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Nest characteristics and associates of *Dolichovespula* (Hymenoptera, Vespidae) in Central Finland

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Abstract

In social vespine wasps, the nest characteristics and associates vary intra- and interspecifically. I studied the nest characteristics and nest associates of three *Dolichovespula* wasp species in boreal Finland. The average number of combs and cells per nest was similar among *D. media*, *D. saxonica* and *D. norwegica*, and similar to *Dolichovespula* in the temperate zone. Most *D. media* and *D. saxonica* colonies produced both gynes and males, whereas *D. norwegica* produced mainly either one. The average colony lifespan of *D. saxonica* was a bit over two months, i.e. shorter than documented for *Dolichovespula* in the temperate zone. The proportion of nests parasitised by the ichneumonid wasp *Sphécophaga vesparum* was 36% in *D. saxonica* and 50% in *D. media*; *S. vesparum* has not been recorded from *D. media* before. The proportion of parasitized cells was 0.6–11% for *D. saxonica* and 0.2–22% for *D. media*. The proportion yellow, overwintering cocoons of *S. vesparum* was highly variable among the nests. The proportion of nests parasitised by the moth *Aphomia sociella* was 36% in *D. saxonica* and 13% in *D. media*. *Sphécophaga* and *Aphomia* were not recorded from *D. norwegica* colonies, which supports studies in the temperate zone. The study adds up to the previous research on the nest structure and nest associates of vespines, and together they indicate that there is geographical variation within Europe and globally in the host use of *Sphécophaga*.

Keywords

Aphomia sociella, colony structure, social wasps, *Sphécophaga vesparum*, Vespinae

Introduction

Social vespine wasps (Vespinae) are divided in four to five genera (Persson 2015; Lopez-Osorio 2017), of which three occur in Finland: *Dolichovespula* (Rohwer, 1916), *Vespa* (Linnaeus, 1758) and *Vespula* (Thompson, 1869). Biology of *Dolichovespula*, especially that of *D. norwegica* (Fabricius, 1781) and *D. media* (Retzius, 1783), is poorly known compared to *Vespula*, partly because of the global invasions of the latter (Beggs et al. 2011). *Dolichovespula* and *Vespula* also differ in their sociality as well as colony and nest characteristics (Foster et al. 2001; Archer 2012) but there are also differences within *Dolichovespula* (Archer 2006). Colony and nest characteristics are biologically interesting as such, and they are needed to interpret possible intra- and interspecific differences in the identity and prevalence of nest associates (parasites, parasitoids, predators and scavengers), which can influence the size, activity and success of vespine colonies (Archer 2012).

In Finland, cuckoo wasps *Dolichovespula adulterina* (Du Buysson, 1905) and *D. omissa* (Bischoff, 1931) parasitize *D. saxonica* (Fabricius, 1793) and *D. sylvestris* (Scopoli, 1763), respectively (Douwes et al. 2012). Cuckoo wasps do not feed on the host larvae but the queen replaces the host queen and use the host workers as slaves to produce reproductive castes. The wasp *Sphecofaga vesparum* (Curtis, 1828) (Hymenoptera: Ichneumonidae) is nearly a cosmopolitan ectoparasitoid of Vespinae (Archer 2012). Two subspecies are known: the European *S. vesparum vesparum* and the North American *S. vesparum burra* (Cresson, 1869). The endoparasitoid beetle *Metoecus paradoxus* (Linnaeus, 1761) (Coleoptera: Ripiphoridae) and related taxa are common parasites of *Vespula* but have rarely been observed from *Dolichovespula* nests (see Carl and Wagner 1982; Makino 1982). Similarly, the syrphid *Volucella pellucens* (Linnaeus, 1758) (Diptera: Syrphidae) parasitizes *Vespula* but not *Dolichovespula*. The moth *Aphomia sociella* (Linnaeus, 1758) (Lepidoptera: Pyralidae) is a common inhabitant of *Dolichovespula* nests (Gambino 1995). It pre-dates eggs, larvae and cocoons, but feeds also on waste found in nests. The species generally attacks declining colonies and thus is likely to have a marginal effect on colony success (Gambino 1995; Archer 2012). The overall prevalence (proportion of occupied nests) of nest associates in vespine nests is usually high but the nest-specific prevalence (proportion of occupied cells or the number of individuals) is usually low (Archer 2012).

