

STEM-NESTING HYMENOPTERA IN IRISH FARMLAND: EMPIRICAL EVALUATION OF ARTIFICIAL TRAP NESTS AS TOOLS FOR FUNDAMENTAL RESEARCH AND POLLINATOR CONSERVATION

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Abstract—Insect pollinators are suffering global declines, necessitating the evaluation and development of methods for long-term monitoring and applied field research. Accordingly, this study evaluated the use of trap nests (“bee hotels”) as tools for investigating the ecology of cavity nesting Hymenoptera within Irish agricultural landscapes. Three trap nests consisting of 110 mm diameter plastic pipe containing 100 cardboard nest tubes of varying diameter were placed at eight apple orchards and eight oilseed rape sites and left in the field for five months. Sealed nest tubes occurred at 15 of the 16 sites, and in 77% of the 48 nests. However, only 7% of the 4800 individual nest tubes were sealed, and only 4% produced cavity-nesting Hymenoptera. Three cavity nesting bee species (*Hylaeus communis*, *Osmia bicornis*, *Megachile versicolor*) and two solitary wasp species (*Ancistrocerus trifasciatus*, *A. parietinus*) emerged from nest tubes. There were significant differences among species in terms of emergence date and the diameter of nest tubes from which they emerged, the latter allowing the calculation of niche width and niche overlap, and informing choice of tube size in future studies/conservation efforts. Trap nests, therefore, offer a valuable tool for fundamental ecological research and a model system for investigating interactions between stem-nesting species within their wider ecological networks. The ability of trap nests to actually increase farmland pollinator abundance and diversity as part of agri-environment schemes requires additional investigation. However, used in sufficient numbers, these trap nests provide valuable biogeographical data for cavity nesting Hymenoptera and offer a viable means for long term monitoring of these species in Irish farmland.

Keywords—*Hylaeus*; insect declines; Ireland; *Megachile*; *Osmia*; solitary bees; solitary wasps

INTRODUCTION

There is growing weight of evidence for dramatic, long-term declines in insect abundance and diversity (e.g. Hallman et al. 2017; Lister & Garcia 2018; van Klink et al. 2020). These general trends corroborate previous reports of declines in insect pollinators, attributed to abiotic and biotic stressors such as agricultural intensification, habitat loss, exposure to chemical pollutants, and emerging pests and diseases (Potts et al. 2010; Roulston & Goodell 2011; Balfour et al. 2018; Dicks

et al. 2021). Although managed bees generally play the major role in pollination of commercial crops, wild pollinators also provide significant - and often complementary - crop pollination services (Brittain et al. 2013; Garibaldi et al 2013; Rader et al. 2020). Thus, in addition to the aesthetic and ethical values associated with preservation of species-rich pollinator assemblages, there are clear economic benefits to be gained from maintaining, or enhancing, a diverse assemblage of insect pollinators associated with commercial farms and horticultural operations (Hanley et al. 2015).

The foundation of many farmland pollinator conservation initiatives is the maintenance of flower-rich field margins or the deliberate sowing of flowering plants that provide ready sources of pollen and nectar for foraging insects, and offer complementary resources to mass flowering crops (Albrecht et al. 2020; Bottero et al. 2021). In addition to nutritional support, successful pollinator conservation schemes must also consider other components of the pollinator life cycle and ecology, such as provision of larval food plants, shelter, and nesting sites (Potts et al. 2005; Kline & Joshi 2020; Requier & Leonhardt 2020). For above-ground cavity nesting bees, man-made structures, such as brickwork or dry-stone walls can provide suitable nesting sites, especially in the absence of natural nesting sites such as hollow stems and tree holes (Xie et al. 2020). Additionally, artificial nests (known as ‘trap nests’ to the scientific community or ‘bee hotels’ to the general public) can be manufactured or bought from commercial suppliers that mimic natural nesting sites, and provide additional nesting resources for a wide range of cavity-nesting bee and solitary wasp species.

Bee hotels or trap nests can be made from a variety of materials, and may involve drilling holes in bricks or wooden blocks, or filling an outer casing with nest tubes made from reeds, bamboo canes or cardboard tubes. As research tools, self-made trap nests can, therefore, provide an easily replicated, cost-effective standardized method for the monitoring of cavity nesting bees and other Hymenoptera over large areas and over long periods (MacIvor 2017; Staab et al. 2018; Prendergast et al. 2020). Trap nests can provide data on how nesting bees and wasps are influenced by intrinsic factors such as the materials used, design, overall dimensions and hole diameter, and by external factors such as nest height, aspect, and local habitat (McIvor 2017; Rahimi et al. 2021). Trap nests can be used to gather information pertaining to species autecology, nesting season, emergence time, and interactions with predators and parasites, and also be adapted for specific purposes, such as biogeographical monitoring, life history research and conservation translocation (Tschardt et al. 1998; MacIvor 2017; Eeraerts et al. 2022). The use of trap nests by different species also allows investigations into fundamental ecological topics,

such as competition between species for nest sites, colonisation and emergence periods, identification of the resources supplied to the developing larvae in terms of pollen or prey, and niche overlap (Budriene et al. 2004; Valdovinos & Marsland 2021).

Members of the public wishing to be actively involved with pollinator conservation efforts or attract additional insect biodiversity into their gardens often use similar artificial nests (‘bee hotels’). However, efforts to support wild bees often go unrewarded because the bee hotels are of an incorrect design or manufactured from inappropriate materials (MacIvor & Packer 2015; von Königslöw et al. 2019; Alton & Ratnieks 2020). Additionally, artificial nests are often criticised because they offer an artificially high density of nesting cavities, they encourage high levels of pathogens and parasites, and may provide data on abundance and diversity that does not necessarily correlate with that obtained by other pollinator sampling methods (Roulston & Karen Goodell 2011; Prendergast et al. 2020).

