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Occupation of wood warbler *Phylloscopus sibilatrix* nests by *Myrmica* and *Lasius* ants

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Abstract

Bird nests can provide habitats for various invertebrates, including ectoparasites, scavengers and predators. Records of ants associating with active bird nests mostly involve the insects searching for food, with some exceptional records of ants raising their broods (eggs, larvae or pupae) within songbird nests in tree cavities. We present data for a previously undocumented, but apparently regular, occurrence of ants and their broods within the active nests of a songbird, the wood warbler *Phylloscopus sibilatrix* (Bechstein, 1793), which builds domed nests on the ground in European forests. Systematic recording found ants, mostly *Myrmica ruginodis* Nylander, 1846, in 43% of 80 wood warbler nests in the primary forest of Białowieża National Park (Poland) during the springs of 2016-2017, including ant broods in 30%. Ad hoc records from this site in 2004-2015 found ants in a further 29% of 163 nests, including broods in 20%, indicating a regular association. However, examination of 37 nests from secondary forest in Switzerland and Great Britain founds ants in only 14%, and broods in just 5%. We discuss the potential drivers and mechanisms of the observed association between breeding wood warblers and ants, including the apparent difference in frequency between the primary and secondary forests.

Keywords: interspecific interactions, nest sites, reproduction, ant broods, wood warbler

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Introduction

Bird nests are constructions that can also provide habitats for many other species, particularly invertebrates. The latter may include ectoparasites that feed on the host birds' blood, scavengers that forage on nest materials or detritus, or predators that hunt other invertebrates inhabiting the nest (e.g. Woodroffe 1953). Although the cohabitation of birds and invertebrates within nests creates opportunities for the development of complex interspecific relationships, studies of these are scarce outside of the literature relating to bird-ectoparasite interactions (reviewed in Clayton and Moore 1997; Deeming and Reynolds 2015).

The associations between social insects, such as ants, wasps, bees or termites, and nesting birds involved bird species situating their nests in close proximity to these insects' colonies, excavating holes and breeding inside insect nests (e.g. reviewed in Myers 1935; Young et al. 1990; Joyce 1993; reviewed in Haemig 2001; Somavilla et al. 2013), or insects appearing inside or nearby bird nests (e.g. Haemig 1999; Lambrechts et al. 2008; DeFisher and Bonter 2013; Lambrechts and Schatz 2014; Broughton et al. 2015; Brown et al. 2015). Due to the increased nest security against predation or parasitism, breeding close to colonies of social insects was advantageous for some bird species, which seemed to be attracted to nesting in such places (e.g. reviewed in Myers 1935; Joyce 1993; reviewed in Heamig 2001). The majority of these studies came from the tropics, however, with only rare records from temperate regions.

To date, observations of the presence of ants inside bird nests mainly comprised adult ants exploring bird nests, presumably in search of food, and sometimes removing ectoparasites (Duffy 1991; Brown et al. 2015) or foraging on dead nestlings (e.g. Lambrechts et al. 2008), but occasionally also showing antagonistic behaviour towards the owners (e.g. Haemig 1999; Lambrechts et al. 2008; DeFisher and Bonter 2013; Lambrechts and Schatz 2014). Such aggression of ants towards nesting birds could be responsible for some chick deaths or erratic incubation behaviour by parent birds (Lambrechts et al. 2008; DeFisher and Bonter 2013), and could also affect nest-site choice by birds (Davis et al. 2008).

The evidence of ants using bird nests to raise their own broods (eggs, larvae or pupae) has been exceptional. To the best of the authors' knowledge, ant broods have only been documented within nest-boxes containing blue tit *Cyanistes caeruleus* broods in Corsica (Lambrechts et al. 2008), and in tree-cavity nests of the great tit *Parus major* and marsh tit *Poecile palustris* in the primeval part of the Białowieża Forest, Poland (9 of 203 nests; Mitrus et al. 2015). Blem and Blem (1994) reported frequent ant colonies (unidentified species) on the side of active nests in nest-boxes of prothonotary warblers *Protonotaria citre*, but without any further details.

The lack of similar reports from the nests of other well-studied songbirds is intriguing, suggesting that this phenomenon is exceptional and occurs only among limited cavity-nesting species. Here, we confound this presumption by presenting the first data on the occurrence and frequency of ants and their broods in nests of the wood warbler *Phylloscopus sibilatrix* (Bechstein, 1793), a small (10 g) migrant songbird breeding in deciduous, mixed or conifer-dominated woodlands of temperate Europe (Cramp 1992). Wood warblers build dome-shaped nests on the forest floor, which are typically hidden among low herb vegetation, and less frequently wedged under fallen branches or logs, or situated on slopes of small hillocks (Wesołowski 1985). The external layer of the nests is usually constructed from dead leaves of trees or grasses (see examples in Fig. 1).

