

The suitability of artificial nests as nesting sites for cavity-nesting wasps and bees (Hymenoptera, Aculeata)

Reima Leinonen^{1,2,*}, Juho Paukkunen³, Henri Vanhanen⁴,
Jarmo K. Holopainen², Jaakko Pohjoismäki⁵ & Jouni Sorvari⁶

¹⁾ Kainuu Centre for Economic Development, Transport and the Environment, Kalliokatu 4, FI-87100 Kajaani, Finland (*corresponding author's e-mail: reima.leinonen@ely-keskus.fi)

²⁾ Department of Environmental and Biological Sciences, University of Eastern Finland, Yliopistonranta 1, FI-70210 Kuopio, Finland

³⁾ Finnish Museum of Natural History, Zoology Unit, P.O. Box 17, FI-00014 University of Helsinki, Finland

⁴⁾ Natural Resources Institute Finland, Yliopistonkatu 6, FI-80100 Joensuu, Finland

⁵⁾ Department of Environmental and Biological Sciences, University of Eastern Finland, Yliopistonkatu 7, FI-80100 Joensuu, Finland

⁶⁾ Natural Resources Institute Finland, Latokartanonkaari 9, FI-00790 Helsinki, Finland

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Populations of several cavity-nesting aculeate wasps and bees have been in decline due to a shortage of nesting sites and changes in agricultural landscapes. We tested the suitability of various natural and non-natural materials as nesting sites for aculeate wasps and bees in Finland. According to our results, natural materials such as reed and cow parsley stems and birch wood with holes, were more suitable for artificial nests than plastic straws. We developed a new type of nest containing natural stems and a wooden cube with drilled holes of various diameters. To compensate for the shortage of nesting sites, artificial nests made of natural materials can be used to provide breeding environments for several species of cavity-nesting aculeate wasps and bees native to the boreal zone. When artificial nests are used for research purposes ('trap nests'), insects should be allowed to hibernate in the artificial nests under natural conditions instead of being frozen.

Introduction

The Hymenoptera order is one of the most species-rich in the world, accounting for up to eight percent of all known organisms (Aguilar *et al.* 2013). Many aculeate species (Hymenoptera: Aculeata) pollinate wild and domestic plants, significantly increasing the yield of many fruits, berries and other crops (Klein *et al.* 2007,

Jones *et al.* 2014, Potts *et al.* 2016). In recent decades, populations of pollinating insects have been monitored with concern because they have decreased and even collapsed at a global level. Suggested reasons for this decline include the chemicalisation of the environment, changes in land use, and a lack of nesting sites and habitat fragmentation (Potts *et al.* 2010, Goulson *et al.* 2015, Artz & Pitts-Singer 2015). Rare ecologi-

cally specialised species are particularly susceptible to population decline (Powney et al. 2019).

In Finland, the most important pollinator groups are bees, bumblebees, parasitic bumblebees and wasps, as well as hoverflies (Diptera: Syrphidae). Of the 7904 currently known Hymenoptera species in Finland, the sawflies (Symphyta) and aculeates (Aculeata) are the best known (Paukkunen 2025). The structural change in Finnish agriculture has been significant in recent decades (Vainio et al. 2001, Paukkunen et al. 2019), and this has clearly impacted the populations of pollinating insects (Teräs 1996). As natural habitats with abundant flowers decrease, substitute habitats such as roadsides, airports, wasteland areas and gravel pits have become important oases for many aculeate wasps and bees (Söderman & Leinonen 2003, Hopwood 2008). It is now recommended that flower strips be planted in uncultivated areas and in the middle of intensively cultivated areas (Benelli et al. 2015). Artificial nests can be used in urban environments to alleviate the shortage of nesting sites for wild pollinators (Gordon et al. 2009, von Königslöw et al. 2019, Prendergast 2023). This can strengthen populations of pollinating insects and is one means of protecting endangered aculeates (Pereira-Peixoto et al. 2014, MacIvor & Packer 2015).

Social bees and wasps build their own nests, which consist of multiple cells, usually in cavities in soil, trees or buildings. In contrast, solitary bees and wasps use available holes and hollow plant stems for nesting (Michener 2000). Some pollinating insects nest in the ground. Around 15% of bees nest in above-ground holes (Michener 2000). Of the 691 aculeate species found in Finland (Paukkunen 2025), 203 mainly use above-ground cavities as their nesting sites. These include certain bee families (e.g. Halictidae and Megachilidae), wasp families (e.g. Vespidae), digger wasp families (e.g. Crabronidae), cuckoo wasp families (Chrysididae), spider wasp families (Pompilidae) and club-horned wasp families (Sapygidae) (Söderman & Leinonen 2003). One hundred and fifty Finnish species that nest in above-ground holes build their nests in decaying wood or ready-made holes created by wood-boring beetle larvae in harder wood, as well as in natural stems (Söder-

man & Leinonen 2003); the rest are nest parasites (Teräs & Leinonen 2010). In addition to kleptoparasites, around 70 species of parasitic wasps and flies associated with aculeates are known. However, the exact number remains unknown due to a lack of information about their lifestyles. The presence of these wasps and flies is entirely dependent on the abundance of their hosts (Ebeling et al. 2012).

Several species of cavity-nesting aculeates, particularly the genera *Osmia*, *Megachile* and *Hylaeus*, pollinate a variety of flowering plants, including edible berries (Pekkarinen & Teräs 1998, Biesmeijer et al. 2006). The presence of a continuum of decaying wood is important for hole-nesting bees, as it increases the number of species and individuals in a given habitat (Tscharntke et al. 1998, Loyola & Martins 2009). Various aculeates use natural tree holes, hollow plant stems (e.g. reeds) and wooden structures (e.g. beetle-damaged logs and drilled logs) as nesting sites (Valkeila 1955, Cane et al. 2007, Loukola et al. 2020). These nesting sites can be supplemented or replaced with various types of artificial nests (Krombein 1967, MacIvor 2017, Khan et al. 2024). Such artificial nests can also be used to monitor trophic interactions in a changing environment (Staab et al. 2018).

