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SHORT COMMUNICATION

Cavity-nesting bees and wasps (Hymenoptera: Aculeata) of xerothermic habitats are unable to use cavities in reed galls

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Abstract

Galls induced by *Lipara lucens* on common reed are adopted by bees and wasps as a nesting cavity. Most of these species occur only in wetlands. Some of them are specialised or show strong preference to nest only in reed galls. In our manipulative study, we deployed trap nests of reed galls to 16 steppic grasslands or open sandy xerothermic habitats in the Czech Republic. Surprisingly, we reared from a total of 1,523 galls only 31 specimens of five nesting species and one predator-inquiline. Trap nests of identical design, which we previously deployed to wetlands, contained four-times more individuals of twice as many nesting species and four parasite species. Moreover, the most abundantly reared species in reed galls deployed to the steppic habitats was *Pemphredon fabricii* (58% of total individuals). This species is strictly specialised for nesting in reed beds. Therefore, this experiment revealed that bees and wasps of xerothermic habitats are likely to have difficulties in finding the gall opening. The cavities of similar size are readily occupied by xerothermophilous bees and wasps when provided. In contrast, despite the *Lipara*-induced reed gall having a broad opening, it is hidden at the top of the gall in fibrous remnants of leaves, and the non-specialist bees and wasps are unable to locate it. This is the first evidence on an overlooked aspect of cavity quality – the cavity may be present and suitable but is too difficult for the insect to find.

Keywords Cavity · Cigar gall · Conservation · *Lipara* · *Pemphredon fabricii* · Steppic grassland

Introduction

Cavity nesters are the second most species-rich ecological group among bees and wasps, outnumbered just by those that dig their nests underground (Michener 2007; Grimaldi & Engel 2005; Bogusch and Horák 2018; Westrich 2018). Diverse cavity types are available and suitable for nesting, which is associated with enormous variability in nesting specialisation of cavity-nesting bees and wasps. Many are non-specialists and place their nests in multiple cavity types, such as cavities in wood, plant stems and stalks, cavities in walls or between stones (Bogusch and Horák 2018; Westrich 2018). Only a few species create their nests both underground and in pre-existing cavities. In Europe, these are represented by several crabronid and pompilid wasps, i.e., *Anoplius nigerrimus* or *Crossocerus elongatulus*. On the contrary, there are ecological guilds of species, which are highly specialised to create their nests only in one narrowly defined cavity type. These include bees and wasps nesting in empty snail shells or those creating their nests inside old galls (Heneberg et al. 2014; Müller et al. 2018; Bogusch et al. 2019).

Specialised species usually evolved very specific behavioural and ecological traits to utilize their favourite cavity type effectively. There are many species nesting in reed or bamboo stalks with existing cavities. However, only a few species nest in stems filled with soft parenchymatic tissue (Mikát et al. 2020; Westrich 2018; Heneberg et al. in press). The inability of excavate the cavities in the parenchyma of stems is thus a limiting factor if the species can nest inside the stems. Most of the species capable of excavating cavities strongly prefer active excavation in stems with parenchyma (e.g., *Ceratina*) or in other materials, in which they must

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create the cavity (e.g. *Xylocopa* in wood). Reviewing the list of species specialised in, or only marginally using, specific cavity types, we find many strictly specialised species and several or more generalists, utilizing nearly any cavity of suitable size. Müller et al. (2018) reviewed all species nesting in empty snail shells and recorded most species to be specialised and only four nesting in shells only occasionally. Bogusch et al. (2020) reviewed species nesting in cigar galls on common reed (*Phragmites australis*) and recorded only several specialists and many species nesting in cigar galls occasionally.