Ireland has approximately 100 species of wild bees, of which around a third are currently considered endangered or at risk of local extinction (Fitzpatrick et al. 2006). Fifteen Irish bee species, primarily in the genera *Megachile* and *Hylaeus*, are considered above-ground cavity nesting species, and will typically nest in hollow plant stems, holes in trees, or cracks in rocks or walls. The red mason bee, *Osmia bicornis* (L.), is considered a recent introduction to Ireland and was first recorded 2003 (Murray et al. 2005). In addition to cavity nesting bees, Ireland is also home to several species of ‘potter wasps’ (Vespididae: Eumeninae) that are commonly found in trap nests intended for solitary bees (e.g. Stanley et al. 2013).

The aim of this study was to examine the use of trap nests by above ground nesting bees and wasps associated with two mass blooming crops, apple (*Malus domestica* Borkh.) and oilseed rape (*Brassica napus napus* L.), in Ireland. In meeting this primary aim, additional data were obtained pertaining to species preferences for nest tubes of a certain diameter or for nests set different heights above the ground, and allowed us to perform some preliminary analysis of niche overlap of Irish cavity nesting Hymenoptera. Based on these results, recommendations are made regarding the

value of trap nests for use as scientific research and monitoring tools, and how the design of nests might be improved for domestic use or for involvement in agri-environment schemes.

MATERIALS AND METHODS

TRAP NESTS

The outer casing of the nests was constructed from 110 mm diameter plastic pipe (Floplast, Screwfix, UK) cut into 185 mm lengths using a bandsaw (Supplementary File S1). A plywood disc (110 mm diameter; 12 mm thickness) was positioned 6 mm from one end of the pipe and fixed using three 20 mm long countersunk screws. For waterproofing, the plywood disc was painted with a preserving wood treatment (Cuprinol, Dulux Paints, UK).

The nest casing was packed with cardboard nest tubes (140 mm long; Stell Cardboard Tubes, UK) of five different widths (inner diameters: 4, 5, 6, 8, and 10 mm). Twenty tubes of each diameter were mixed and fastened into a bundle using four 6 mm wide elastic bands. The bundle of nest tubes was placed into the pipe casing so that the tubes were in contact with the plywood end piece. Extra cardboard and tissue paper was used to fill any gaps between the casing and the cardboard tubes, and to secure the bundle of tubes in place.

In the field, three trap nests were attached to the same side of an 1800 x 100 x 100 mm wooden fence post using standard 110 mm plastic pipe brackets (FloPlast SP82BL, Screwfix.com, UK) so that all three nests faced the same direction (Supplementary File S1). The brackets were angled so that the casing tilted downwards slightly to help prevent rain entering the open face of the nest tubes. The nests were spaced 25 cm apart from the top of the post so when the fence post was in position the nests were at heights of 1.0, 1.25 and 1.5 m above the ground.

The fence post was positioned along a field boundary so that the nests faced south east. If access restrictions meant the fence post had to be positioned on a north-facing boundary, the nests were arranged so they still faced south east but were positioned in a gap in the hedge so insects would have clear access to the nesting tubes.

STUDY SITES, NEST EXPOSURE, AND REARING OF OCCUPANTS

Field sampling was conducted between March and September 2019 at 16 study sites in Ireland (Fig. 1; Hodge & Stout 2019). Eight sites consisted of fields of winter-sown oilseed rape (OSR) which represented an annual mass-flowering crop, and eight sites were apple orchards which represented a perennial mass-flowering crop (Fig. 1; Supplementary File S1). Study sites ranged in size from 0.4 ha to 22 ha and were a minimum distance of 3 km apart.

The nests were placed at the OSR sites between 30/3/19 and 3/4/19 and at the apple sites between 4/4/19 and 19/4/19 and meant that the nest tubes were available for colonization just as flowering of the crops was commencing (Supplementary File S1). The nests were left in the field until early September so that any hymenopteran larvae present in the nest tubes would have reached pupation and be less susceptible to damage during transit.

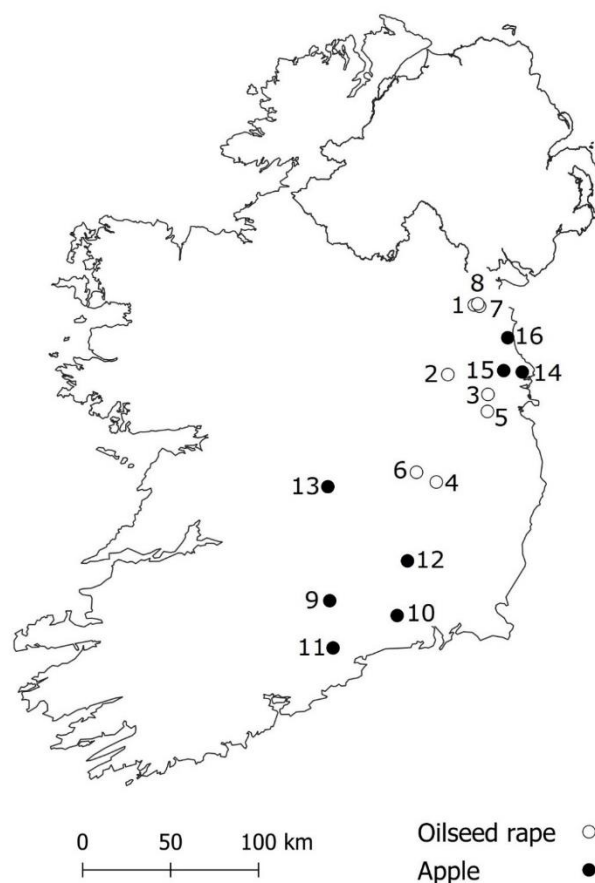


Figure 1. Locations of 16 field sites used to evaluate the use of trap nests by stem nesting Hymenoptera in the spring/summer of 2019. Closed circles represent apple orchards, and open circles oil seed rape fields.