The selection of nesting materials affects the attractiveness and nesting success of solitary aculeates. Krombein (1967) stated that nesting materials for artificial nests should be natural, as moisture problems often occur in plastic nests. In nature, habitat heterogeneity enables the co-occurrence of multiple species (Pianka 1966). Therefore, artificial nests containing a wide variety of nesting materials and hole sizes could attract a wider variety of aculeates.

The aim of this study was twofold: first, to evaluate suitable materials for artificial nests; and second, to explore the utilisation of artificial nests by Finnish Hymenoptera species as trap nests. We first tested whether natural materials were preferred to plastic straws by comparing artificial plastic straws with natural materials: hollow cow parsley and reed and raspberry stems (*Anthriscus sylvestris*, *Phragmites australis* and *Rubus idaeus*, respectively). Second, we tested whether artificial nests with heterogeneous hole sizes and nesting materials were more

attractive than artificial nests made from a single material. This was tested by comparing 1) more homogeneous-sized reeds with heterogeneous-sized cow parsley, 2) birch log nests with differently sized drilled holes, and 3) single-material nests with multiple-material nests.

Material and methods

Trap nests and sampling design

This study tested the suitability of different artificial nesting materials for cavity-nesting aculeates. Both artificial and natural materials were used. The research material was collected from several locations in Finland (Fig. 1 and Appendix 1) in 2001, 2002 and 2010 using various types of artificial nests (Fig. 2 and Table 1). All straws, stems and drilled holes used in the nests were 12 cm long, in line with recommendations from previous studies (Müller *et al.* 1997). The Hymenoptera nomenclature follows Paukkunen (2025).

Natural stem vs. plastic straw nests

In 2001, six different types of artificial nests were placed at ten sites (Appendix 1). Nine of these sites represented rural landscapes, while one (site 5) was an old forest that had been cut down, with dead and fallen aspens left in place (Appendix 1). Before the willows (*Salix* spp.) flowered in May, we installed a total of six artificial nests at each site on narrow tree trunks or thick bush stems at the height of 1 to 1.5 m. This ensured that the tubes' openings faced the morning sun (Budriene *et al.* 2004, Staab *et al.* 2018). We constructed the artificial nests using paraffin-coated cardboard milk cartons to protect them from birds, small rodents and rain, and placed various tubes inside them. Three of the nests contained tubes made from natural materials: one contained reed straws from common reed (*Phragmites australis*, diameter 2–4 mm, approximately 210 tubes per nest); one contained soft-core raspberry stems (*Rubus idaeus*, diameter 4–8 mm, approximately 60 tubes per nest); and one contained cow parsley stems (*Anthriscus sylvestris*, diameter 6–12 mm, approximately 35 tubes per nest) (Fig. 2). The

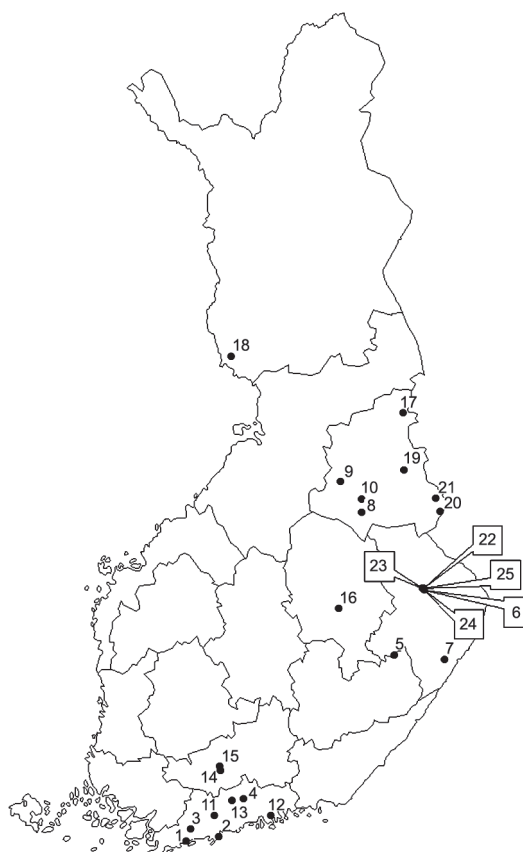


Fig. 1. The study sites in Finland in 2001 (numbers 1–10), the natural stem nests in 2002 (5, 7 and 11–18), the birch block nests in 2002 (8–10 and 19–21), and the combination nests and nest blocks in 2010 (7 and 22–25).

tubes in the other three artificial nests were plastic: one contained small straws (diameter 2.5 mm, approximately 460 tubes per nest), one contained medium-sized straws (diameter 4 mm, approximately 150 tubes per nest), and one contained large straws (diameter 5 mm, approximately 135 tubes per nest) (Fig. 2).

At the beginning of September, when the pollinators were already overwintering, we removed the artificial nests from the field and inspected them visually. During this inspection, we only counted 'plugged' tubes, i.e. those that were completely built and had a visible plug of clay or other material. Nests that were only partially built were not included in this count.

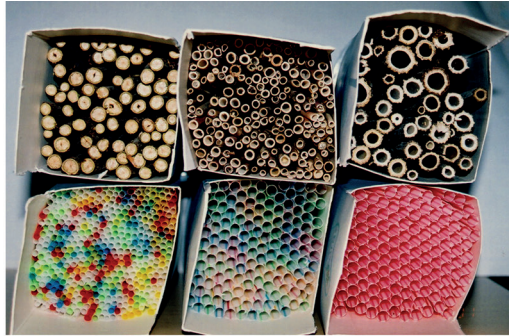
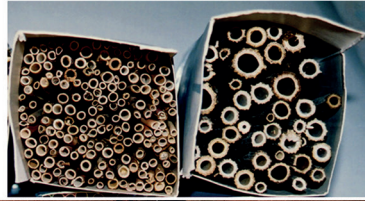
2001**Natural vs. plastic****2002****Reed vs. cow parsley****Birch logs****4 mm vs. 6 mm holes****2010****Combination vs. nest blocks**

Fig. 2. Trap nest types and comparison pairs used in the three study seasons. 2001: natural stems (top row, left to right: raspberry, reed and cow parsley) and plastic straws (bottom row, left to right: 2.5 mm, 4 mm and 5 mm in diameter). 2002: reed and cow parsley stems, and birch logs with 4 mm and 6 mm holes. 2010: newly developed combination nests with stem and birch log modules, and nest blocks.