The nest characteristics and associates of *Dolichovespula* are poorly studied in comparison with *Vespula*, especially in the boreal region. The extant studies have been conducted in very different geographical locations and suggest geographical variation in the biology of *Dolichovespula* (e.g. US, Greene et al. 1976; Gambino 1995; Japan, Makino 1982; UK, Archer 2000, 2002; Poland, Pawlikowski and Pawlikowski 2010; Nadolski 2012, 2013). I studied the colony and nest characteristics, as well as the nest associates, of *D. saxonica*, *D. media* and *D. norwegica* in boreal Central Finland.

Methods

The study was conducted in the province of Central Finland, which belongs to the middle boreal zone. During 2019–2022 *Dolichovespula* nests were located based on public information and active searching. All nests were within 60 km (mostly within 5 km) from the Jyväskylä city centre. Nests were in a variety of natural and anthropogenic locations, mostly in semiurban broadleaved or mixed forests. Most *D. saxonica* nests were inside wooden bird nest boxes (1.3–2.0 m above ground) that were used for a bird study (Komonen and Tornainen 2022). The nests were removed and their characteristics (number of combs and cells), and the number of nest associates or parasitized cells, were recorded in the laboratory. Small supplementary combs (one *D. saxonica* nest) between the main combs were not counted as separate combs but they were included in the total cell counts. The number of small and large cells in each comb was also counted or estimated but because they are difficult to distinguish in combs having intermediate-sized cells (Greene et al. 1976; Archer 2006), I do not provide quantitative estimates of small-to-large cell ratios. Interspecific differences in the colony size (total number of combs and cells) were analysed with the non-parametric Kruskal-Wallis test. The sample size may vary in different analyses and data summaries because not all characteristics were recorded from every nest for varying reasons. Nest characteristics are available in the Suppl. material 1.

Lifespan was documented for seven *D. saxonica* colonies in bird nest boxes ($n = 7$), which were monitored about once a week for a bird study from April 2021 onwards. Colony lifespan was determined as the difference between the first date the wasp was observed and the date of colony removal. Because the colonies were initiated earlier than observed at the first time, I estimated the date of colony initiation: the number of days between the date a nest box was observed occupied and the previous date the nest box was empty, divided by two). At the time of removal, four colonies had just ceased and three were still active, although at their final phase with males and gynes.

To make colonies comparable they should be in the same developmental phase. This was not fully possible. Thus, in analyses I focused on the mature colonies, which were determined as having large cells containing sealed brood or large cells from which the adults had emerged (see Archer 1981). All *D. media* ($n = 8$) and *D. norwegica* ($n = 4$) nests were mature, whereas two *D. saxonica* ($n = 31$) nests had only small cells, one had only large cells and two were destroyed by *A. sociella*. To document, if the nests produced both males and gynes, I recorded the adults and opened the closed cells. I also examined each nest for nest associates, of which *S. vesparum* and *A. sociella* were abundant and could be identified to species. All open and closed host cells were examined for *S. vesparum* cocoons. I recorded the number of cocoons (one host cell may host several parasitoid cocoons), the colour of the cocoon (white or yellow), and whether the parasitoid had emerged from the cocoon (i.e. there was an exit hole; Fig. 1). *Sphecophaga vesparum* lays three kinds of eggs: those that produce 1) white cocoons and then brachypterous females; 2) those that produce weak, yellow cocoons and then winged



Figure 1. White *Sphecophaga vesparum* cocoons from which the parasitoid has emerged, and closed yellow cocoons in a nest of *Dolichovespula media*. A host cell may have both white and yellow cocoons. Photo: Atte Komonen.

females and possibly males; and 3) resistant yellow, overwintering cocoons (Donovan 1991). I classified the cocoons as white or yellow because I was not confident in separating the two types of yellow cocoons, except in one nest. *Aphomia sociella* larvae were counted or the past presence of the species was determined by the silk spun by the larvae.