Reed galls are induced by frit flies of the genus *Lipara* (Diptera: Chloropidae) (Tscharntke 1994; Nartshuk 2006; Westrich 2008; Heneberg et al. 2014; Bogusch et al. 2015). There are several species that occur in Europe and differ in gall size, shape and wall thickness. Especially large galls with a prominent cavity, which are induced by *Lipara lucens*, are frequently used as nesting cavities by multiple species of bees and wasps. Astapenková et al. (2017) and Bogusch et al. (2020) reviewed the species nesting inside these galls and found that these species can be divided into three groups according to their preferences of reed galls: (1) specialists nesting only, or predominantly, in reed galls (*Stenodynerus clypeopictus*, *Pemphredon fabricii* and *Hylaeus pectoralis*); (2) species nesting both in reed galls and reed stalks but not in other cavity types (*Trypoxylon deceptorium*, *Hylaeus moricei*, *Passaloecus clypealis*); (3) generalists nesting in multiple cavity types and using reed galls for their nesting often or occasionally (*Hoplitis leucomelana*, *Symmorphus bifasciatus*, *Trypoxylon minus*). The number of species that are specialised for nesting in reed galls is not high compared to the list of generalists. However, many generalists can be considered as satellite species with regards to their presence in reed galls, as they were recorded only once, or several times, as nesting in reed galls. Only the three above-named generalist species were recorded frequently in reed galls (see Bogusch et al. 2020).

Reed gall is thus the limiting nesting resource for many species that are restricted to wetlands (Tscharntke 1994; Heneberg et al. 2017; Bogusch et al. 2020). However, there are many other abundant wetland species, which do not nest inside reed galls despite the presence of reed galls in their habitats (e.g., *Anoplius caviventris*) (Heneberg et al. 2014). On the other hand, several species recorded quite frequently nesting inside reed galls occur mainly in xerothermic sites (*H. leucomelana*) or have broad spectrum of habitats, where they occur (*S. bifasciatus*, *T. minus* and *Heriades rubicola*) and certainly nest in other cavity types in other habitats (Bogusch et al. 2015, 2020; Astapenková et al. 2017). Here we performed a manipulative experiment, in which we deployed trap nests in xerothermic habitats (both steppic and sandy formations) with an absence of reed beds with *Lipara*-induced cigar-shaped galls. The deployed trap nests consisted, however, of the *Lipara*-induced cigar-shaped galls only. We hypothesized that the species of xerothermic habitats can readily adopt reed galls for their nesting because they contain cavities similar to those known to be occupied by these species.

Materials and methods

We performed the field study at 16 localities that were located throughout the Czech Republic. Of these localities, ten were steppic grasslands that developed on southern-orientated hilly slopes, and another six localities were sandy habitats with bare sand patches. The presence of rich communities of bees and wasps including rare species was documented at all the examined sites; the evidence was available from mostly unpublished field surveys for conservation authorities. All except three studied localities were > 1 km away from the nearest reed bed, where the reed galls could be naturally present. The list of localities, their characters, dates of deployment and collection of trap nests and GPS coordinates are provided in Table 1.

In winter 2018–2019, we collected reed galls at two Czech localities with very abundant galls of *L. lucens* (Holice, GPS 50.0826603N, 15.9720972E and Pardubice-Semtín, GPS 50.0458333N, 15.6967608E). We collected galls induced by *L. lucens* in 2018 or older but did not collect damaged galls (e.g., destroyed by birds). We cut out the deformed reed shoots about 10 cm under the gall, and also removed protruding leaves. We immediately moved the collected galls to the emergence traps, stored in a well aired place, side-exposed to daylight, at a temperature between 15 and 23 °C, and sprayed with water at least once a week. Such treatment allowed any *Lipara* flies and other invertebrates to emerge. Therefore, the galls were ready to be deployed without any unwanted invertebrates inside, which would otherwise affect the results and support undesirable dissemination to the sampling sites. At the end of April 2019, we removed the galls from the emergence traps and constructed the trap nests. Each trap consisted of a bunch of ten well-developed cigar-shaped galls that were attached to a 0.5–1.2 m long bamboo stick by a tape (see Heneberg et al. 2017 for a detailed description of the method used).

