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Novel nesting of ants in bee cocoons in empty shells of terrestrial gastropods

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Summary. Several species of ants were reported to place their nests inside empty shells of larger terrestrial gastropods. The structure of their nests was never studied in detail. We recorded 14 species of ants nesting in empty shells of terrestrial gastropods in various habitats of the Czech Republic, of which especially small species of the genus *Temnothorax* were the most numerous. In steppic habitats, nests of *Temnothorax unifasciatus* were placed inside the cocoons of the shell-nesting solitary bee *Osmia bicolor* in several cases. This bee is a specialist for nesting inside empty shells and is locally common and numerous in steppic habitats in Central Europe. In two nests, remnants of a dead bee were found inside the cocoon, together with the colony of *T. unifasciatus.* The adult of *O. bicolor* probably died inside the nest and was partly eaten by the ants suggesting a scavenging behaviour. This finding is unique and interesting, brings new insight to the biology of ants and a challenge for further studies on ants nesting in empty shells of gastropods.

Résumé. Nidifications inédites de fourmis dans des cocons d'abeilles, dans des coquilles vides de gastéropodes terrestres. Plusieurs espèces de fourmis ont été signalées comme installant leurs nids dans des coquilles vides de gastéropodes terrestres de grande taille. La structure de leurs nids n'a jamais été étudiée en détail. Nous avons recensé 14 espèces de fourmis nichant dans des coquilles vides de gastéropodes terrestres dans divers habitats de République tchèque, parmi lesquelles les plus nombreuses étaient les petites espèces du genre *Temnothorax*. Dans les habitats steppiques, des nids de *Temnothorax unifasciatus* ont été placés à plusieurs reprises dans les cocons de l'abeille solitaire *Osmia bicolor*, nicheuse dans des coquilles. Cette abeille, spécialiste de la nidification dans des coquilles vides, est localement commune et abondante dans les habitats steppiques d'Europe centrale. Dans deux nids, les restes d'une abeille morte ont été retrouvés à l'intérieur du cocon, avec la colonie de *T. unifasciatus*. L'adulte d'*O. bicolor* est probablement mort à l'intérieur du nid et a été partiellement mangé par les fourmis, suggérant un comportement charognard. Cette découverte est unique et intéressante, elle apporte de nouvelles perspectives sur la biologie des fourmis et constitue une base pour de futures études sur les fourmis nichant dans des coquilles vides de gastéropodes.

Keywords: *Osmia bicolor*; *Helix pomatia*; *Caucasotachea vindobonensis*; *Temnothorax unifasciatus*; *Lasius alienus*; biology; colony

Empty shells of larger terrestrial gastropods are utilised by many groups of invertebrates as natural cavities, used for overwintering, pupation or nesting (Szinetár et al. 1998; Moreno-Rueda et al. 2008; Bogusch et al. 2019). Around 50 species of solitary bees and wasps place their nests exclusively into empty snail shells and several other species nest in empty gastropod shells occasionally (for review, see Müller et al. 2018). In Central Europe, four species of the genus *Osmia* Panzer, 1806 – *O. aurulenta* (Panzer, 1799), *O. bicolor* (Schrank, 1781), *O. rufohirta* Latreille, 1811 and *O. spinulosa* (Kirby, 1802) – place their nests only into empty gastropod shells and are relatively common in steppic habitats. They usually place their nests into the shells of larger common species of snails, such as *Caucasotachea vindobonensis* (C. Pfeiffer, 1828), *Helix pomatia* Linnaeus, 1758 and *Xerolenta obvia* (Menke, 1828), while the nesting behaviour of these bees differs among the species in the size of shell, nest structure, nesting habitat and nesting behaviour (Bellmann 1981; Müller 1994; Müller et al. 2018; Bogusch et al. 2019; Heneberg et al. 2020). All these bees are currently spreading because of the overgrowing of steppic habitats by shrubby vegetation and are responding to an increase in availability of empty shells in their nesting sites (Bogusch et al. 2020a).