After counting the number of plugged tubes, we placed the artificial nests in a freezer at -10 to -18 °C for two to three weeks. We then brought the artificial nests to room temperature in gauze bags. We kept a hatching diary and recorded all hatched individuals, including parasites, for identification purposes. Finally, after three months with no further hatching, we cut open the stems and examined and recorded the contents of nests containing immature stages under a stereo microscope.

Reed vs. cow parsley stem nests

In the second year of developing the method (2002), we placed straw nests made from reed and cow parsley (Fig. 2) at ten sites (Appendix 1). The reed straws had a diameter of 2–4 mm (approx. 210 tubes per nest) and the cow parsley straws had a diameter of 6–12 mm (approx. 35 tubes per nest). The trap nests were otherwise the same as last year, but we only used natural stems. At each site, three artificial

nests contained reeds and three cow parsley. Two of the sites were excluded from the analysis because the artificial nests had been destroyed by birds. The artificial nests were set out in May and removed in September for visual inspection.

Before transferring the artificial nests to cold outdoor storage for winter, we counted the number of plugged tubes. At the end of March, we brought the artificial nests inside to room temperature and preserved the hatched individuals for identification. In June, we cut open the stems and examined the nests containing any undeveloped stages under a microscope. Results were pooled by site to compare cow parsley and reed nests (three each).

Birch log nests with different hole diameters

In 2002, we made trap nests from drilled birch logs (Fig. 2) and placed them in pairs at six sites across the Kainuu region (Fig. 1, Appendix 1). Birch was used instead of conifer because our previous experience had shown that solitary bees and wasps prefer birch over conifers. Each site contained a log with drilled holes 4 mm in diameter spiralling outwards from the centre at 2 cm intervals (61 holes in total), and a log with drilled holes 6 mm in diameter arranged similarly at 5 cm intervals (14 holes in total).

In May, we placed the birch logs on the trees at the height of about 1 m, facing the morning

sun horizontally, and removed them from the field at the same time as the stem nests. The birch logs were kept in gauze bags in outdoor storage over winter and brought to room temperature alongside the stem nests. We recorded and identified the hatching individuals. After all the aculeates had hatched, we examined some nests with immature stages.

Combination nests vs. nest blocks

In 2010, we used combination nests and nest blocks (Fig. 2). Two nests of each type were placed at five sites in the clearings and meadows of the former slash-and-burn forests of Koli National Park (*see* Vainio *et al.* 2001 for habitat data and Appendix 1 for sites).

The nest blocks were comprised of birch wood laths with one hole per lath. The first nest block comprised four laths with 4 mm holes and four laths with 6 mm holes, and the other four laths with 8 mm holes and four laths with 10 mm holes. The combination nests included a birch log with 42 drilled holes measuring 4–8 mm in diameter and 160 stems (reed and cow parsley) measuring 4–10 mm in diameter. The nest blocks and combination nests were in the field from the end of May to the beginning of September. We conducted a visual inspection of the artificial nests immediately after retrieving them from the field. We placed the nests in gauze bags

Table 1. Nest characteristics and nesting percentages of tubes and drilled holes in the trap nests used in this study. Nesting % refers to the percentage of plugged tubes or holes.

Nest type	Year	Material	Holes per nest	Hole diameter (mm)	Nesting %
Plastic tubes	2001	plastic small	460	2.5	0.3
Plastic tubes	2001	plastic medium	150	4	0.13
Plastic tubes	2001	plastic large	135	5	3.4
Raspberry stems	2001	raspberry	60	4–8	2.6
Reeds	2001	reed	210	2–4	1.8
Cow parsley	2001	cow parsley	35	6–12	3.4
Reeds	2002	reeds	210	2–4	8.5
Cow parsley	2002	cow parsley	35	6–12	13.9
Birch log 4 mm	2002	birch wood	61	4	7.4
Birch log 6 mm	2002	birch wood	14	6	27.4
Nest block	2010	birch wood	8	4–10	28.8
Combination nest	2010	reed/cow parsley	160	4–10	14.1*
Combination nest	2010	birch wood	42	4–8	14.1*

*Nesting percentage for combination nests is the combined percentage of the tubes and holes.

and put the laths from the nest block in separate gauze bags. We also counted the number of empty nest blocks. The combination nests and nest blocks overwintered in outdoor storage and were taken to hatch at room temperature at the end of February. The results for the combination nests and nest blocks were combined for each site.

Statistical methods

Statistical analyses were carried out using SPSS Statistics version 30 software (IBM Corp.). Due to the low number of replicates and non-normally distributed variables, like the numbers of individuals and species and proportions ranging between zero and one, we used distribution-free nonparametric tests. The related-samples Wilcoxon test was used for paired analyses and pairs of treatments (Conover 1980). We calculated effect size as Cohen's d using means and standard deviations (SD) of paired differences (Cohen 1988).

Due to the different sample sizes, we used rarefaction (e.g. Hurlbert 1971, Gotelli & Colwell 2001) to compare the number of taxa between nest types. The smaller sample size was scaled to correspond with the larger one. The effectiveness of different methods or materials was evaluated using the 95% confidence limit of the sample with the higher taxon number. The position of the species accumulation curve of the smaller sample outside the confidence limits indicates a difference. Rarefactions were performed using formulas from Colwell *et al.* (2004, 2012) and Chao *et al.* (2014). Rarefaction curves with 95% confidence intervals were produced using EstimateS software (version 9.1.0; Colwell 2013).