Methods

Observations of wood warbler nests were conducted in the strictly protected part of the Białowieża National Park, Poland (47 km2, hereafter BNP; coordinates of Białowieża village: 52°42' N and 23°52' E), a remnant of the lowland European primeval forests. Here, the animal community is mostly intact, with species interactions and natural processes being largely unaffected by direct human activity (e.g. Tomiałojć et al. 1984). The occurrence of ants, including their broods, in wood warbler nests in BNP was discovered accidentally during long-term study of the birds' breeding ecology in 2004-2015. This prompted systematic documentation in 2016-2017 to determine the frequency of this phenomenon.

Additionally, during 2017, checks of wood warbler nests were commissioned from collaborators at the Jura Mountains in Switzerland (coordinates of Olten town: 47°20' N, 7°54' E; for details see Grendelmeier et al. 2015) and four areas of Great Britain: Highland in Scotland (vicinity of Tomich village: 57°17' N, 4°47' W), Gwent in Wales (vicinity of Parc-Seymour village: 51°37' N, 2°49' W), Devon (vicinity of Haytor Vale: 50°34' N, 3°43' W) and New Forest (vicinity of Lyndhurst: 50°52' N, 1°34' W) in southern England, to determine whether the presence of ants and their broods occurs more widely across the wood warbler's breeding range. Sampling sites were located mostly in deciduous woodland, and occasionally in mixed or coniferous stands.

During observations the nest structure was carefully examined and disassembled soon after it was vacated by the birds, typically 1-7 days following fledging of the young or nest failure if this occurred > 8 days post-hatching, and the presence or absence of adult ants and their brood was noted. In 2016-2017, adult ant specimens were systematically collected from nests in BNP, and preserved in ethanol for identification by a specialist. Specimens were also obtained from eight nests in BNP from 2004-2015, and four British nests from 2017.

Results

Of 80 nests from BNP examined in 2016-2017, 43% contained ants and 30% contained ant broods (larvae or pupae). In all of these cases, the ant brood was located within the sidewalls of the warbler nest (see example in Fig. 2), at or just above the ground level. The majority of specimens collected from the 34 nests were identified as *Myrmica ruginodis* Nylander, 1846 (65%, including 16 ant broods) or *M. rubra* (Linnaeus, 1758) (18%, six broods), with three cases of *Lasius niger* (Linnaeus, 1758) (one brood), two of *L. platythorax* Seifert, 1991 (one brood) and a single case of *L. brunneus* (Latreille, 1798) adults.

During the unsystematic observations in BNP (2004-2015), the proportion of wood warbler nests containing ants was only slightly lower than in 2016-2017, at 29% of 163 nests (Fisher's exact test, $p = 0.060$), with 20% of the total containing ant broods (Fisher's exact

test, p = 0.11). Specimens collected from the eight nests in 2004-2015 were all identified as *M. ruginodis.*

The results from the near-pristine forest of BNP contrasted with those commissioned from other parts of Europe, which all took place in human-modified, fragmented woodlands. In the Swiss uplands, only one of 12 nests examined contained adult ants (without a brood), and in Britain four of 25 nests contained adult *M. ruginodis*, including two nests with ant larvae. All observations of ants in the British nests came from the New Forest in the lowlands of southern England (n = 5 nests inspected), with none from higher altitudes in the west (Gwent, Wales: n = 12, Devon: n = 4) or north (Highland, Scotland: n = 4).

Discussion

These first records of the occupation of wood warbler nests by ants raising their broods suggest that this phenomenon could be relatively common in some areas and may be underreported. Thus, the presence of ant broods on or inside the nests of other bird species might be more widespread in these environments than the available records (Blem and Blem 1994; Lambrechts et al. 2008; Mitrus et al. 2015) would suggest. Similar associations may also occur in bird species that often build their nests at or just above the ground, but this would require confirmation. Those nests with a construction resembling that of the wood warbler's, i.e. domed-shaped and constructed of leaves or grasses, can be found in several other European woodland species, such as the willow warbler *Phylloscopus trochilus,* common chiffchaff *Ph. collybita*, or European robin *Erithacus rubecula* (Cramp 1988, 1992), and so ant broods could also be present in such nests. Studies involving systematic inspection of nests belonging to different bird species would be worthwhile to reveal the true frequency of this phenomenon.

The very low incidence of ants in wood warbler nests in Western Europe, compared to the much greater frequency in BNP, may reflect lower densities of wood warblers in the declining populations of Switzerland and Britain (BirdLife International 2004), and/or possible differences in densities of ant nests in the human-altered habitats (reviewed in Elmes et al.

1998). Both possibilities could indicate disruption of the association between ground-nesting birds and ants in transformed woodlands, but further studies are necessary to confirm this.

The occurrence of ant broods inside walls of wood warbler nests showed that ants clearly colonised nests following their construction and, at least in some cases, while they were still occupied by the birds; this was indicated by testing in 2017, when a probe delicately inserted into the walls of several nests resulted in ants emerging (M. Maziarz, pers. obs.). Despite this apparently defensive reaction, no aggressive behaviour by ants towards the warblers was observed in BNP.