On retrieval, all cardboard nest tubes were removed from the outer casing and checked for occupants. Sealed nest tubes were then placed into individual glass tubes (150 mm long; 15 mm diameter) and the open end of the glass tubes sealed with cotton wool. These glass tubes were then placed in large plastic boxes to protect them from predators and excessive moisture and maintained in an outdoor storage facility at ambient temperature. The tubes were inspected weekly to check for damage, any emerged insects, or the presence of parasites/ predators.

On 24th March 2020, the tubes were moved into an indoor rearing facility and maintained under ambient lighting at room temperature (approx. 17-21°C). Tubes were checked twice a day, and any emergent insects collected and euthanized by freezing. This process was repeated until 6th June 2020 by which time no further insects had emerged for four weeks. All cavity nesting bees and wasps that emerged from the tubes were sexed and identified to species with reference to Else & Edwards (2018), Yeo & Corbet (1995), and Archer (2014).

STATISTICAL ANALYSIS

All statistical analyses were performed using Genstat v21 software (VSN International Ltd., UK). To assess which factors influenced the occupation of the nest tubes, a generalized linear mixed model (GLMM) was performed where the number of sealed tubes of each diameter in each nest was treated as count data with a Poisson distribution. In this GLMM, crop type, nest height, and tube diameter were treated as fixed categorical explanatory factors, and individual nests and study sites were included as random factors. The GLMM dispersion parameter was estimated so as to account for any overdispersion of the data.

For each of the main cavity-nesting Hymenoptera species, separate GLMMs were performed to investigate the effects of crop type and trap height on nest tube occupation. In these GLMMs the response variable was the number of tubes in each of the 48 nests from which the species emerged. The models used a Poisson error structure and site was included as a random factor.

To assess whether the cavity-nesting species preferentially used nest tubes with different diameters, the nest-tube diameters from which

each species emerged were pooled across all 16 sites to create a workable data set. As tube diameter in this instance could be considered an ordinal variable, a non-parametric Kruskal-Wallis test was then performed to compare the diameters of tubes from which each bee or wasp species emerged. As the Kruskal-Wallis test indicated highly significant differences in tube use among the five species, the nest tube diameters used by each species were subsequently compared in a pairwise fashion using Mann-Whitney tests. Because 10 pairwise tests were required, we used a Bonferroni adjustment to shift the level of statistical significance from $P < 0.05$ to $P < 0.005$.

To assess whether crop type or tube diameter affected the number of adults that emerged from occupied nest tubes, a GLMM was performed for each species. These GLMMs used a Poisson error structure with log link function, with crop and tube diameter included as fixed factors, and site included as random factor. The GLMM dispersion parameter was estimated so as to account for any overdispersion of the data. Only tubes from which specimens emerged were included in these analyses.

To compare emergent times among the different cavity-nesting species and between males and females, a residual maximum likelihood model (REML) was fitted with species and sex as fixed factors, and individual nest tubes as a random factor. For the response variable, as date is an interval scale measure, relative emergence time (days) for each individual was calculated as that relative to 31st March 2020, and then a mean relative emergence time calculated for the individuals of the same sex emerging from the same tube.

TUBE DIAMETER NICHE OVERLAP

The relative niche width (NW) of a species i in terms of nest tube diameter can be estimated by:

$$NW_i = \frac{1}{\sum_{k=1}^n P_{ik}^2}$$

where n represents the different levels of the shared resource k , and P the proportion of individuals of species i using each resource level. In our system, k represents the nest tubes and n represents the five different diameters (Case 2000; Budriene et al. 2004).

To assess pairwise species niche overlap based on nest tube diameter we first used the simplified symmetrical Morisita-Horn index (Budriene et al. 2004), where overlap, O , between two species, i and j , who share the resource k , is given as:

$$O_{ij} = \frac{2 \sum_{k=1}^n P_{ik} P_{jk}}{\sum_{k=1}^n (P_{ik}^2) + \sum_{k=1}^n (P_{jk}^2)}$$

With this model, the overlap of any one species with itself, O_{ii} , is equal to 1 (Case 2000).

As species with different niche widths can interact with each other in an asymmetrical manner, this can be reflected by calculation of O_{ij} using the slightly different formula:

$$O_{ij} = NW_i \sum_{k=1}^n P_{ik} P_{jk}$$

where $O_{ji} \neq O_{ij}$ unless species i and j have exactly the same niche (Case 2000).

The niche width based on nest tube diameters was calculated for each of the five bee and wasp species that emerged from the nest tubes, and the symmetrical and asymmetrical indices of niche

overlap were then calculated for each of 10 pairwise combinations of these five species.

RESULTS

NEST TUBE OCCUPATION

A total of 332 ($\approx 7\%$) of the 4800 nest tubes were found to be sealed with mud, clay, or leaves, when the nests were retrieved from the field. Sealed tubes were found at 15 of the 16 sites and in 37 (77%) of the 48 nests (Table 1). The highest number of sealed tubes found at a single site was 46 (15%), and the most in a single nest was 24 (24%).

There was no significant difference between the overall proportion of occupied tubes in the apple sites (8.4%) and the OSR sites (5.5%; $F_{1,13} = 0.49$, $P = 0.206$; Table 1). Nest height had a significant effect on tube occupancy, with the nests positioned at the middle height (1.25 m) having lower occupancy than the highest (1.5 m) and lowest (1.0 m) nests (GLMM $F_{2,23} = 2.4$, $P = 0.017$; Table 1). There was also a highly significant difference among the different diameter tubes in terms of the proportion that were occupied: for example, 16.4% of 4 mm diameter tubes were sealed compared with less than 2% of the 8 mm and 10 mm diameter tubes ($F_{4,173} = 20.6$, $P < 0.001$; Table 1).

Table 1. Proportion (%) of sealed cardboard nest tubes set at three heights at eight apple (APP) and eight oil seed rape (OSR) sites in Ireland from March to September 2019. There were 20 tubes of each diameter at each height at each site (4800 tubes in total).