Results

Natural stem vs. plastic straw nests

In 2001, overwintering the nests in the freezer for a few weeks was unsuccessful, with only a few individuals hatching (*see also* Budrys *et al.* 2010). When the stems and plastic straws were

opened, some of the aculeates could be identified to species level. In total, 309 individuals belonging to nine species were observed (Appendix 2). These included 201 bee specimens representing two species, 73 specimens of three solitary wasp species, 31 specimens of three crabronid wasp species and four specimens of a single parasitic wasp species. The most abundant species were the leafcutter bee *Megachile lapponica* (Megachilidae) and the solitary wasp *Symmorphus bifasciatus* (Vespidae).

Due to failed overwintering, some of the specimens could only be identified to genus level, and some could not be identified at all. Additionally, it was not possible to precisely count the specimens in some of the plastic straws because nesting failed due to moisture. Statistical testing was not conducted due to limited data.

The proportions of plugged tubes were compared between natural and artificial materials because the number of tubes in the different materials varied. Since the smallest plastic straws might have been too small for the nesting species, the proportion of plugged tubes was also compared using corrected data from which the proportion of the smallest plastic straws had been removed. The percentage of plugged tubes was higher in natural materials than in plastic straws. However, when the small plastic straws were removed from the analysis, this difference no longer existed in the corrected data (all stems and plastic straws: $n = 10$, $Z = -2.191$, $p = 0.028$, $d = 0.78$; corrected: $n = 10$, $Z = -0.663$, $p = 0.508$, $d = 0.29$; Fig. 3).

Reed vs. cow parsley stem nests

In 2002, a total of 1000 specimens belonging to 42 species were observed in stems and birch log nests (Appendix 2). Of these, 178 belonged to four bee species, 391 to six species of solitary wasps, 74 to six species of kleptoparasites and 71 to 12 species of parasites. A total of 584 specimens belonging to 29 species hatched from reed nests, while 267 specimens belonging to 16 species hatched from cow parsley nests. Forty-eight specimens belonging to four species hatched from small-holed (4 mm) birch

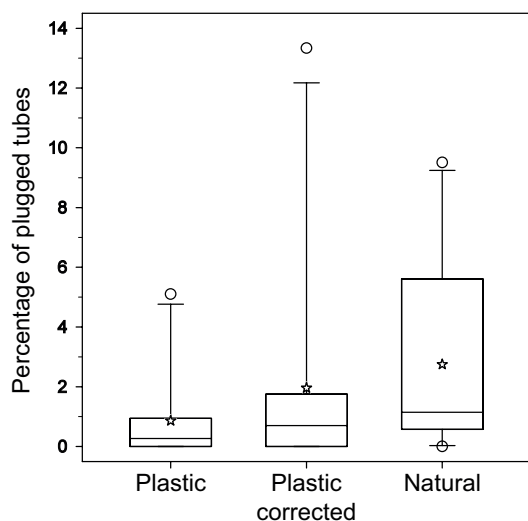


Fig. 3. Percentages of plugged plastic and natural tubes ($n = 10$), with and without the smallest straws (plastic corrected). The star indicates the mean value, and the circles show values that fell outside 90% of the data.

logs and 101 specimens belonging to 16 species hatched from large-holed (6 mm) birch logs. The most abundant species found in the straws were the leaf-cutting bee *Megachile lapponica*, the solitary wasp *Symmorphus bifasciatus*, the nest parasite *Chrysis angustula* (Hymenoptera: Chrysididae) and the parasitic wasp *Ephialtes* sp. (Ichneumonidae). The most abundant species in birch logs were the Pemphredonid wasp *Pemphredon lugens*, the Crabronid wasp *Rhopalum clavipes* and the inquiline parasitoid *Gasteruption assectator* (Hymenoptera: Gasteruptiidae). One vulnerable species, the nest parasite *Chrysis ignita*, was found in both the stems and the birch logs. In 2002, the peak of hatching in the birch logs and stem nests occurred approximately one month after they were brought inside. We observed the last hatchings two months later.

The number of specimens in the nests did not differ significantly between the reed and cow parsley stems ($n = 8$, $Z = 1.262$, $p = 0.207$, $d = 0.72$). When we analysed the numbers of host and parasite specimens separately, there was no significant difference between reed and cow parsley stems ($n = 8$, hosts: $Z = 1.540$, $p = 0.123$, $d = 0.70$; parasites: $Z = 1.363$, $p = 0.173$, $d = 0.76$). The number of all species and host species was higher in reed stems than

in cow parsley stems, but the differences were only marginally significant ($n = 8$, all species: $Z = 1.761$, $p = 0.078$, $d = 0.94$; host species: $Z = 1.913$, $p = 0.056$, $d = 0.92$; Figs. 4A and B). The number of parasite species was similar in reed and cow parsley stems ($n = 8$, $Z = 0.921$, $p = 0.357$, $d = 0.70$). The proportion of plugged tubes was also similar between the two types of stems ($n = 8$, $Z = 1.352$, $p = 0.176$, $d = 0.38$).

One possible source of error was that the diameters of the reeds and the cow parsley stems were different, resulting in a greater number of reed stems per nest, potentially increasing specimen numbers. Therefore, we compared rarefied species numbers between reed and cow parsley stems. The rarefied species curve for cow parsley remained below the lower 95% confidence interval of the reed curve (Fig. 4C), indicating that cow parsley was slightly less attractive for nesting.

Birch log nests with different hole diameters

Birch logs with 6 mm holes had a significantly higher proportion of plugged holes and a higher number of species than those with 4 mm holes. However, the difference in species richness was marginally non-significant ($n = 6$; proportion of plugged holes: $Z = -2.032$, $p = 0.042$, $d = 1.46$; number of species: $Z = -1.826$, $p = 0.068$, $d = 0.77$; Fig. 5). The number of specimens did not differ between birch logs with 4 mm and 6 mm holes ($n = 6$, $Z = -1.095$, $p = 0.273$, $d = 0.51$).