Ants (Formicidae) are a cosmopolitan group of insects, typical by their eusocial life (Hölldobler & Wilson 1990). There are more than 15,000 species known worldwide (Schultheiss et al. 2022) with variable life strategies. They inhabit various habitat types and differ by their

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nest placing – from underground to tree crowns (Hölldobler & Wilson 1990). From the order Hymenoptera, ants (Formicidae) are the second most numerous group of shell-adopters behind the bees (Tluste & Birkhofer 2021); however, this topic remains understudied. Robla et al. (2025) in their current survey focused on myrmecophily of snails reported that use of empty shells for nesting is one of the four main interactions of ants and snails.

Only a few authors reported cases of nesting of single or several species of ants in empty gastropod shells (Headley 1943; Fokuhl et al. 2007; Bogusch et al. 2019; Tluste & Birkhofer 2021). Bogusch et al. (2019) in their comprehensive study on insects inhabiting empty snail shells reported nine species, of which *Temnothorax unifasciatus* (Latreille, 1798) was the most numerous. Most recorded species nested inside or fertilised queens overwintered in empty snail shells. However, the nesting biology of ants in empty snail shells was never studied in detail, maybe because most species usually create their nests in other types of cavities or semicavities and they probably utilise snail shells only occasionally (Bogusch et al. 2019; Tluste & Birkhofer 2021).

In this study, we are bringing an interesting report of nesting of two ant species in empty snail shells and their association with nests of the solitary bee *O. bicolor*. We also have reviewed our results of ants nesting in empty gastropod shells.

Materials and methods

Empty snail shells were collected in steppic habitats of the Czech Republic in one locality in České středohoří Protected Landscape Area (Raná National Nature Reserve, a steppic grassland on southern-oriented hill slope, GPS: 50.4080428°N, 13.7756464°E), and in one unprotected locality nearby (Patokryje, steppic grassland with shrubs on south-western oriented hill slope, GPS: 50.5085247°N, 13.7059350°E; 12 km far from the first locality) in March 2025. For the same research, empty shells were collected in other steppic regions in Czechia but ant nests were not investigated. At each locality, we collected as many empty shells of larger gastropods as were available – *H. pomatia*, *C. vindobonensis*, *X. obvia* and other species of similar size and structure. Because bee nests were usually placed inside the shell and invisible without extraction, we collected all unbroken shells available at the locality.

The collected shells were within 1–3 days transferred to the laboratory where they were cut using tweezers and their inner contents were studied. The research was focused on solitary bees nesting in empty shells so the methodologies followed Heneberg et al. (2020) and Bogusch et al. (2020b). Each shell with bee nest (cocoons) inside is described in Supplementary Table 1. We counted the number of bee cocoons inside, their positions, and identified the species. Then the cocoons were extracted, and bee brood identified by the first author. If bee adults were not inside the shell, we (1) let the larvae and pupae to finish their development to adults, or (2) identified the owner of the nest by the matters used for closing plugs and septa between brood cells, number and orientation of brood cells, and pollen remnants (methodology developed by the first author combining information from multiple studies and his own experience).

Because of finding many ant nests in shells, these ant nests were separately transferred into 100 ml plastic vials and each nest was separately studied. Only ant communities with the presence of the queen and/or ant brood were reported as ant colonies. If the shell contained both bee cocoons and ant individuals/brood, we studied the positions of ant queen and brood and the number of workers inside the nest.

Representative nests were put into the fridge and stored at a temperature of 5°C. Nest contents were photographed using the photographic microscope Keyence VHX-100 (Osaka, Japan). Ants were determined to the species level by the third author using Seifert (2018). Preferences of shells were tested using Fisher's exact test (Omni Calculator 2025).

Results

We collected 647 gastropod shells in two studied localities. Of these shells, 440 belonged to *Helix pomatia*, 176 to *Caucasotachea vindobonensis*, 25 to *Xerolenta obvia* and the remaining six to *Euomphalia strigella* (Draparnaud, 1801). We recorded 32 ant colonies inside the shells, with *Temnothorax unifasciatus* being more numerous (24 colonies) than *Lasius alienus* (Foerster, 1850) (eight colonies). Most colonies were in the shells of *H. pomatia* (17 of *T. unifasciatus* and seven of *L. alienus*); the rest were in *C. vindobonensis.* Testing of shell preferences using one-tailed Fisher's exact test did not show any differences between these two ant species ($p = 0.33$). Thus, both ant species probably do not prefer larger shells of *H. pomatia* (shell dimensions according to Nica et al. (2011) are: height 39 mm, diameter 34 mm, aperture size 25 mm) or smaller shells of *C. vindobonensis* (shell dimensions according to Kowalewska-Groszkowska et al. (2018) are height 18 mm, diameter 24 mm, aperture size 14 mm).