Crop	Height	Tube diameter					Grand Total
		4 mm	5 mm	6 mm	8 mm	10 mm	
APP	1.0 m	18.1	13.8	10.6	4.4	4.4	10.3
	1.25 m	18.8	8.1	2.5	0.6	2.5	6.5
	1.5 m	16.3	13.1	8.8	2.5	1.3	8.4
	All APP	17.7	11.7	7.3	2.5	2.7	8.4
OSR	1.0 m	23.1	5.0	7.5	1.9	3.1	8.1
	1.25 m	5.6	3.1	3.8	0.0	0.0	2.5
	1.5 m	17.5	6.3	5.4	0.0	0.0	5.8
	All OSR	15.4	4.8	5.2	0.6	1.0	5.5
All sites		16.6	8.2	6.4	1.6	1.9	6.9

Table 2. Summary of emergence data for five species of stem-nesting Hymenoptera from trap nests set at three different heights in eight oil seed rape (OSR) and eight apple (APP) sites in Ireland.

		<i>Osmia bicornis</i>	<i>Megachile versicolor</i>	<i>Hylaeus communis</i>	<i>Ancistrocerus trifasciatus</i>	<i>Ancistrocerus parietinus</i>
Sites present (x/8)	OSR	3	1	5	6	4
	APP	3	3	4	5	4
	Total	6	4	9	11	8
Tubes emerged: crop (x/2400)	OSR	13	5	28	36	6
	APP	11	9	19	61	11
Tubes emerged: height (x/1600)	1.50 m	8	1	10	46	8
	1.25 m	5	2	8	20	5
	1.00 m	11	11	29	31	8
	Total	24	14	47	97	17
Total individuals emerged	OSR	54	23	198	152	19
	APP	44	49	112	220	52
	Total	98	72	310	372	71
Mean individuals per tube	OSR	4.2	4.6	7.1	4.2	3.2
	APP	4.0	5.4	5.9	3.6	4.7
	Total	4.1	5.1	6.6	3.8	4.2
Maximum individuals per tube	OSR	7	7	17	14	5
	APP	9	7	16	11	11
	Total	9	7	17	14	11
Overall sex ratio (F:M)	OSR	0.4	1.6	1.0	1.4	2.8
	APP	0.3	1.2	1.9	1.0	2.3
	Total	0.3	1.3	1.3	1.2	2.4

FAUNA

Of the 332 tubes that were sealed with mud or leaves, 199 produced stem-nesting bees or wasps (Table 2). The most common bee species was *Hylaeus communis* Nylander (Colletidae; 310 specimens), followed by *Osmia bicornis* L. (Megachilidae; 98 specimens), and *Megachile versicolor* Smith (Megachilidae; 72 specimens). Two solitary wasp species also emerged from the nest tubes: *Ancistrocerus trifasciatus* (Müller) (Eumenidae; 372 specimens) and *A. parietinus* (L.) (71 specimens).

The number of tubes from which each species emerged was not influenced by whether the nests

were situated in OSR or apples (Table 2; GLMM; $P > 0.40$ for all species). *Osmia bicornis*, *A. trifasciatus* and *A. parietinus* were not significantly affected by the height of the trap nests (GLMM; $P > 0.08$). However, both *M. versicolor* (GLMM; $P < 0.001$) and *H. communis* (GLMM; $P = 0.008$) were significantly more likely to emerge from the lowest (1 m high) trap nest, than both the 1.25 m and 1.5 m high nests (Table 2).

Many of the remaining 133 sealed tubes that produced no stem-nesting Hymenoptera proved to be empty. The common earwig (*Forficula auricularia* L.; Forficulidae; Dermaptera) emerged from several tubes collected from orchard sites, although it is unknown whether they were using

the tubes for reproduction or as an overwintering shelter site. Several tubes produced hymenopterous parasitoids, belonging to families Ichneumonidae, Pteromalidae, and Chalcididae. Ruby tailed wasps (*Chrysis* spp.; Chrysididae), which are known to parasitize species of *Ancistrocerus*, emerged from eight tubes. One tube produced a specimen of the tachinid fly, *Tiarthria setipennis* Fallén, which is a parasitoid of *F. auricularia*.

EFFECT OF NEST TUBE DIAMETER ON ADULT EMERGENCE

For each species, when considering only the tubes that produced adults, there was no difference between crops (Table 2; $P > 0.25$) or among the different diameter tubes (Supplementary File S2; $P > 0.20$) in terms of the numbers of adults that emerged per tube. However, there were highly significant differences among the five stem-nesting species with respect to their preferred tube diameters (Fig. 2; Kruskal-Wallis, $H = 119$, 4 df, $P < 0.001$). *Hylaeus communis* primarily used the smallest 4 mm tubes, which overlapped with the range of small diameter tubes used by *A. trifasciatus* (Fig. 2). *Osmia bicornis* emerged only from the 5 mm and 6 mm tubes, whereas *A. parietinus* used of the 5 mm, 6 mm and the 8 mm tubes. The largest bee species, *Megachile versicolor*, emerged from only the larger 8 mm and 10 mm diameter tubes (Fig. 2). In terms of pairwise comparisons, almost all the species were significantly separated from each other in terms of their nest tube size distributions (Mann-Whitney tests, $P < 0.001$); only *O. bicornis* and *A. trifasciatus* were not statistically different in terms of the nest tube diameters from which they emerged (Mann-Whitney, $P = 0.414$; Fig. 2).

EMERGENCE TIME

After the tubes were moved to the indoor rearing room on 24th March, the first *O. bicornis* emerged on 29th March, with the first *A. trifasciatus* emerging 11 d later on 9th April, followed by *A. parietinus* and *H. communis* on 11th April. (Fig. 3). The first *M. versicolor* emergence did not occur until 21st April (Fig. 3). Apart from *A. trifasciatus*, emergence patterns tended to occur in two or several peaks, often associated with emergence from different nest tubes (Fig. 3). The overall emergence of *O. bicornis* and *H. communis* occurred over a period of 19 d, whereas that of *A. trifasciatus* and *M. versicolor* occurred over narrower periods of 11 d and 10 d.