We deployed the trap nests in transects of ten trap nests, which formed a line of approximately 120–200 m in length. We deployed all the trap nests between 2 and 15 May 2019. We retained the trap nests onsite through the summer and removed them from the transects between 17 October and 2 November 2019. We placed the removed trap nests into enclosed black plastic bags to avoid cross-contamination and contact with other insects until examined. We then

Table 1 List of localities studied

Locality	GPS	Distance to nearest reed bed [m]	Nests deployed	Nests collected	Character	Note
Báň	50.1586769 N, 15.2748264E	2486	02.05.2019	18.10.2019	Steppic	Steppic grassland on hilly slope
Boří Les	48.7362192 N, 16.8694961E	573	12.05.2019	22.10.2019	Sandy	Spoil heap on sandy substrate
Bzenec	48.9587975 N, 17.2913008E	1357	11.05.2019	22.10.2019	Sandy	Bare sandy site
Čeperka	50.1277239 N, 15.7693019E	1414	02.05.2019	17.10.2019	Sandy	Sands at forest
Dunajovické kopce	48.8480047 N, 16.5523100E	4519	15.05.2019	23.10.2019	Steppic	Loess steppic formations
Kleneč	50.3900117 N, 14.2564842E	1307	04.05.2019	01.11.2019	Sandy	Bare sandy site above steppe
Kunětická hora	50.0797761 N, 15.8132625E	2355	02.05.2019	17.10.2019	Steppic	Bazaltic steppe on a hill
Pálava, Soutěska	48.8657839 N, 16.6434769E	3168	11.05.2019	23.10.2019	Steppic	Limestone steppe
Pánov	48.8863256 N, 17.1409169E	1366	11.05.2019	22.10.2019	Sandy	Bare sandy site
Písečný vrch	50.4234019 N, 13.7348056E	4248	04.05.2019	02.11.2019	Steppic	Steppic grassland on hilly slope
Pouzdřany	48.9473536 N, 16.6438217E	2189	11.05.2019	23.10.2019	Steppic	Loess steppic formations
Prokopské údolí	50.0358736 N, 14.3501622E	4224	04.05.2019	02.11.2019	Steppic	Limestone steppe
Raná	50.4073522 N, 13.7768078E	3149	04.05.2019	02.11.2019	Steppic	Loess steppic formations
Stroupeč	50.3593994 N, 13.4979533E	2135	04.05.2019	01.11.2019	Steppic	Loess steppic formations
Velká Klajdovka - Hády	49.2169928 N, 16.6754658E	180	12.05.2019	23.10.2019	Steppic	Limestone steppe
Vesecký kopec	50.0456331 N, 15.8540794E	561	02.05.2019	17.10.2019	Sandy	Sand dune in a forest

placed the trap nests in a shaded place at ambient temperature and, within a week, we longitudinally cut all the collected galls and analysed their contents. We put all the larvae of bees and wasps, as well as their parasites into 1.5 ml tubes, enclosed the tubes with cotton plugs, and stored them for two months in a fridge. Then, we allowed all the insects to develop until the end of June 2020. We fixed and stored all the reared insects in 75% ethanol until identified to species level by the first author. We stored the specimens in the collection of the University of Hradec Králové. We compared the species composition of reared specimens with that of the insects that had been reared from identically constructed trap nests that were previously deployed in wetlands and reed beds (Heneberg et al. 2017).