Results

The number of combs and cells was variable among nests but there were no interspecific differences ($H = 1.1$, $p = 0.57$ and $H = 0.7$, $p = 0.72$, respectively, $df = 2$, $n = 38$;

Table 1. Characteristics of the studied nests, the percent parasitized nests, the mean (min–max) percent of parasitized cells in occupied nests, and the mean (min–max) number of individuals per occupied nest.

	Nest n	Combs Mean (SD)	Cells		<i>S. vesparum</i>		<i>A. sociella</i>	
			Med, Mean (SD)	% nests	% cells	Exx./nest	% nests	Exx./nest
<i>D. saxonica</i>	31	3.7 (1.2)*	854, 739 (420)	36 ^e	4 (0.6–11) ^g	19 (2–48) ^e	36 ^e	33 (2–94) ^g
<i>D. norwegica</i>	4	4.3 (0.5)	712, 1079 (762)	0	0	0	0	0
<i>D. media</i>	8	4.1 (0.8)	626, 674 (275)	50	11 (0.2–22)	104 (1–256)	13	1

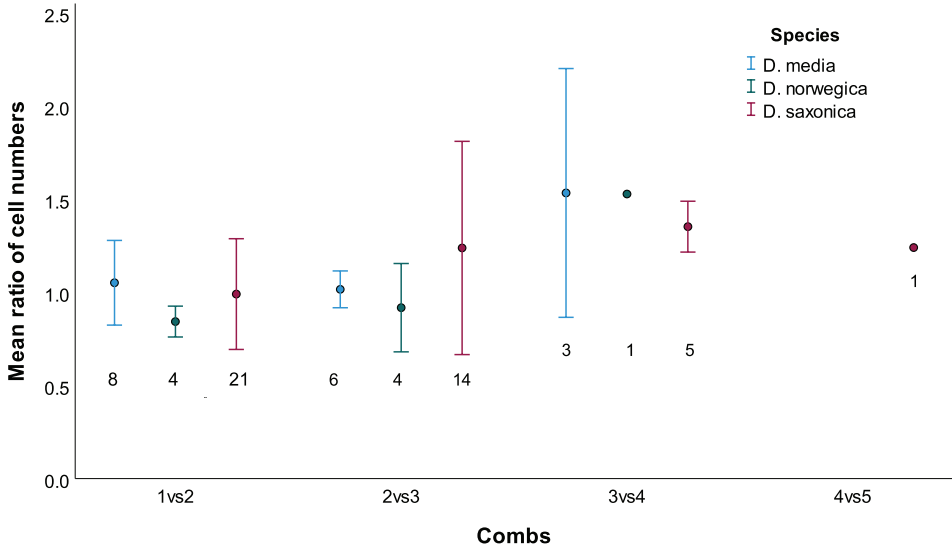
*n = 26; ^an = 28; ^bn = 9; ^cn = 10; ^dn = 4**Figure 2.** The mean ratio (\pm 1SD) of the cell numbers in adjacent combs (1 is the basal, oldest comb). Numbers give the number of nests.

Table 1). Of the basal combs ($n = 32$), 88% had only small cells, and of the newest comb, 47% consisted only of small cells. The middle combs had generally large or medium cells, and if there were small cells (63% of nests), they were peripheral. The mean ratio of cell numbers in adjacent cells was similar among the species and increased from the basal (oldest) towards the outer (newest) combs (Fig. 2). The mean \pm SD lifespan of *D. saxonica* colonies was 70 ± 4 days ($n = 7$).