Combination nests vs. nest block

In 2010, we monitored aculeate wasps and bees in Koli National Park using two combination nests and two nest blocks at five sites. In total, 582 specimens belonging to 16 species were recorded in the 10 combination nests (made of birch wood and natural stems) and 10 nest blocks. Of these, two specimens represented one species of bees, 259 specimens four species of solitary wasps, 228 specimens five species of crabronid wasps, 18 specimens three species of kleptoparasites and 75 specimens three

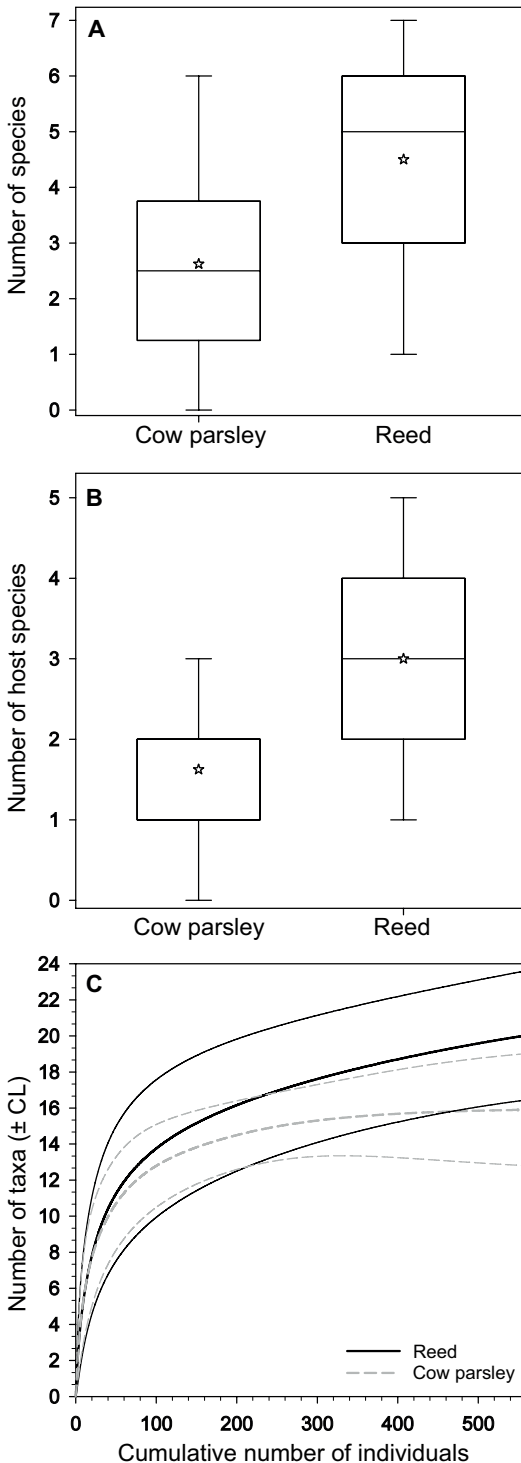


Fig. 4. Numbers of species (**A**) and host species (**B**) in cow parsley and reed stems ($n = 8$). Stars indicate the mean values. — **C**: Rarefaction of the species accumulation curves for reed and cow parsley stems with 95% confidence intervals.

species of parasites (Appendix 2). A total of 50 specimens belonging to six species were found in nest blocks. The most abundant species were the solitary wasp *Ancistrocerus trifasciatus* in nest blocks, and the solitary wasp *Symmorphus bifasciatus* and the crabronid wasp *Passaloecus eremita* in combination nests. One near-threatened crabronid wasp species, *Psenulus pallipes*, occurred in nest blocks. Results were pooled by site to compare combination nests with nest blocks.

Combination nests had significantly higher numbers of species and specimens than nest blocks ($n = 5$; specimens: $Z = -2.023$, $p = 0.043$, $d = 1.72$; species: $Z = -2.023$, $p = 0.043$, $d = 1.60$; Figs. 6A and B). However, the proportion of plugged tubes did not differ between nest types ($Z = -1.483$, $p = 0.138$, $d = 0.84$; $n = 5$). As there were more specimens in combination nests than in nest blocks, we compared species richness using rarefied species numbers. The rarefied species curve for nest blocks remained below the lower 95% confidence interval of the combination nest curve, indicating that combination nests provided a more attractive nesting habitat for a wider range of species (Fig. 6C).

Discussion

Natural straws are better than plastic straws

When developing the methods, we compared plastic straws of three different sizes, as well as cow parsley, reed and raspberry stems at altogether ten sites. Nest counts were successful for plastic straws, even though some of the nest cells were at the back of the straws and lacked protective plugs. In the case of natural stems, examining nest cells without plugs was not possible, so only tubes with end plugs were counted. We observed collapsed back walls and incomplete nests in some plastic straws, leading us to conclude that nesting had failed due to moisture in the material (*see also* Krombein 1967).

Leafcutter bees (*Megachile* spp.) could also nest in large plastic straws; however, the comb cells were partially moulded due to humidity. Reed stems were the most popular for nest-

ing, with nests observed at two sites. In 2001, the willow mason-wasp (*Symmorphus bifasciatus* Linnaeus, 1761), a solitary wasp species, only nested in reed stems. All nesting materials were used for nesting by aculeate species, but soft-core raspberry stems were less popular for nesting. At site 5 (Muhamäki), no nests occurred within the raspberry stems, but leafcutter bees nested in the spaces between the stems. Nests were occupied at a high rate in clear-cut forests, and previous studies have also observed a variety of pollinator species visiting flowers in logging areas (Korpela *et al.* 2014).