Results and discussion

In the 1,523 galls collected from trap nests, we recorded only 31 individuals of five species of bees and wasps. Of these species, *Pemphredon fabricii* was surprisingly the most abundant, with 18 reared individuals (58% of the total). We also reared *Nitela spinolae*, *Trypoxylon minus*, *Chelostoma campanularum* and a predator-inquiline *Gasteruption assectator* (Table 2). In total, trap nests from ten of the 16 examined localities were completely empty. Of the six localities with bees and wasps present, *P. fabricii* was recorded in four localities (Boří Les, Bzenec, Kleneč and Pánov) in numbers of 12, 11, 5 and 3 individuals, respectively. This corresponds to the occupancy of only one to four galls per locality. The inverse relationship between distance to the nearest reed bed and the number of *P. fabricii* was statistically significant. The sites within 180–2,000 m from the nearest reed bed hosted significantly more *P. fabricii* compared to sites that were 2,000–4,519 m from the nearest reed bed (Mann-Whitney $U = 13.5$, $5 = 77.5$, $p = 0.015$) (Fig. 1). *Nitela spinolae* was recorded in Boří Les and Velká Klajdovka in four and two individuals (each in one gall), *T. minus* in Bzenec and Pouzdřany both in two individuals and *C. campanularum* in Pouzdřany. We reared more individuals from galls that were deployed in sandy habitats within a flat landscape (3 species, 32 individuals) compared to habitats at hill slopes (4 species but 11 individuals), although the numbers of localities were 6/10. However, this difference could be fully attributed to differences in *P. fabricii* abundance. Only approximately two individuals were recorded in every 100 galls.

The species richness and abundance of bees and wasps that were recorded in trap nests constructed from reed galls placed in xerothermic habitats were low. The trap nests were exposed in places where we expected them to attract multiple cavity nesting species. Similarly placed nests that were made from reed stalks and goldenrod stems attracted at the same places high numbers of individuals or multiple cavity nesting species in our previous studies (Bogusch et al. 2017; Heneberg et al. in press). The majority of galls remained empty and only 16 galls of a total of 1,523 galls (1%) contained nests of bee or wasp species. Therefore, we conclude

Table 2 Species composition of trap nests in xerothermic habitats compared with the species composition in similarly constructed trap nests located in wetland habitats (data from wetlands adopted from Heneberg et al. (2017)). Two columns show numbers of specimens of each species reared in xerothermic habitats and wetlands, respectively. Third and fourth column show the number of specimens of each species per gall

Species	No. of individuals		Number of individuals per gall * 100	
	Xerothermes	Wetlands	Xerothermes	Wetlands
Chelostoma campanularum	2	3	0.13	0.08
Gasteruption assectator	1	2	0.07	0.05
Gasteruption nigrescens	0	2	0	0.05
Gasteruption sp.	0	5	0	0.13
Hoplitis leucomelana	0	7	0	0.18
Hylaeus moricei, EN	0	4	0	0.10
Hylaeus pectoralis, CR	0	119	0	3.05
Nitela spinolae	6	3	0.40	0.08
Passaloecus clypealis, VU	0	23	0	0.59
Pemphredon fabricii	18	1055	1.20	27.05
Stelis ornatula	0	2	0	0.05
Symmorphus bifasciatus	0	6	0	0.15
Trypoxylon deceptorium	0	4	0	0.10
Trypoxylon minus	4	0	0.27	0
Gen. sp.	0	5	0	0.13
Total individuals found	31	1240		
Total galls	1523	3900		

that bees and wasps occurring in xerothermic habitats are unable to adopt reed galls as their nesting resources. However, this result does not agree with our previous results, as summarized by Bogusch et al. (2020), and with results of other researchers who focused on bee and wasp species in reed galls (Wolf 1988; Westrich 2008; Nartshuk and Andersson 2013). The previous studies suggested that the specialised wetland species, or those with strong preferences for wetlands, were not the only occupants of reed galls. Other species were found in small numbers but repeatedly recorded as nesting in reed galls. Concerning these previously reported habitat generalists known to use reed galls for their nesting in wetlands, we recorded only *Trypoxylon minus*. Beyond *T. minus*, all other species recorded in the present study were previously recorded nesting in reed galls in reed beds (Bogusch et al. 2020). Therefore, deployed reed galls lacked not only the characteristic steppic cavity nesters, but also common habitat generalists among cavity nesters, such as *Hoplitis leucomelana* and *Symmorphus bifasciatus* (Macek et al. 2010; Westrich 2018). The two named species were previously repeatedly recorded as nesting in reed galls, particularly in cigar-shaped galls induced by *L. lucens* on thin reed shoots (Bogusch et al. 2015).