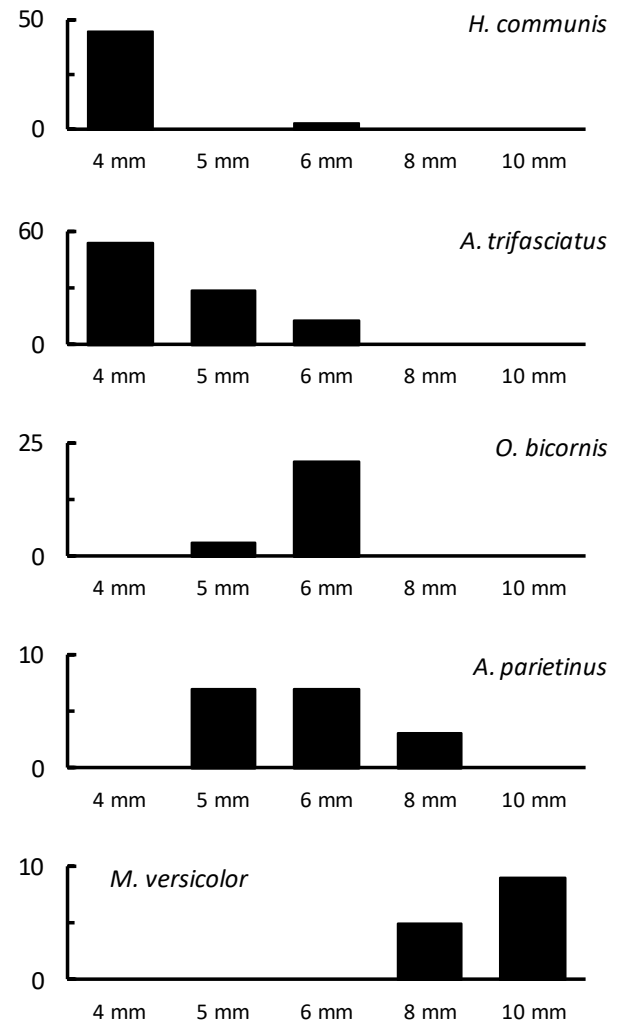


Figure 2. Distribution of nest tube diameters used by different species of stem-nesting Hymenoptera across 16 farmland sites in Ireland. Figures given are the total numbers of tubes used from 960 of each diameter. Species are presented in the order of their median nest tube diameters.

In terms of individual emergents, there was generally some overlap in emergence times between species, with only *O. bicornis* and *M. versicolor* being completely separated (Fig. 3). When considering mean emergence times per tube, however, there were clear significant differences among species (REML; $P \ll 0.001$) and between sexes of the same species for all five species (REML; $P \ll 0.001$; Fig. 4). The smallest mean separations of males and females of the same species were 2.4 d and 2.6 d for *A. trifasciatus* and *H. communis*, whereas the largest mean separations were 4.5 d and 5.3 d for *M. versicolor* and *O. bicornis* (Fig. 4).