Artificial plastic materials are not ideal for aculeates that nest in tubes because moisture tends to accumulate inside them, causing the nest cell partitions to collapse. Aculeates may therefore abandon plastic tubes and select natural materials, where the nest structure collects less moisture. Likewise, although not experimentally confirmed, resinous woods such as pine can lead to moisture retention and fungal growth. Thus, breathable hardwoods such as birch are less prone to mould.

Stems and birch wood logs

Due to their performance, we only compared two natural materials, cow parsley and reed, as these are also used as nesting sites in nature (Merisuo 1943, 1973). Of these two materials, reed appeared to be more suitable for nesting, possibly due to its size, which suits most species. However, holes of different sizes attract a wider range of species that nest in similar-sized holes and stems in nature. Therefore, stems and holes of different sizes, for example made from reed and cow parsley, should be offered.

Birch logs with 4 mm and 6 mm drilled holes were readily used for nesting. The 6 mm holes, that were spaced more widely, were clearly the most popular and attracted more species. Nest cells were also present deeper inside the holes, where no entrance plug was visible. In nature and in the wooden walls of log buildings, the potential density of nests is largely determined by the density of beetle-made holes.

We also used birch wood cubes with drilled holes of 4 mm, 6 mm, 8 mm and 10 mm, com-

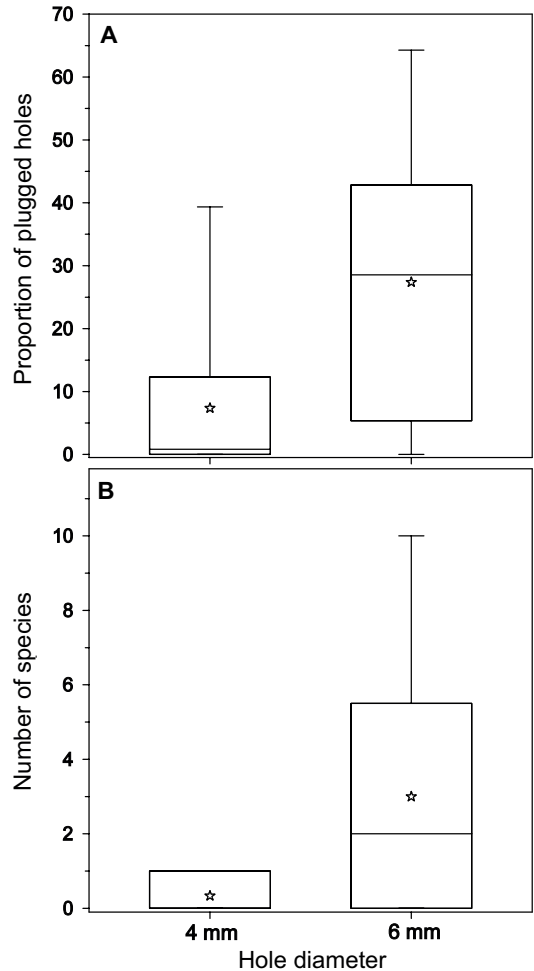


Fig. 5. Proportion of plugged holes (**A**) and the number of species (**B**) in birch logs with 4 mm and 6 mm diameter holes ($n = 6$). Stars indicate the mean values.

bined with reed and cow parsley stems in the combination nests. This provided a variety of materials and hole diameters and may explain why combination nests were preferred over nest blocks.

We also observed strong variation in nest numbers among the combination nests we developed. This indicates that the placement of artificial nests strongly influences nesting activity. It has been suggested that the nests should be placed near flowering plants or berry bushes (e.g., raspberry or currant), with the holes oriented horizontally, preferably on south-facing walls or along the edges of warm meadows, facing the morning sun (Budriene *et al.* 2004, Staab *et al.*

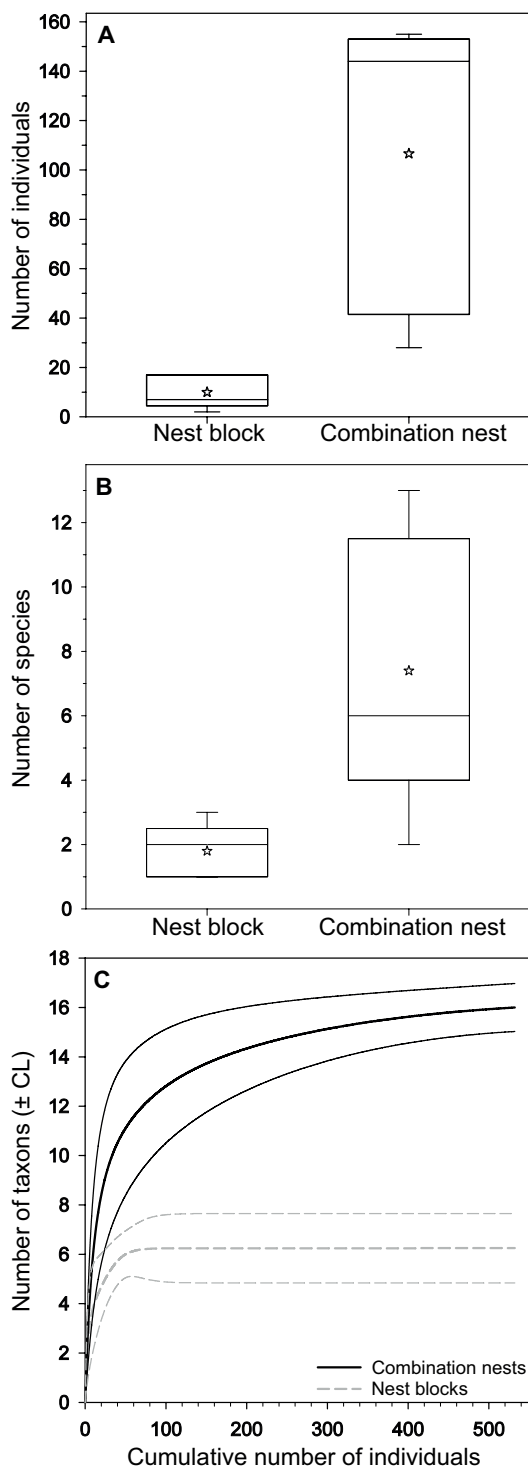


Fig. 6. Numbers of specimens (A) and species (B) in nest blocks and combination nests ($n = 5$). Stars indicate the mean values. — C: Rarefaction of species accumulation curves of combination nests and nest blocks with 95% confidence intervals.