The most frequent and abundant nest associates were *S. vesparum* and *A. sociella*. These attacked *D. saxonica* and *D. media*, whereas no nest associates were found in *D. norwegica* nests. Both in *D. media* and *D. saxonica*, *S. vesparum* parasitized large and small cells. In *D. media*, there was an average of 1.5 (max. = 8) parasitoid individuals per host cell, and in *D. saxonica* 1.1 (max. = 4). In both species, there was generally more yellow than white *S. vesparum* cocoons (Table 2). In *D. media* colonies, the ratio of white to yellow cocoons was highly variable. The proportion of white or yellow cocoons, from which the parasitoid had emerged, was less variable. Most of the white cocoons were empty, whereas the yellow cocoons were still inhabited. In *D. saxonica*

Table 2. The number and ratio of white and yellow cocoons of *S. vesparum*, and the proportion of open (parasitoid emerged) white and yellow cocoons in *D. media* (Dm) and *D. saxonica* (Ds) nests.

Nest	White	Yellow	Ratio	Empty (%)	
				White	Yellow
Dm1	15	21	0.71	0.93	0
Dm2	25	231	0.11	0.76	0.02
Dm3	65	55	1.18	0.89	0.11
Dm4	0	1	0	na	0
Ds1	2	31	0.06	0.5	0.06
Ds2	10	21	0.48	0.9	0.05
Ds3	11	37*	0.30	1	0.27
Ds4	4	1	4	0.25	0
Ds5	1	1	1	1	1
Ds6	0	2	0	na	0.5
Ds7	2	22	0.09	0	0
Ds8	0	7	0	na	0.86

* 8 of these were yellowish.

colonies, the ratio of white to yellow cocoons was less variable than in *D. media*. The proportion of white or yellow cocoons, from which the parasitoid had emerged, was more variable than in *D. media*; exceptionally large or small proportions were associated with small number of parasitoids. Similar to *D. media*, white cocoons were more often empty than yellow cocoons. No social vespine parasites were observed.

Discussion

Nest characteristics

The nest locations were variable. All *D. norwegica* nests were aerial in trees or bushes. All *D. media* nests were aerial in natural or anthropogenic objects. Nest locations of *D. saxonica* were the most variable and generally aerial. In addition to natural objects, they were found in many anthropogenic objects. The results underscore flexibility in nesting locations and ability to utilize anthropogenic locations (at least *D. saxonica* and *D. media*; see also Archer 2006; Nadolski 2012). Because nest location can affect colony size, nest characteristics, and the production of sexual castes (for *D. saxonica* see Nadolski 2012), some interspecific differences may result from the ecological context rather than being evolutionary traits. The lifespan of *D. saxonica* colonies was about a month shorter than that of *Dolichovespula* in the temperate zone (cf. Archer 2006). Because the summer of 2021 was record-warm in Central Finland, this might have sped up the colony development and shortened the lifespan.

The studied *Dolichovespula* species had more similarities than differences and the colonies were of typical size for *Dolichovespula* (see Archer 2006). The typical number of combs was three to five in all the studied species (see also Archer 2012; Nadolski 2012). The number of combs in *D. saxonica* nests varied the most, which may result from the diverse nest locations (Nadolski 2012) and larger number of prematurely ceased or

collected nests. The average number of cells corroborates those documented for these species in the temperate zone (Makino 1982; Archer 2000, 2006; Nadolski 2012). Although there were no interspecific differences in the average number of cells (see also Makino 1982), *D. media* combs had less cells per unit of comb area than *D. norwegica* and *D. saxonica*, which can be explained by its larger body size. The ratio of cell numbers in adjacent combs was also very constant among the species. Because the newest, outermost combs was left out from this analysis, this result is not biased if some nests were still being enlarged (nest growth at the final stage is mostly enlarging the newest comb).

