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and *Lasius* ants.**

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

2

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10

## 11 **Abstract**

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

27

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

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40 request from Marta Maziarz ([mart.ann.maz@gmail.com](mailto:mart.ann.maz@gmail.com)).

41

## 42 **Introduction**

43 Bird nests are constructions that can also provide habitats for many other species,  
44 particularly invertebrates. The latter may include ectoparasites that feed on the host birds'  
45 blood, scavengers that forage on nest materials or detritus, or predators that hunt other  
46 invertebrates inhabiting the nest (e.g. Woodroffe 1953). Although the cohabitation of birds  
47 and invertebrates within nests creates opportunities for the development of complex  
48 interspecific relationships, studies of these are scarce outside of the literature relating to  
49 bird-ectoparasite interactions (reviewed in Clayton and Moore 1997; Deeming and Reynolds  
50 2015).

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

62 To date, observations of the presence of ants inside bird nests mainly comprised adult  
63 ants exploring bird nests, presumably in search of food, and sometimes removing  
64 ectoparasites (Duffy 1991; Brown et al. 2015) or foraging on dead nestlings (e.g. Lambrechts  
65 et al. 2008), but occasionally also showing antagonistic behaviour towards the owners (e.g.  
66 Haemig 1999; Lambrechts et al. 2008; DeFisher and Bonter 2013; Lambrechts and Schatz  
67 2014). Such aggression of ants towards nesting birds could be responsible for some chick  
68 deaths or erratic incubation behaviour by parent birds (Lambrechts et al. 2008; DeFisher and  
69 Bonter 2013), and could also affect nest-site choice by birds (Davis et al. 2008).

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

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

88

## 89 **Methods**

90 Observations of wood warbler nests were conducted in the strictly protected part of the  
91 Białowieża National Park, Poland (47 km<sup>2</sup>, hereafter BNP; coordinates of Białowieża village:  
92 52°42' N and 23°52' E), a remnant of the lowland European primeval forests. Here, the  
93 animal community is mostly intact, with species interactions and natural processes being  
94 largely unaffected by direct human activity (e.g. Tomiałojć et al. 1984). The occurrence of  
95 ants, including their broods, in wood warbler nests in BNP was discovered accidentally  
96 during long-term study of the birds' breeding ecology in 2004-2015. This prompted  
97 systematic documentation in 2016-2017 to determine the frequency of this phenomenon.

98 Additionally, during 2017, checks of wood warbler nests were commissioned from  
99 collaborators at the Jura Mountains in Switzerland (coordinates of Olten town: 47°20' N,  
100 7°54' E; for details see Grendelmeier et al. 2015) and four areas of Great Britain: Highland in  
101 Scotland (vicinity of Tomich village: 57°17' N, 4°47' W), Gwent in Wales (vicinity of Parc-  
102 Seymour village: 51°37' N, 2°49' W), Devon (vicinity of Haytor Vale: 50°34' N, 3°43' W) and  
103 New Forest (vicinity of Lyndhurst: 50°52' N, 1°34' W) in southern England, to determine  
104 whether the presence of ants and their broods occurs more widely across the wood  
105 warbler's breeding range. Sampling sites were located mostly in deciduous woodland, and  
106 occasionally in mixed or coniferous stands.

107 During observations the nest structure was carefully examined and disassembled soon  
108 after it was vacated by the birds, typically 1-7 days following fledging of the young or nest  
109 failure if this occurred > 8 days post-hatching, and the presence or absence of adult ants  
110 and their brood was noted. In 2016-2017, adult ant specimens were systematically collected  
111 from nests in BNP, and preserved in ethanol for identification by a specialist. Specimens  
112 were also obtained from eight nests in BNP from 2004-2015, and four British nests from  
113 2017.

114

## 115 **Results**

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

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

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

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

135

## 136 **Discussion**

137 These first records of the occupation of wood warbler nests by ants raising their broods  
138 suggest that this phenomenon could be relatively common in some areas and may be  
139 underreported. Thus, the presence of ant broods on or inside the nests of other bird species  
140 might be more widespread in these environments than the available records (Blem and Blem  
141 1994; Lambrechts et al. 2008; Mitrus et al. 2015) would suggest. Similar associations may  
142 also occur in bird species that often build their nests at or just above the ground, but this  
143 would require confirmation. Those nests with a construction resembling that of the wood  
144 warbler's, i.e. domed-shaped and constructed of leaves or grasses, can be found in several  
145 other European woodland species, such as the willow warbler *Phylloscopus trochilus*,  
146 common chiffchaff *Ph. collybita*, or European robin *Erithacus rubecula* (Cramp 1988, 1992),  
147 and so ant broods could also be present in such nests. Studies involving systematic  
148 inspection of nests belonging to different bird species would be worthwhile to reveal the true  
149 frequency of this phenomenon.

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

154 1998). Both possibilities could indicate disruption of the association between ground-nesting  
155 birds and ants in transformed woodlands, but further studies are necessary to confirm this.

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

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

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



182 2001), the same mechanism of nest site-selection may also operate in wood warblers. A  
183 greater frequency of bird nests in the vicinity of ant nests than random would support this  
184 idea.

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

193 Another potential benefit to ants in colonising wood warbler nests might be the presence  
194 of other invertebrates, which may constitute a source of protein-rich food for ants (Dussutour  
195 and Simpson 2009). If this resulted in reduced numbers of ectoparasites (see e.g. Duffy  
196 1991; Lambrechts et al. 2014; Brown et al. 2015), then the presence of ants in the nests  
197 could also be advantageous for the hosting birds. Such a reduced ectoparasite infestation  
198 could improve the growth and survival rates of warbler chicks, thereby enhancing the  
199 parents' breeding productivity, although the effect may be subtle (see e.g. Lambrechts et al.  
200 2014; reviewed in Deeming and Reynolds 2015). Nevertheless, the reduction of ectoparasite  
201 numbers in nests occupied by ants in comparison to those without might confer a fitness  
202 advantage of the bird-ant cohabitation (e.g. Lambrechts et al. 2008; Brown et al. 2015).

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

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

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

219

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283



284



285

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

291

292



293 **Fig. 2** Numerous ant *Myrmica* spp. larvae (centre-left of the image) and well-  
294 grown (3<sup>rd</sup> 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