The flagship species of reed galls, crabronid wasp *P. fabricii*, was the most abundant species using reed galls that were deployed to xerothermic habitats. This species occurs mostly in wetlands, while its relative, *P. lethifer*, occurs in xerothermic habitats (Blösch 2000). However, Heneberg et al. (in press) confirmed that trap nests of reed stalks contained numerous brood of *P. fabricii* both in wetlands and steppic habitats (133/427 individuals) and *P. lethifer* was recorded only in three individual galls in wetlands. However, the trap nests were exposed in xerothermic habitats neighbouring with wetlands, so females of *P. fabricii* could simply find trap nests without flying large distances.

As per recent knowledge, *P. fabricii* is a species preferring reed galls but abundantly nesting also in reed stalks (Bogusch et al. 2020), and it occurs in the landscape nearly everywhere due to its ability to occupy very small reed beds with a few galls suitable for its nesting (P. Bogusch, unpublished observations). Therefore, it probably has a good dispersion ability and is able to search for alternative patches of nesting resources (reed galls) within relatively broad range around their existing nest sites. Note that we recorded this species in three flat sandy sites and one small hilly locality but it was absent in steppic formations on larger hills studied in this survey (Pouzdřany, Raná, Pálava-Děvín and many others) where dispersion would be more difficult or require them to travel greater distances both horizontally and vertically.

Heneberg et al. (2014) mentioned that reed galls are specific cavity types, in which the entrance is hidden among dry leaves (Fig. 2) and many species cannot use them for their nesting. This is valid especially for those hunting larger prey, for example spider wasps. Thus, quite common and numerous species *Anoplius caviventris* and *Priocnemis fennica* frequently occurring in reed beds were never recorded nesting in reed galls, as well as other species of family Pompilidae. On the other hand, these species, including rare wetland specialists (e.g., *Myrmecodipogon pannonicus*) and other spider wasps with different habitat requirements, were captured in coloured pan traps in wetlands in our studies