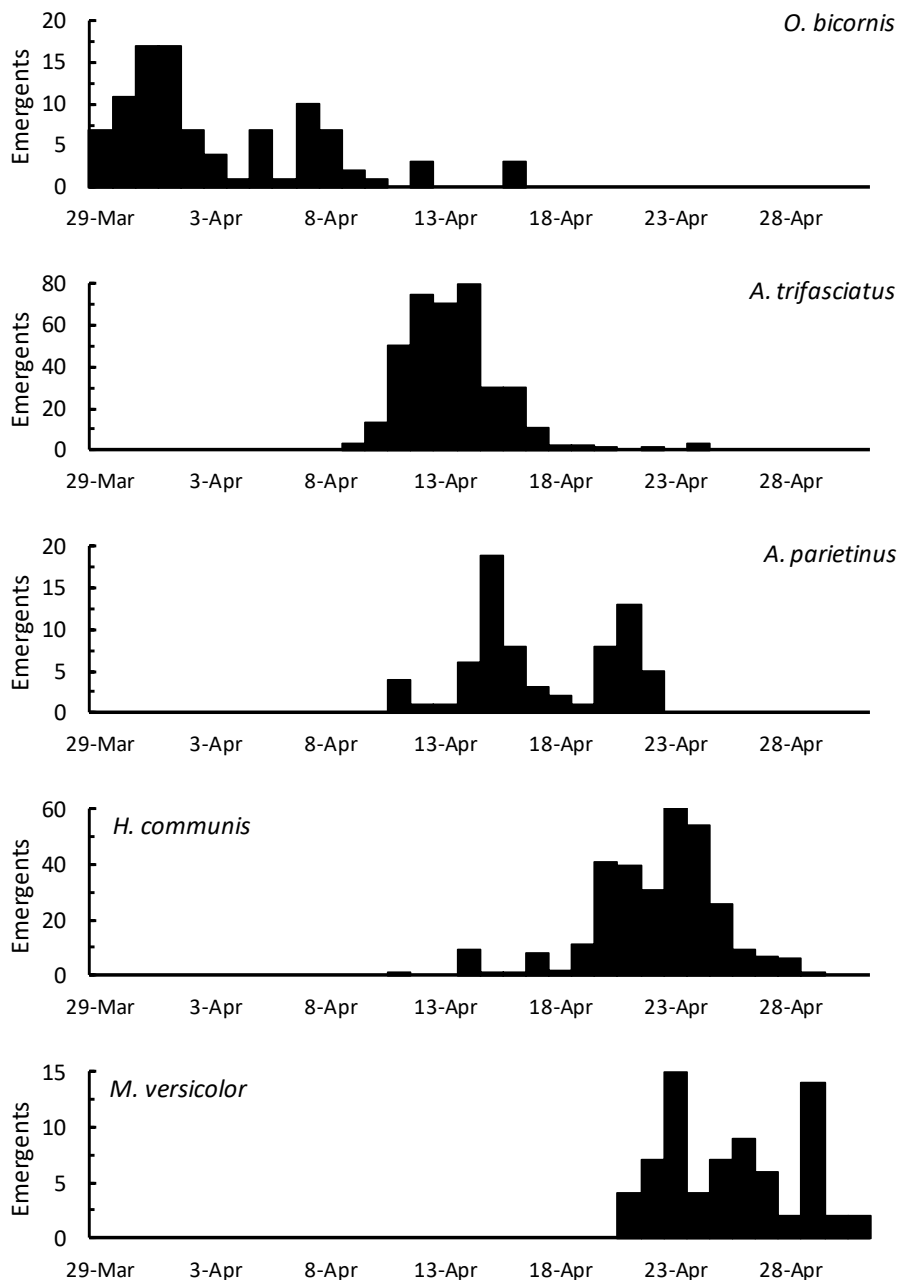


Figure 3. Total numbers of stem-nesting Hymenoptera emerging each day from cardboard nest tubes from March 29th to 1st May 2020. The nest tubes were placed out at 16 Irish farms during spring/summer 2019, maintained outdoors from September 2019, and moved to an indoor rearing facility on 24th March 2020.

NICHE WIDTH AND NICHE OVERLAP

In terms of nest tube diameter, *H. communis* and *O. bicornis* had the narrowest niche widths and the two wasps, *A. trifasciatus* and *A. parietinus* had the widest (Table 3). With respect to niche overlap, *M. versicolor* had zero overlap with *H. communis*, *O. bicornis* and *A. trifasciatus*, whereas the highest levels of niche overlap occurred between *H. communis* and *A. trifasciatus* and between *O. bicornis* and *A. parietinus* (Table 3; Fig. 2).

The overall picture of niche overlap among the five species obtained from the symmetrical overlap

model was generally similar to that when using the asymmetric niche overlap model. For example, the symmetrical niche overlap obtained for the interaction between the two wasps, *A. trifasciatus* and *A. parietinus*, of 0.452, was very similar to the asymmetric niche overlap estimates of 0.487 and 0.423 (Table 3). However, the asymmetrical niche overlap models also resulted in species with the narrower niche widths, for example *H. communis* and *O. bicornis*, having a greater impact on species with the wider niches, *A. trifasciatus* and *A. parietinus*, than was seen in the reciprocal situations.

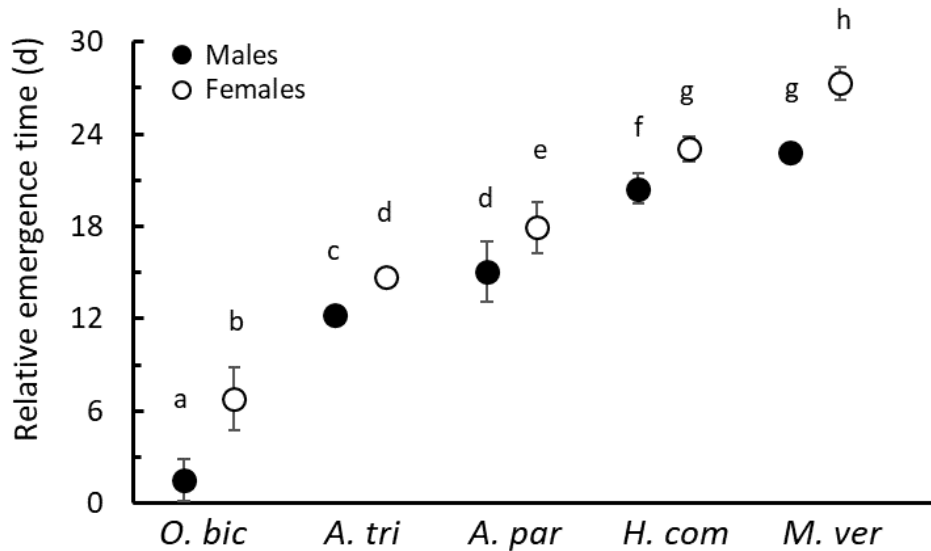


Figure 4. Relative emergence time (d; mean \pm 95% CI) of male (closed circles) and females (open circles) of five species of stem-nesting Hymenoptera from cardboard nest tubes. Mean emergence times were calculated for males and females emerging from a single tube, and are relative to 31st March 2020. Letter codes separate groups based on LSD values from REML analysis at $P < 0.05$.

O. bic - *Osmia bicornis*; *A. tri* - *Ancistrocerus trifasciatus*; *A. par* - *Ancistrocerus parietinus*; *H. com* - *Hylaeus communis*; *M. ver* - *Megachile versicolor*.

DISCUSSION

During this investigation we recorded three species of cavity nesting bees and two species of cavity nesting wasps in trap nests consisting of a plastic outer casing with cardboard nesting tubes. The data obtained allowed us to separate these five species in terms of the diameter of nest tubes they preferred and their relative emergence times. Although the occupation rate of whole nests was high (77%), the occupation rate of individual tubes by stem-nesting Hymenoptera was relatively low (7%). Additionally, only 60% of sealed tubes produced stem-nesting bees or wasps, resulting in an overall emergence rate of 4%. Low occupation rates of nest tubes have been reported in several previous studies (Rahimi et al. 2021), for example 0.7% (Gathmann et al. 1994), 1.5% (MacIvor 2017) and 3.5% (Alton & Ratnieks 2020). Conversely, high levels of colonisation (30%) were reported for nests in urban settings (30%; von Königslöw et al. 2019) and in commercial *Osmia* operations (100%; Seidelmann et al. 2016). The low nest-tube occupancy rates in our study may have occurred for a variety of reasons, including that many of the solitary bees and wasps that could potentially use these trap nests are uncommon, and some species

may be reticent to use the cardboard tubes for nesting. Additionally, it must be acknowledged that the occupation rate is a function of both the number of occupied tubes and the number of tubes made available: it is probable that we would have recorded higher occupation rates had we used fewer than the 300 tubes provided at each site, which appeared far in excess of what was required.