2018, Khan *et al.* 2024). The service life of the nests has not been tested over consecutive years, but they may remain usable as long as some holes remain open and the structures remain intact.

Stem nests made of natural materials, log nests made from hardwood and combination nests were suitable for a large number of species (Fig. 2) and could help to alleviate the shortage of nesting sites. Combination nests with a wider variety of nesting materials and hole sizes attracted more species than wooden nest blocks alone. Therefore, we recommend artificial nests with multiple materials and hole sizes, such as our combination nest design. Artificial nests particularly suitable for certain solitary wasps, solitary bees and sphecids wasps, and their kleptoparasites. Further research is needed on the use of artificial nests to enhance pollination and increase berry yield. Initially, such nests could be placed in clear-cut areas or rural landscapes; once occupied, for example by leafcutter bees, they could be moved to nearby raspberry, currant, strawberry or apple orchards. Crop yields should be monitored before and after nest placement to assess their effectiveness.

Many cavity-nesting aculeates have recently become highly endangered (Potts *et al.* 2010, Goulson *et al.* 2015). The artificial nest method presented here may assist in the conservation of endangered species, as several species readily used stems and birch logs for nesting. We observed one vulnerable species (*Chrysis ignita*) and one near-threatened species (*Psenulus palipes*, Appendix 2) in the nests. There were very few parasites in the artificial nests, a finding also reported in previous Central European studies. It has been suggested that parasites initially find trap nests poorly and that their abundance increases if nests are kept in the same areas for several years (Freeman & Jayasingh 1975). The abundance of parasites follows that of the host with a slight delay (Pohjoismäki & Raper 2012).

Further development of trap and artificial nests

Based on our research, artificial nests are a useful tool for alleviating the nest shortage of aculeates, as they were suitable for several spe-

cies. In our study, the most frequently occupied hole diameters in artificial nests were 6–8 mm, and on average 9.3% of the available tubes and drilled holes were used for nesting. It is important to place artificial nests in the field in spring before willows bloom, as many cavity-nesting wasps begin collecting nectar and pollen from willows at that time.

A review by Rahimi *et al.* (2021) found that the average occupancy rate of artificial nests was over 30%, which is notably higher than the 9.3% recorded in our study. One likely explanation is that our study sites were within the boreal zone, where both species richness and the number of individuals searching for nesting sites is lower.

Further development of trap and artificial nests is needed, as are efforts to find solutions for soil-nesting aculeates (*see also* Dylewski *et al.* 2024). Longer-term testing with the same nests should also be carried out, and a wider range of wood types evaluated for the wooden blocks used in the combination nest. The weakness of the straw nest structures was evident in some areas where the straw was pecked and scattered by small birds; therefore, the straw should be glued to the shelter container. Although plastic straws proved unsuitable for trap and artificial nests, other artificial materials, such as cardboard tubes, paper straws or lightly rolled-up corrugated cardboard, could be tested. However, trap nests containing straw should be protected from bird damage, for example by using a plastic container or metal mesh.

If trap nests are not overwintered under natural conditions, they should be placed in a refrigerator or an adjustable climate chamber before being transferred to the freezer. This ensures a more gradual decrease in temperature, similar to that experienced outdoors. In spring, the hatching peak occurred, on average, one month after the trap nests were brought to room temperature. Under natural conditions, the hatching peak in spring occurs over a slightly longer period due to natural weather fluctuations.

Conclusion

The results of our study are consistent with those of previous studies conducted in Europe,

although the number of species is lower in Northern than in Central Europe (*see also* MacIvor *et al.* 2017). There are still significantly fewer studies on artificial nests in Northern Europe. When using artificial nests, it is recommended to use local natural materials such as deciduous tree wood and natural stems, which are inexpensive and require little maintenance (Krombein 1967, MacIvor *et al.* 2017). Artificial nests could also be part of national pollinator strategies to improve pollination and restore areas where pollinator populations have declined (IPBES 2016, Ministry of the Environment 2022).

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Appendix 1. Locations of sampling sites, their numbers as shown in Fig. 1, habitat types and years of sampling.

Location	Number	WGS °	Habitat	Years
Backaviken	1	60.004, 23.823	rocky meadow	2001
Dåvits	2	60.075, 24.607	overgrown pasture	2001
Kivelä	3	60.159, 23.916	overgrown meadow	2001
Sandberginpelto	4	60.542, 25.174	abandoned field	2001
Muhamäki	5	62.281, 29.000	forest clear-cut	2001
Koli, Havukka-aho	6	63.056, 29.864	glade	2001, 2010
Jalajavaara	7	62.202, 30.302	rocky meadow	2001, 2002
Isoaho	8	64.030, 28.224	pasture with alders	2001, 2002
Melalahti	9	64.402, 27.659	pasture with alders	2001, 2002
Naapurinvaara	10	64.183, 28.230	pasture with alders	2001, 2002
Hulttila	11	60.324, 24.480	mesic brook side forest	2002
Virvik	12	60.343, 25.856	gravel pit margin	2002
Nukari	13	60.520, 24.902	brook valley	2002
Hakoinen	14	60.873, 24.584	broad-leaf woodland	2002
Kalpalinna	15	60.927, 24.562	gravel pit margin	2002
Neulamäki	16	62.859, 27.566	aspen forest	2002
Juntusranta	17	65.217, 29.475	pine forest margin	2002
Kalkkima	18	65.898, 24.450	aspen forest	2002
Viinämäki	19	64.527, 29.433	spruce forest clear-fell	2002
Kelovaara	20	64.005, 30.390	clear-fell with aspen trees	2002
Leppivaara	21	64.160, 30.286	clear-fell with aspen trees	2002
Koli, Mustanniityt	22	63.088, 29.837	meadow	2010
Koli, Mäkränaho	23	63.083, 29.815	meadow	2010
Koli, Ikolanaho	24	63.073, 29.828	glade	2010
Koli, Purolanaho	25	63.078, 29.822	meadow	2010

Appendix 2. List of taxa encountered in this study in stems and plastic straws in 2001, stems and wood in 2002, and birch block and combination (comb.) nests in 2010, and their life-history strategies (kleptop. = kleptoparasite).