All shells with colonies of *L. alienus* were empty with no remnants of nests of solitary bees; the ants probably adopted empty shells or cleaned their inner contents. This species is bigger than *T. unifasciatus* and the cocoon of *O. bicornis* is probably too small for the colony. Five nests of *T. unifasciatus* (two in *H. pomatia* and three in *C. vindobonensis* shells) were placed inside bee cocoons (Figure 1A, B). In three nests, the cocoons were empty but it was not possible to recognise if these were cocoons from emerged bees or the bees died inside the cocoon and the ants ate their bodies or remnants. In the two other nests, we recognised remnants of dead females of *O. bicolor.* These remnants represented about a half of the bee body (head and most of mesosoma), which was not influenced by weather and time, but certainly partly eaten by the ants.

During our studies on insects in empty shells from the years 2016–2017, we recorded in winter time 50 ant nests

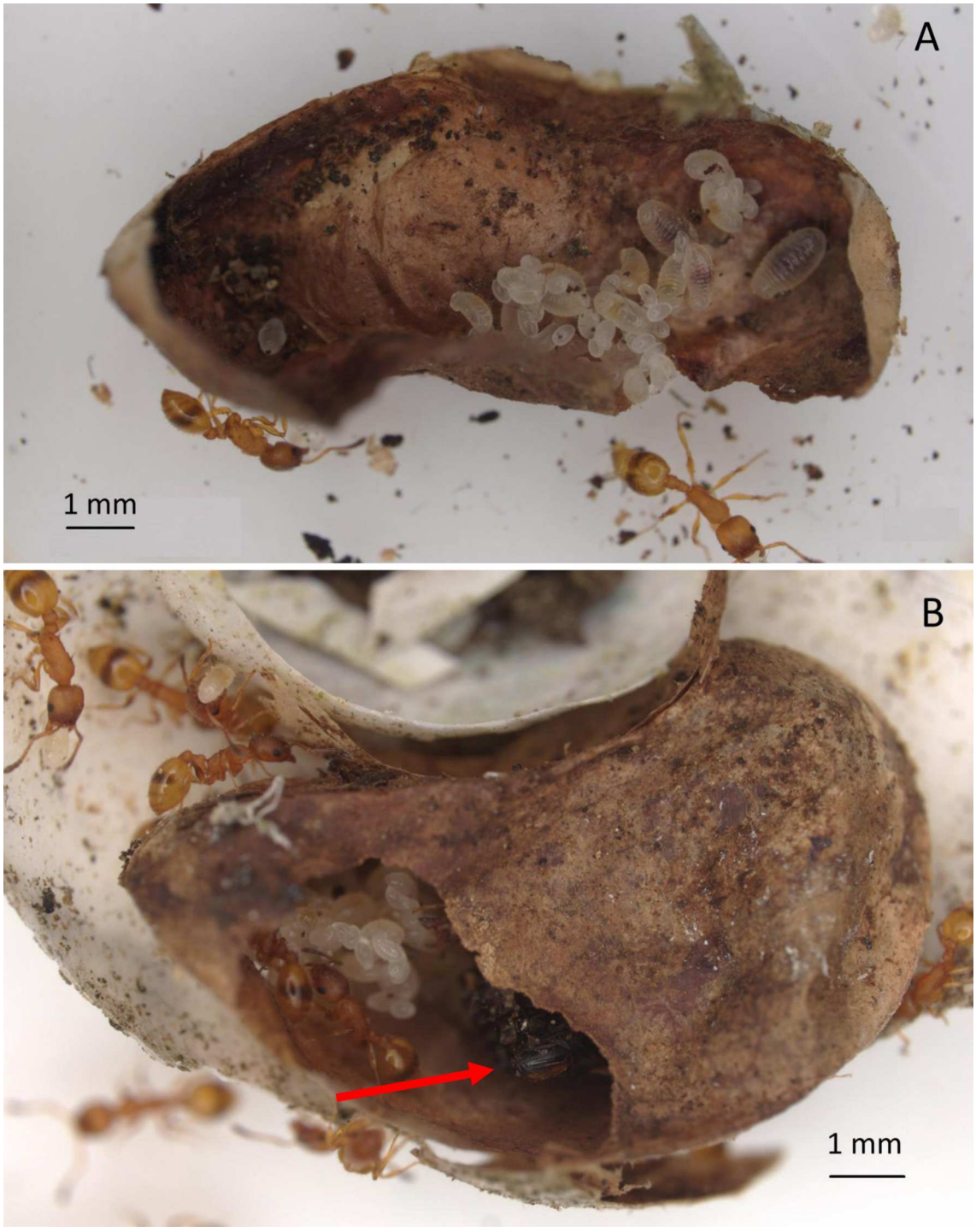

Figure 1. **A**, Empty cocoon of *Osmia bicornis* with adults and brood of *Temnothorax unifasciatus.* **B**, Shell of *Caucasotachea vindobonensis* with nest of *Temnothorax unifasciatus* in the cocoon of *Osmia bicolor.* Remnants of the head of the bee are visible (red arrow). Author Petr Bogusch.

in empty shells in 30 localities in Czechia. Of these nests, 23 were of *Temnothorax crassispinus* (Karavajev, 1926), 11 of *T. unifasciatus*, five of *T. parvulus* (Schenck, 1852), two of *Lasius alienus*, *Myrmica ruginodis* Nylander, 1846, *M. sabuleti* Meinert, 1861 and *Temnothorax nigriceps* (Mayr, 1855), and one nest each of *Lasius psammophilus* Seifert, 1992, *Tapinoma erraticum* (Latreille, 1798) and *Temnothorax tuberum* (Fabricius, 1775). The numbers of individuals differed from those with only one individual (usually the queen) to 635 individuals of

T. unifasciatus (probably complete nesting colony) in the shell of *H. pomatia.* Whole colonies of *T. unifasciatus* were recorded in all 11 shells, with 93–635 individuals in one colony, mean 244 ± 154 individuals, median 222. Very similar numbers of individuals were recorded in shells with *T. crassispinus* with 5–493 individuals in one colony, mean 188 ± 146 individuals, median 212. Small species of *Temnothorax* thus belong to the most numerous ants nesting in empty gastropod shells with lower hundreds of individuals per shell.