Most nests, especially the larger ones, had more than one comb that were dominated by small cells (usually the first and the last). Although the middle combs consisted generally of large or medium cells, mixed combs were common. These results support previous studies indicating intra- and interspecific variation in the distribution of cell sizes among combs (Greene et al. 1976; Makino 1982; Archer 2000, 2006; Nadolski 2012). The result that the newest comb was dominated by small cells agrees with that observed for *D. saxonica* (Nadolski 2012). The newest comb is probably used to produce males by the reproductive workers, which can be related to limited queen control in declining colonies or typical kin structure of *Dolichovespula*, resulting in limited worker policing (Foster et al. 2001). In the mixed combs, the small cells were usually peripheral, which differs from previous studies of *Dolichovespula* (Archer 2006). Because it is not always easy to distinguish different cell sizes in mixed combs, especially if there are cells of intermediate size (Archer 2006; Nadolski 2012), I refrain from more quantitative conclusions.

The production of males and gynes varied among species. 75% of the *D. media* nests had both males and gynes; it is likely that also the other two colonies produced or would have produced both sexes, but in one of these nests most individuals had already left and the other was heavily parasitized. 55% of the *D. saxonica* colonies that had sexual castes produced both males and gynes; all the single-sex colonies produced only males. Because larvae were still present it is possible that some would have produced gynes later. It is known, however, that *D. saxonica* colonies usually produce more males than gynes (Nadolski 2012). My results support the observations that colonies of *D. norwegica* often specialize as male-producing or gyne-producing (Archer 2000, 2006), but occasionally both sexes can be produced. Because gynes and males can be produced in phases (Greene et al. 1976; Archer 2002, 2006), prematurely ceased or collected nest may give biased data about the production of sexual castes. Unfortunately, most studies (including this one) cannot conclude anything quantitative about the production of gynes and males, because this would require continuous monitoring of the production of sexual castes.

Nest associates

The most common nest associates were *S. vesparum* and *A. sociella*, whereas no social vespine parasites were observed. *Sphécophaga vesparum* parasitized both *D. media* and *D. saxonica*. To my knowledge, *S. vesparum* has not been recorded from *D. media* before (see also Archer 2012). The lack of parasitism in *D. norwegica* may result from a small sample size, rather than lack of suitability as a host; however, *S. vesparum* has not been

recorded from *D. norwegica* in England despite extensive sampling (Archer 2000, 2012), which suggests that there indeed are differences in host suitability. Similarly, *S. vesparum* has not been documented from *D. saxonica* nests in the UK (Archer 2012) but has been observed from those in Poland (Pawlikowski and Pawlikowski 2010; Nadolski 2013). Although *S. vesparum* has also been found from *D. sylvestris* and *Vespula* nests with low prevalence (Archer 2002, 2012), I have not recorded the species from *V. vulgaris* nests in Finland ($n = 10$). The proportion of nests parasitized by *S. vesparum* was higher in *D. media* (50%) than in *D. saxonica* (36%), which may result from the smaller sample size in *D. media*. These figures are somewhat higher than in other studies on *Dolichovespula* (Greene et al. 1976; Archer 2012; Nadolski 2013). In North American *Vespula*, there seems to be much higher prevalence of *S. v. burra* (up to 80%; MacDonald et al. 1975; Roush and Akre 1978; MacDonald et al. 1980; Akre et al. 1982; Reed and Akre 1983). It is known that the cuticular hydrocarbons of *S. vesparum* differ depending on their *Vespula* host species (Oi et al. 2020), so it is possible that the same phenomenon applies also to *S. vesparum* in different *Dolichovespula* hosts; yet, the acquisition and role of hydrocarbon signatures in host discrimination is not understood. Furthermore, given the geographic variation in morphology and host use of *Sphécophaga*, it is possible that there are more than two subspecies (see Berry et al. 1997).