The diversity of stem-nesting Hymenoptera we recorded was also low when compared with other trap nest studies: for example 47 species in Canada (MacIvor 2019), 33 species in Lithuania (Budriene et al. 2004), and 22 species in Germany (von Königslöw et al. 2019). This low diversity generally reflects the low number of stem nesting species which occur in Ireland, and the results are similar to a previous study on Irish farmland where only two species of bees, *M. versicolor* and *H. communis*, emerged (Stanley et al. 2013).

We found no significant differences between the OSR or apple sites with respect to overall occupation rates of nest tubes or the occurrence of any of the five stem nest nesting species. There was, however, some indication that two of the bee species, *M. versicolor* and *H. communis*, were more frequent in the lowest trap nests, set at 1 m above

Table 3. Niche width and niche overlap among five species of stem-nesting Hymenoptera based on nest tube diameter. See Methods for details of calculations. Sp – species; Hc - *Hylaeus communis*; Mv - *Megachile versicolor*; Ob - *Osmia bicornis*; At - *Ancistrocerus trifasciatus*; Ap - *Ancistrocerus parietinus*.

		Sp <i>i</i>				
		Hc	Mv	Ob	At	Ap
Niche width		1.13	1.85	1.28	2.35	2.70
Niche overlap						
Symmetrical	Hc	1				
	Mv	0	1			
	Ob	0.066	0	1		
	At	0.819	0	0.259	1	
	Ap	0.041	0.009	0.715	0.452	1
Sp <i>i</i> → Sp <i>j</i>	Hc	1				
	Mv	0	1			
	Ob	0.070	0	1		
	At	1.258	0	0.367	1	
	Ap	0.070	0.011	1.112	0.487	1
Sp <i>i</i> → Sp <i>j</i>	Hc	1				
	Mv	0	1			
	Ob	0.062	0	1		
	At	0.607	0	0.200	1	
	Ap	0.029	0.007	0.527	0.423	1

the ground, compared with nests set at 1.25 m and 1.5 m. Budriene et al. (2004) found the majority of stem-nesting Hymenoptera preferred to nest within a 1-2 m height range, with no species preferring relatively lower (< 1 m) nests, and only one species (the wasp *Symmorphus crassicornis*) preferring higher (> 2 m) nests. It has been suggested there could be a height limit for some species of stem-nesting Hymenoptera (McIvor 2016), but this is unlikely to be the case in our study where the highest nests were positioned at 1.5 m. It can be speculated that female bees foraging on ground vegetation would encounter the lowest nests first, or that the lowest nests were slightly more sheltered from the nests above, but these patterns in height preferences require further study to demonstrate repeatability and/ or clarify any mechanisms.

In contrast to ground nesting bees, which manufacture their own nest cavity to the required

size and structure, the dimensions of the cavities used by above-ground nesting bees are generally predetermined. If the internal dimensions of the cavity are too small then this can limit brood size, and affect the sex ratio and body size of the offspring, whereas if the nest cavity is too large then the female bee may have to collect additional nesting materials and spend more time reducing the diameter and capping the entrance (Seidelmann et al. 2016). As observed in several previous papers, the majority of occupied tubes were in the 4-6mm diameter range, with much lower occupation rates at 8 mm and 10 mm diameter (e.g. Gathmann et al. 1994; Budriene et al. 2004; Königslöw et al. 2019). In our study, these patterns are related to the relative abundance of the different Hymenoptera species, for example only *M. versicolor* used the 10 mm diameter tubes, and as this was the least common species these tubes had the lowest occupation rates. Conversely, the two most common species, *H. communis* and *A.*

trifasciatus, were responsible for the high occupation rate of the 4 mm diameter tubes.

There were distinct differences among species in terms of their nest tube diameter preferences, and this led to various degrees of niche overlap based on this resource. *Megachile versicolor* was the only species to use the 10 mm diameter tubes and so had little niche overlap with the other species. Conversely, high levels of niche overlap occurred between *H. communis* and *A. trifasciatis* based on their mutual use of the 4 mm diameter tubes, and between *O. bicornis* and *A. parietinus* based on their shared use of the 5 mm and 6 mm diameter tubes. Budriene et al. (2004) also calculated niche overlap based on nest tube diameter use, and also found significant overlap between *A. trifasciatis* and *H. communis*, but with a value of 0.54, lower than the value of 0.82 obtained here. They also reported some niche overlap between *A. trifasciatis* and *O. bicornis* ($O = 0.53$) which was also present, although not as significant, in our study ($O = 0.26$). Finally, the low niche overlap based on tube diameter between *O. bicornis* and *H. communis* was common to both studies (this study, $O = 0.07$; Budriene et al. 2004, $O = 0.04$).

The calculation of niche width and niche overlap demonstrates the potential of trap nests as a tool for fundamental ecological research, and provides a simple but valuable measure of the potential interaction strength between species. These basic niche overlap indices are based on proportional resource use by each species, but they do not consider the relative abundances of species and whether the shared nesting resources, both natural and artificial, are in limited supply (Case 2000; Roulston & Goodell 2011). In our artificial nests, although niche overlap between two species might be high, interspecific competition was unlikely to occur as nest cavities were far in excess of what was required and thus did not represent a limiting resource (Roulston & Goodell 2011). However, the calculation of niche width based on one resource highlights the need to also examine other factors, such as habitat preferences, larval resources, and activity periods. Stem nesting bees and wasps would tend to separate based on larval diet, although there might still be competition within each taxon for shared pollen resources or prey items. Temporal separation of species could also influence interspecific competition for larval

provisions, for example if pollinators avoided direct competition by harvesting pollen from different flower species, or even the same flower species, but at different times of the year. Alternatively, early emerging species may obtain a temporal competitive advantage by accessing nutritional resources and suitable nest cavities prior to later emerging species (Hodge et al. 1996). Ultimately, more complete analysis can describe how species overlap in multi-dimensional niche space and how this, in turn, influences the structure and composition of the cavity-nesting community (Vickruck & Richards 2012; Valdovinos & Marshland 2021).

