.1 | 0-1 | McComb and Noble (1981) |
| None | 1 | 3.3 x 3.3 | 11 x 11 | wood | in ≤ out | in > out | 17 | 12 | 1.4 | -1-0 | Olszewski (1971) |
| None | 1 | 4.7 x 4.7 | 13 x 13 | wood | in ≤ out | in < out | 10 | 12 | 0.8 | -1-0 | Olszewski (1971) |
| None | 1 | 4.7 x 4.7 | 13 x 13 | sawdust concrete | in ≤ out | in > out | 15 | 12 | 1.3 | 0-1 | Olszewski (1971) |
| None | 4 | 10 x 10 | 26 x 25 | plywood | in ≤ out | in > out | 20 | 16 | 1.3 | 0 | Ellis (2016) |
| None | 4 | 10 x 10 | 25 x 25 | plywood | in ≤ out | in > out | 20 | 16 | 1.3 | 0 | Ellis (2016) |
| None | 4 | 6 x 6 | 20 x 25 | plywood | in ≤ out | in > out | 20 | 16 | 1.3 | 0 | Ellis (2016) |
| None | 4 | 8 x 8 | 25 x 25 | plywood | in ≤ out | in > out | 20 | 16 | 1.3 | 0 | Ellis (2016) |
| None | 4 | 15 x 10 | 26 x 25 | plywood | in ≤ out | in > out | 20 | 16 | 1.3 | 0 | Ellis (2016) |
| None | 4 | 5 x 5 | 31 x 15 | plywood | in ≤ out | in > out | 20 | 16 | 1.3 | 0 | Ellis (2016) |
| <i>Athene noctua</i> | 18 | 6.5 x 6.5 | 18 x 83 | wood | in ≤ out | in > out | 6 | 5 | 1.2 | 0-1 | Grüebler et al. (2014) |
| <i>Coracias garrulus</i> | 17 | 6 x 6 | 21 x 21 | wood | – ^a | – | 14 | 13 | 1.1 | – | Amat-Valero et al. (2014) |
| <i>Poecile palustris</i> | 18 | 2.6 x 2.6 | 8 x 8 | wood | in > out | in > out | 13 | 13 | 1.1 | 0-1 | this study |
| <i>Passer montanus</i> | 3 | 3.2 x 3.2 | 11 x 11 | woodcrete | – | – | 18 | – | – | – | García-Navas et al. (2010) |
| <i>P. montanus</i> | 3 | 3.2 x 3.2 | 12 x 12 | wood | – | – | 15 | – | – | – | García-Navas et al. (2010) |

641 ^a data unavailable