Tribe	Species/taxon	Strategy	Stems and straws	Stem/wood	Block/comb.
Chrysididae	<i>Chrysis angustula</i> Schenck, 1856	kleptop.		x/-	-/x
Chrysididae	<i>Chrysis ignita</i> (Linnaeus, 1758)	kleptop.		x/x	
Chrysididae	<i>Chrysis schencki</i> Linsenmaier, 1968	kleptop.			-/x
Chrysididae	<i>Omalus aeneus</i> (Fabricius, 1787)	kleptop.			-/x
Chrysididae	<i>Pseudomalus triangulifer</i> (Abeille de Perrin, 1877)	kleptop.		-/x	
Vespidae	<i>Ancistrocerus antilope</i> (Panzer, 1798)	host			-/x
Vespidae	<i>Ancistrocerus trifasciatus</i> (Müller, 1776)	host	x	x/x	x/x
Vespidae	<i>Symmorphus allobrogus</i> (Saussure, 1856)	host			x/x
Vespidae	<i>Symmorphus bifasciatus</i> (Linnaeus, 1761)	host	x	x/x	-/x
Vespidae	<i>Symmorphus connexus</i> (Curtis, 1826)	host		x/-	
Vespidae	<i>Symmorphus crassicornis</i> (Panzer, 1798)	host		x/-	
Pompilidae	<i>Deutragenia bifasciata</i> (Geoffroy, 1785)	host	x	x/-	
Crabronidae	<i>Crossocerus subulatus</i> (Dahlbom, 1845)	host		x/-	
Crabronidae	<i>Crossocerus vagabundus</i> (Panzer, 1798)	host		x/-	
Crabronidae	<i>Rhopalum clavipes</i> (Linnaeus, 1758)	host	x	x/x	x/x
Crabronidae	<i>Trypoxylon</i> sp. Latreille, 1796	host	x		
Crabronidae	<i>Passaloecus</i> sp. Shuckard, 1837	host	x		-/x
Crabronidae	<i>Passaloecus corniger</i> Shuckard, 1837	host			-/x
Crabronidae	<i>Passaloecus eremita</i> Kohl, 1893	host			x/x
Crabronidae	<i>Passaloecus monilicornis</i> Dahlbom, 1842	host		x/x	x/x
Crabronidae	<i>Pemphredon lugens</i> Dahlbom, 1842	host		-/x	
Crabronidae	<i>Pemphredon lugubris</i> (Fabricius, 1793)	host		x/x	
Crabronidae	<i>Psenulus pallipes</i> (Panzer, 1798)	host			x/-
Megachilidae	<i>Coelioxys inermis</i> (Kirby, 1802)	kleptop.		x/-	
Megachilidae	<i>Megachile lapponica</i> Thomson, 1872	host	x	x/-	
Apidae	<i>Anthophora furcata</i> (Panzer, 1798)	host		x/-	
Colletidae	<i>Hylaeus</i> sp. Fabricius, 1793	host	x		
Colletidae	<i>Hylaeus annulatus</i> (Linnaeus, 1758)	host		x/x	-/x
Colletidae	<i>Hylaeus cardioscapus</i> Cockerell, 1924	host		x/-	
Gasteruptiidae	<i>Gasteruption assectator</i> (Linnaeus, 1758)	kleptop.		-/x	
Gasteruptiidae	<i>Gasteruption subtile</i> (Thomson, 1883)	kleptop.		-/x	
Ichneumonidae	Ichneumonidae Latreille, 1802	parasitoid	x		-/x
Ichneumonidae	<i>Poemenia notata</i> Holmgren, 1859	parasitoid			-/x
Ichneumonidae	<i>Poemenia hectica</i> (Gravenhorst, 1829)	parasitoid			x/x
Ichneumonidae	<i>Alexeter</i> sp. Foerster, 1869	parasitoid		-/x	
Ichneumonidae	<i>Perithous scurra</i> (Panzer, 1804)	parasitoid		-/x	
Ichneumonidae	<i>Ephialtes</i> sp. Gravenhorst, 1829	parasitoid		x/x	
Ichneumonidae	<i>Isadelphus gallicola</i> (Bridgman, 1880)	parasitoid		x/-	
Ichneumonidae	<i>Demopheles corruptor</i> (Taschenberg, 1865)	parasitoid		x/x	
Ichneumonidae	Hemigastrini sp. Smith & Shenefelt, 1955	parasitoid			-/x
Ichneumonidae	<i>Ischnus alternator</i> (Gravenhorst, 1829)	parasitoid		x/-	
Ichneumonidae	Cryptini sp. Kirby, 1837	parasitoid		x/-	
Eulophidae	<i>Melittobia acasta</i> (Walker, 1839)	parasitoid			-/x
Bombyliidae	<i>Anthrax anthrax</i> (Schrank, 1781)	parasitoid		x/x	
Anthomyiidae	<i>Eustalomyia histrio</i> (Zetterstedt, 1838)	parasitoid		-/x	
Anthomyiidae	<i>Eustalomyia hilaris</i> (Fallén, 1823)	parasitoid		x/-	
Sarcophagidae	<i>Oebalia cylindrica</i> (Fallén, 1810)	parasitoid		x/-	
Drosophilidae	<i>Cacoxenus indicator</i> Loew, 1858	parasitoid		x/-	