Beside this systematic winter research, the search in our database of ant findings provided additional 24 records of ants in shells from 12 localities in the period 2007–2014: 12 of *T. crassispinus*, three of *T. parvulus*, two of *M. ruginodis*, one of *L. alienus*, *Lasius niger* (Linnaeus, 1758), *Myrmica rubra* (Linnaeus, 1758), *Myrmecina graminicola* (Latreille, 1802), *Plagiolepis taurica Santschi*, 1920, *T. nigriceps*, and *T. tuberum*. These ants occupied in seven cases shells of *H. pomatia*, five of *Cepaea hortensis* (O. F. Müller, 1774), three of *C. vindobonensis*, two of *Fruticicola fruticum* (O. F. Müller, 1774) and one of *Cepaea nemoralis* (Linnaeus, 1758), *E. strigella*, *Helicigona lapicida* (Linnaeus, 1758) and *X. obvia*. Ants with larger body (genera *Lasius*, *Myrmica*) tend to occupy larger shells: only one queen of *M. ruginodis* was found in *C. hortensis* shell, four other records of *Myrmica* and *Lasius* were from shells of *H. pomatia*. Ants utilise shells not only in dry steppic localities, but also in forest habitats. The species list of ants recorded in empty gastropod shells with numbers of their findings is included in Table 1.

Discussion

Finding of ant colonies inside bee cocoons is novel and very interesting, showing that ants not only utilise empty gastropod shells for their nesting, which is known from the literature (Bogusch et al. 2019; Tluste & Birkhofer 2021). We first reported that remnants of nests of bees can serve for ants as a brood chamber and dead bees or their brood as a food. It is interesting that this behaviour was recorded only in the case of the smaller *T. unifasciatus*. Ants of this genus are well known to utilise very small cavities for their whole nest, as various types of galls (Bogusch et al. 2016; Giannetti et al. 2019, 2022) or snail shells (Bogusch et al. 2019). They also do not search for their prey over larger distances than 1–2 m (Bengston & Dornhaus 2013) so the presence of bee remnants in the shell is possibly advantageous for them.