In terms of temporal niche separation among species, although this could be implied based on their emergence patterns, the use of emergence date as the sole indicator of activity periods would substantially underestimate the degree of temporal overlap in the field (S MacIvor *pers. comm.* 1/10/21). Temporal overlap in nesting activity is a function of both the emergence date and adult longevity, and would therefore require some estimate of longevity for each species or data on activity obtained from field records. For example, in our study, the first species to emerge was *O. bicornis*, and the last was *M. versicolor*, which began emerging 5 d after the last *O. bicornis* had emerged. However, Strobl et al. (2020) found that median longevity of female *O. bicornis* maintained under laboratory conditions was 21 d, and that some individuals lived for 70 d, suggesting these species could easily overlap in terms of adult activity periods.

A further component of species temporal separation relates to the asynchronous emergence patterns of males and females. Protandry, the arrival of males at breeding sites prior to females, is often observed for solitary bees, and for all the Hymenoptera species we recorded the males emerged slightly, but significantly, earlier than the females (e.g. Bartomeus et al. 2011; MacIvor 2019). Based on our emergence data, this resulted in some overlap between pairs of species, but primarily between the females of an earlier emerging species with the males of a subsequently emerging species. When assessing potential competition for nesting resources from field data, it would, therefore, be important to separate the sexes, as only female

activity and/ or abundance would be a measure of contemporary nest site demand.

Because occupation rates can be so low, ecological surveys using trap nests may be problematic, requiring high numbers of distinct nests which may still produce sparse data. The species colonising the nests may represent only a small subset of the cavity nesting species actually present, and more complete coverage of the solitary bee assemblage may be achieved using alternative methods such as pan-traps and timed transect surveys (MacIvor 2019; Prendergast et al. 2020). Low occupancy also has implications for the inclusion of trap nests in agri-environment schemes aimed at improving farmland pollinator diversity. Trap-nests could provide a valuable method for assessing the success of initiatives aimed at improving farmland pollinator diversity, such as species-rich hedgerows or the creation of florally-rich field margins success (Diekötter et al. 2013; Requier & Leonhardt 2020). On the other hand, agri-environment scheme payments to growers that are based on the perceived success of biodiversity initiatives would need to consider that occupation of any artificial nesting structure is not guaranteed.

The frequent use of trap nests by solitary wasps, rather than solitary bees, has also been reported in previous studies. In an extensive Canadian study, MacIvor (2019) recorded 22 species of solitary bees with an additional 16 species of cavity-nesting wasps, and, similarly, in Lithuania, Budriene et al. (2004) found only seven species of bees emerged from reed trap nests compared with 26 wasp species. The presence of so many wasps could be considered a failure for initiatives aimed specifically for the conservation of wild bees or to promote pollinator abundance and diversity. However, rather than seen as an issue, the presence of solitary wasps offers additional opportunities for biodiversity conservation, and to examine potential interactions between different taxonomic and functional groups of cavity nesting Hymenoptera. This idea can be extended to consideration of all occupants, including the numerous parasites and predators of the stem nesting species and inhabitants such as spiders, earwigs, woodlice, and flies, as contributing to the biodiversity

benefits of the installed nesting structure (Barthell et al. 1998; Tschardt et al. 1998; Staab et al. 2018).

It is frequently suggested that trap nests or bee hotels have great potential as educational resources and as tools for citizen science research (e.g. Staab et al. 2018). Nevertheless, based on our results it would appear prudent to accept that occupancy rates of bee hotels can be very low, but also that their success rate might be improved if certain criteria are met. Some solitary bees show clear preferences for trap nests made from certain materials (e.g. Eeraerts et al. 2022), and many commercial bee hotels are made from unsuitable materials or contain cavities of inappropriate dimensions (often too large) for most domestic Irish bee species (Alton & Ratnieks 2020; Requier & Leonhardt 2020). So, in addition to setting nests correctly in terms aspect and height, using a wide range of cavity diameters and/ or different nests of different materials would tend promote a higher diversity of occupants, or at least make the nests accessible to a wider range of species (e.g. von Königslöw et al. 2019; AIPP 2021). Additionally, many solitary bees have short foraging ranges so the positioning of nests close to floral resources and nesting materials would also promote nest occupation (Gathmann & Tschardt 2002; Kline & Joshi 2020).

In summary, although we acknowledge the many issues associated with trap nests and extrapolating data to real-world population sizes and species diversity, our findings suggest that these techniques offer a valuable, low cost, standardized method for investigating the autecology of stem-nesting Hymenoptera in Irish landscapes. Future work into Irish stem nesting Hymenoptera would benefit from incorporating trap nests made from different materials (e.g. cardboard tubes, bamboo canes, wooden blocks) in order to achieve better coverage of the community present. The nests are easily replicated, can be modified to answer specific research objectives, and can be adapted to specifically investigate the nesting preferences and autecology of individual species. Trap nests also provide a powerful tool for studying fundamental ecological topics, the investigation of a range of interspecific interactions, and descriptions of ecological networks involving competition, predation, parasitism, and mutual use of floral resources.

Finally, trap nests provide a straightforward means of involving the public in pollinator conservation and citizen science schemes which can provide a means of method refinement and valuable data regarding biogeography and nesting behaviour of these understudied species.

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APPENDICES

Additional supporting information may be found in the online version of this article:

Supplementary File S1. Photographs of trap nests used in this study.

Supplementary File S2. Summary of study site information including area and dates related to flowering period and trapping period.

Supplementary File S3. Numbers of adults of five species of stem-nesting Hymenoptera which emerged from nest tubes of different diameters.

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