



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



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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.

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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

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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; Erbeling-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; Gruebler 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 km² 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

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