We cannot answer the question if small *Temnothorax* species kill bee brood or emerged bees waiting in their cocoons. We have only the experience that the proportion of bees unable to finalise their metamorphosis and dying inside their nests in empty shells is very high (in the two studied localities it is 67 of 221 bees, 30%). Our current study confirmed that many nests of bees inside empty gastropod shells contained dead individuals of bees – mostly the adults. Several were adults reared one or more years ago and then destroyed by parasitic mites, fungi or other organisms, but many individuals were fresh adults that finalised their metamorphosis and died inside their nests. Heneberg et al. (2015) reported quite a high mortality of *Pemphredon fabricii* (M. Müller, 1911) in reed galls. Many pathogens are connected with other bee species, including the honeybee (Gillian & Prest 1987); other bees have also their specific parasitic mites, e. g. *Chaetodactylus osmiae* (Dufour, 1839) in nests of mason bees (Van Asselt 2009). Because managed mason bees *Osmia bicornis* (Linnaeus, 1758) and *Osmia cornuta* (Latreille, 1805) are closely phylogenetically related to the bees nesting in empty gastropod shells, it is likely that the same or similar pathogens and parasites can also affect their nests. From our first research on bees nesting in empty gastropod shells (Bogusch et al. 2019), we have collected brood affected by pathogens but the research is not finished and published. However, several different types of infection (caused probably by different species of pathogens) were observed and can be one of the most frequent reasons of death of bee larvae. In our field observations, the proportion of infected brood is higher in more humid habitats, but the sample is too small to be statistically tested.

Three of most common bees nesting in empty shells (*O. aurulenta*, *O. bicolor* and *O. rufohirta*) create their nests in spring (April to June), their brood finalises the metamorphosis in summer and fresh adults overwinter in the nests and wait to the spring of the next season to abandon the shell (Bellmann 1981; Westrich 2018). This means the adults spend 6–9 months inside the shell, which can influence their vitality. Moreover, Bogusch et al. (2019) reared the insects from the shells without extraction of their inner contents and recorded 196 bees from 27,650 shells (which means one bee in every 141 shells). In our current research with opening shells and extracting their inner contents, we recorded 621 nests in 5656 shells (a nest in every ninth shell). Our current research is certainly methodically influenced by our better experience: we chose localities previously rich in bee nests and focused on larger shells that are more often utilised by nesting bees.

Ants very often interact with bees. Robbing of provisions in honeybee hives (Seeley 1982; Landa & Wallis 1988), nests of stingless bees (Lehmberg et al. 2008) or bumblebee nests (Spangler 1970) by ants is well known and was repeatedly published. Ants often rob pollen and other provisions from nests of cavity nesting bees and wasps, especially in insect hotels (Harris et al. 2021) and certainly in nests of bees and wasps placed underground. However, the interaction between ants and nesting bees is understudied and hopefully new studies in connection with modern insect hotels will be soon published.

Table 1. Species of ants reported nesting in empty gastropod shells.

Species name	Number of nests
Temnothorax crassispinus	35
Temnothorax unifasciatus	35
Lasius alienus	11
Temnothorax parvulus	8
Myrmica ruginodis	4
Temnothorax nigriceps	3
Myrmica sabuleti	2
Temnothorax tuberum	2
Lasius niger	1
Lasius psammophilus	1
Myrmecina graminicola	1
Myrmica rubra	1
Plagiolepis taurica	1
Tapinoma erraticum	1

Ants are certainly a group of invertebrates which frequently utilise empty gastropod shells for nesting. Several smaller species (*T. unifasciatus*) probably prefer empty shells before other cavity types. Bogusch et al. (2019) and Heneberg et al. (2020) reported that shell occupation by nesting bees decreases with number of shells available at the locality – there are many localities, where the number of empty shells available for nesting is much higher than can be utilised by nesting bees. Thus, some competition between ants and bees can be real only in localities, where number of shells available for nesting is very small. In our study, 647 shells included 32 colonies of ants but 104 nests of bees and wasps. Similar situation was observed in reed galls (Bogusch et al. 2016), oak galls, termite mound (de Bruyn & Conacher 1990; Tuma et al. 2020), beetle galleries (Satoh et al. 2016) or other types of cavities used by nesting bees and wasps and also by ants.

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Supplemental data

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