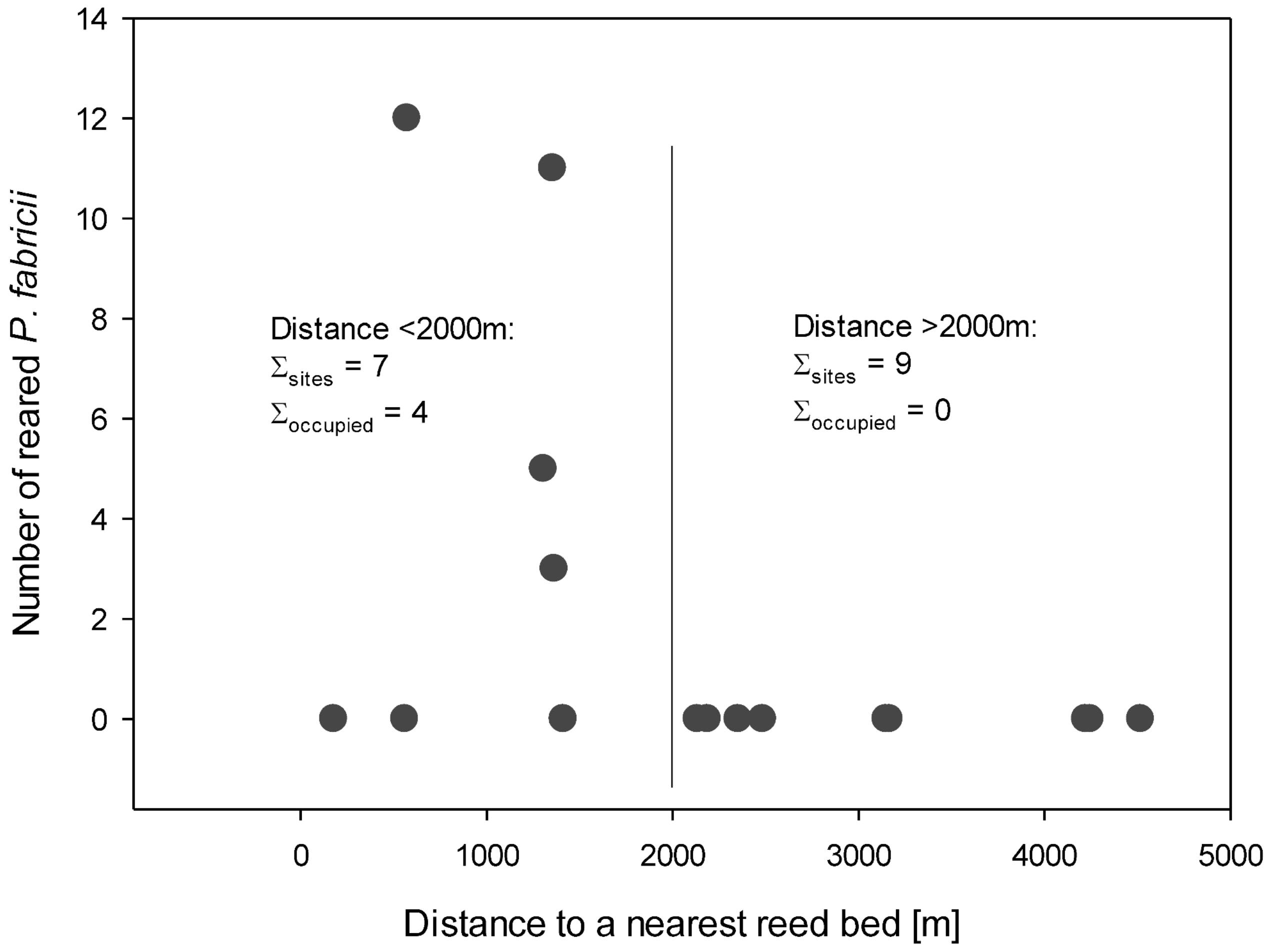

Fig. 1 Inverse relationship between the distance to the nearest reed bed and the number of reared *Pemphredon fabricii* surprisingly applies even at large distances, and we recorded nesting *P. fabricii* up to 1366 m from the nearest reed bed

(Bogusch et al. 2020). Many gall specialists are known among species collecting pollen and nectar (all non-parasitic bees) and hunting small prey (e.g., *P. fabricii* hunts aphids). For species of bees and wasps occurring in xerothermic habitats, reed galls are probably a strange cavity type that is problematic to get inside and so they prefer other cavity types, which are abundantly available at the respective sites. Species nesting sporadically in reed galls in wetlands (e.g., *H. leucomelana* or *S. bifasciatus*) have many other nesting possibilities in xerothermic habitats and may therefore consider reed galls as low-quality nesting resources.

In conclusion, the present study revealed reed galls are cavities that are not adopted for nesting by the generalist cavity adopters in habitats where other cavity types are abundant. We speculate that many bee and wasp species simply cannot get inside the gall and make their nests there or are unable to locate the opening. Nevertheless, reed galls are important for rare Red-Listed specialists that nest only, or mostly, in this cavity type (*Hylaeus pectoralis*, *Stenodynerus clypeopictus*, *Pseudoanthidium tenellum*), as well for other more common species that use both, reed galls and reed stalks, for their nesting (*P. fabricii*, *Trypoxylon deceptorium*, *Heriades rubicola* or *Hylaeus moricei*). These species of bees and wasps can profit from the fact that their preferred cavity type is useless for most of other species, i.e. is forming a specific niche. Well-applied conservation measures can help us to protect this specialized guild of insects. Similarly, wide spectra of cavity nesters from xerothermic habitats need to have the possibility to find dead wood, exposed stems and stalks, empty snail shells and other cavities in their habitats to survive (Fortel et al. 2016; Bogusch and Horák 2018; Westerfelt et al. 2018).

Fig. 2 Comparison of the nesting cavity and entrance of a reed stalk (left) and cigar gall (right)

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Declarations

Conflict of Interest The authors declare no conflicts of interest. The research did not involve humans and/or animals.

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