This coexistence of birds and ants could be coincidental, due to co-selection of sites and overlap in the phenology of breeding wood warblers and ants raising their young. The timing of the wood warblers' arrival in spring to begin nest-building in Europe (from about mid-April to mid-May; Cramp 1992), coincides with the period when ant workers place their larvae in temporary brood chambers, which are parts of the underground nests situated just above the ground surface, under fallen bark, twigs, logs, leaves or moss, in which the ants incubate their broods (Elmes et al. 1998; M. Maziarz, pers. obs.). By building their domed nests of grass, leaves and moss on the ground, and often next to or under fallen twigs or logs (Wesołowski 1985; M. Maziarz, pers. obs.; see examples in Fig. 1), wood warblers create structures that may resemble brood chambers of ants. As such, incidental creation by the birds of a potentially suitable microhabitat in the vicinity of ant nests might facilitate nest colonisation by the insects.

Another possibility is that the cohabitation of ants and birds would give potential advantages to one or both parties in the system, leading to one- or two-way interspecific attraction. The birds may preferentially select nest sites in the vicinity of ant nests to facilitate their colonisation, and ants may preferably occupy the wood warbler nests. Such behaviour was frequently reported in bird species that place their nests close to colonies of various social insects (e.g. reviewed in Myers 1935; Young et al. 1990; Joyce 1993; reviewed in Haemig 2001; Somavilla et al. 2013). Although the main drivers of these associations appear to involve the avoidance of predation or parasitism (e.g. Joyce 1993; reviewed in Haemig

2001), the same mechanism of nest site-selection may also operate in wood warblers. A greater frequency of bird nests in the vicinity of ant nests than random would support this idea.

Additionally, the heat generated by birds within the nest might create favourable thermal conditions in the nest walls, providing conditions that promote rapid development of the ant larvae (Elmes and Wardlaw 1983). The elevated temperature of the nest walls, relative to ambient conditions, could be particularly important for ants in cool spring weather, with limited direct sunlight warming nest chambers on the forest floor. In such conditions, the active nests of wood warblers may provide a reliable and attractive heat source. More frequent ant colonisation of occupied nests heated by bird owners, rather than empty, without eggs or nestlings, would support this hypothesis.

Another potential benefit to ants in colonising wood warbler nests might be the presence of other invertebrates, which may constitute a source of protein-rich food for ants (Dussutour and Simpson 2009). If this resulted in reduced numbers of ectoparasites (see e.g. Duffy 1991; Lambrechts et al. 2014; Brown et al. 2015), then the presence of ants in the nests could also be advantageous for the hosting birds. Such a reduced ectoparasite infestation could improve the growth and survival rates of warbler chicks, thereby enhancing the parents' breeding productivity, although the effect may be subtle (see e.g. Lambrechts et al. 2014; reviewed in Deeming and Reynolds 2015). Nevertheless, the reduction of ectoparasite numbers in nests occupied by ants in comparison to those without might confer a fitness advantage of the bird-ant cohabitation (e.g. Lambrechts et al. 2008; Brown et al. 2015).

Although some bird species may gain protection from predators by nesting close to ant colonies, due to aggressive behaviour of the ants if disturbed by a predator approaching the nest area (e.g. Myers 1935; Joyce 1993; Haemig 1999; Somavilla et al. 2013), it is rather doubtful that this situation could apply to wood warblers. This is because the ant broods are situated within the walls of the wood warbler nest, and so workers will become aggressive only when the nest structure is seriously disturbed or already destroyed (M. Maziarz, pers.

obs.). By this stage, the warblers' eggs or chicks would generally be killed already, rendering any defence by the ants as somewhat redundant.

Thus, we hypothesise that the reasons for ants colonising wood warbler nests may involve three potential scenarios: a coincidental convergence in the phenology and nesting behaviour of wood warblers and ants, exploitation by the ants of the heated nest structures provided by the warblers, and/or mutual exploitation with ants gaining access to a food source, including parasitic invertebrates, while the warblers gain improved nest sanitation and a reduction of ectoparasites. Additional studies are required to test these hypotheses and further investigate the drivers and mechanisms of this colonisation process, as well as the ecological implications for both parties in this system.

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Fig. 1 Examples of wood warbler *Phylloscopus sibilatrix* nests in the Białowieża National Park (Poland). The nests are composed of a dome of leaves, grass and moss with a well concealed entrance, and they are hidden among the vegetation or leaf litter, often under or near fallen branches or logs (Wesołowski 1985; photos: Richard K. Broughton and Marta Maziarz)

293 **Fig. 2** Numerous ant *Myrmica* spp. larvae (centre-left of the image) and two larger, well-
294 grown (3rd instar) blow fly *Protocalliphora* spp. larvae (centre) in the wall material of a wood
295 warbler *Phylloscopus sibilatrix* nest in the Białowieża Forest (Poland). (photo: Marta Maziarz
296 and Richard K. Broughton)
297