The nest-specific rate of parasitism was variable but generally low. Again, the average rate of parasitism was higher in *D. media* (11%) than in *D. saxonica* (4%). These figures are like, or slightly higher (*D. media*) than in other studies of *Dolichovespula* (Greene et al. 1976; Pawlikowski and Pawlikowski 2010; Archer 2012). The proportion of parasitized cells was 22% in the smallest *D. media* nest (277 cells), which suggests that parasitism had a significant negative effect on the colony fitness. In North American *Vespula*, there seems to be similar or slightly lower prevalence of *S. v. burra* (Roush and Akre 1978; MacDonald et al. 1980; MacDonald and Matthews 1981; Akre et al. 1982; Reed and Akre 1983). Because I did not record the larvae of *S. vesparum*, the true parasitism rate is higher, but this applies to other studies as well. Furthermore, I estimated parasitism as the proportion of parasitized cells to all cells, not to the cells occupied by the host larvae (see also Akre et al. 1982; Reed and Akre 1983), which also underestimates fitness consequences. Apparently, there are either differences in host suitability and preference, or spatial variation in the distribution of *S. vesparum*, since even closely-related vespines may have different prevalence of *S. vesparum* (MacDonald and Matthews 1976; this study). Although *S. vesparum* can occasionally cause complete mortality of worker larvae in queen-phase nests (Archer 2012), its overall effect in mature colonies seems minor.

In general, there were more yellow than white cocoons. Yellow cocoons are those in which the adult parasitoid overwinters (Donovan 1991), which suggests that most *S. vesparum* overwinter inside the nest in Central Finland. *Sphécophaga vesparum* had emerged from much larger proportion of the white than yellow cocoons, which agrees well with the overwintering scenario. The proportion of white or yellow cocoons from which the parasitoid had emerged was more variable in *D. saxonica* than in *D. media*; exceptionally large or small proportions were associated with small number of parasitoids, so they are likely artefacts of small sample size. It is likely that the yellow

cocoons, from which *S. vesparum* had emerged, were weak yellow cocoons, which I generally could not distinguish from the resistant yellow ones. However, the empty yellow cocoons in one *D. saxonica* colony were yellowish cocoons, i.e. probably weak yellow cocoons sensu Donovan (1991). However, many yellow but empty cocoons were not visually different from the closed yellow cocoons.

The prevalence of *A. sociella* was similar to *S. vesparum* in *D. saxonica* nests but lower in *D. media* nests. Low prevalence in *D. media* nests may be explained in that proportionally more nests were active when collected, because *A. sociella* predominantly colonize declining colonies. *Aphomia sociella* was not found from *D. norwegica* nests, and it remains unknown if the species can colonize *D. norwegica* nests. Although *M. paradoxus* has been occasionally observed from the nests of *Dolichovespula* in other parts of the world, no individuals were observed in this study, although the species is common in *V. vulgaris* nests in the study region (Komonen 2022). This indicates that *M. paradoxus* is very rare in *Dolichovespula* nests in Finland and possibly does not parasitize them at all. This supports previous observations from the temperate zone (Carl and Wagner 1982; Makino 1982).

Conclusions

To establish any pattern in biology, studies must be replicated in space and time. This study supports some earlier studies about the biology of *Dolichovespula* but also suggests that some issues need more studies so that their generality can be evaluated. Particularly, the variation in the host use of *S. vesparum* needs more research attention, which requires that different *Dolichovespula* species are studied in the same regions. It is also clear that observed level of parasitism cannot cause significant year-to-year variation in *Dolichovespula* abundance but can occasionally cause moderate damage in individual colonies. Furthermore, more studies are needed on the other *Dolichovespula* than *D. saxonica*, especially since *D. norwegica* has no documented nest associates.

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Supplementary material I

Nest characteristics

Author: Atte Komonen

Data type: Nest characteristics

Explanation note: Nest locations, combs and cell numbers, and nest associates.

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