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Population dynamics of the social wasps, *Vespula vulgaris* and *Dolichovespula media* (Vespidae), in Finland

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Global change affects species in many ways. To understand spatio-temporal changes in population dynamics, monitoring data are needed. Social wasps (Vespidae) are ubiquitous in many environments. Using beer traps, we studied annual and seasonal population dynamics of workers of two social wasp species, *Vespula vulgaris* and *Dolichovespula media*, in south-central Finland over six years. The abundance of both species fluctuated annually. That of *Vespula vulgaris* displayed some cyclicity, unlike that of *D. media*; fluctuations were not fully synchronous among locations. Also, seasonal fluctuations were spatially and temporally variable. *Vespula vulgaris* was active later in the season, had longer flight period, and more abundance peaks than *D. media*, which generally had one short abundance peak. Our study suggests great spatio-temporal variation and species-specificity in the population dynamics of social wasps, which should be considered in designing monitoring protocols.

Introduction

Global change affects species distribution and abundance, and social wasps (Vespinae) are no exception. Although social wasps are widespread in anthropogenic environments, can reach high local densities, have invaded new regions, and are often considered a nuisance (Masciocchi *et al*. 2016, Sumner *et al*. 2019, Santaoja *et al*. 2023), their population fluctuations are still poorly documented (*see* Archer 2012). Many extant studies were not species specific, did not use systematic sampling, focused only on a few species or were geographically limited (Akre & Reed 1981, Archer 2012). Knowledge about spatio-temporal variation in population dynamics is important for understanding the impacts of environmental change and developing monitoring protocols.

The annual abundance of social wasps fluctuates greatly (Archer 2012). Although there is some indication of cyclic fluctuations, especially over short time periods, the cycle length and amplitude vary in time and space (Akre & Reed 1981, Pawlikowski & Pawlikowski 2006, Sorvari 2013, Masciocchi *et al*. 2016, Lester *et al*. 2017). Annual population fluctuations can be driven by extrinsic environmental factors (e.g. weather) and/or intrinsic density dependence; the latter is generally the prerequisite for cyclic fluctuations.

In social wasps, winter weather affects mortality of overwintering queens, whereas spring and early summer weather affects the number and size of successful colonies (Kasper 2004, Archer 2012, Masciocchi *et al*. 2016, Sorvari 2018). For social wasps, the most important weather factor is probably temperature. Although individual wasps are rather tolerant to low temperatures (Heinrich 1984, Coelho & Ross 1996, Kasper *et al*. 2008), cool spring and summer can cause colony failures or slow down colony growth and hence affect the number of individuals.

Of the intrinsic density-dependent factors, competition for nest sites and food, as well as parasites and pathogens, are possible reasons for (cyclic) fluctuations. Because social vespine wasps are generalist predators (Torniainen & Komonen 2021), competition for food is less likely a regulating factor than competition for nest sites (*see* Archer 2012). Parasitoids and predators, such as Lepidoptera, Diptera, Hymenoptera and Coleoptera, are common in nests but are rarely so abundant that they could be the primary cause of fluctuations (Donovan 1991, Gambino 1995, Komonen 2022, Komonen 2023). Little is known about microbes, fungi and viruses in wasps' nests (but *see* Rose *et al*. 1999). As suggested by Pawlikowski and Pawlikowski (2006), it seems likely that there is some density-dependent factor(s) that cause inherent cyclicity, but weather eventually determines if the abundance peak is realized or not; favourable weather can also compensate for inherently low-abundance years.

The abundance of social wasps varies also seasonally. A new colony is established in spring by an overwintering, mated queen (Archer 2012). After the first workers emerge, the queen remains in the nest and focuses on egg laying. Colonies are annual and grow larger until the late summer or autumn collapse (Archer 2012, Masciocchi *et al*. 2016). In the northern temperate and boreal zones, there are evidence that colony growth is affected by weather (Akre & Reed 1981, Pawlikowski & Pawlikowski 2006, Sorvari 2018; but *see* Fox-Wilson 1946). Just before the collapse, colonies produce sexual castes, which mate in autumn; only the queens overwinter. In Finland, the number of workers reach their peak in late July to mid-September, depending on the species and year (Pekkarinen & Huldén 1995); especially those species, which are readily beer-trapped, typically peak in August (Sorvari 2013, but *see* Komonen *et al*. 2020).

In Finland, there are 12 species of social vespine wasps (Douwes *et al*. 2012). Most species have a nation-wide distribution, whereas *Vespula germanica* and *Vespa crabro* have a southern distribution. Probably due to climate change, both species are extending their ranges (Teräs *et al*. 2003, Sorvari 2013, 2018, Komonen *et al*. 2020) which may also affect their dynamics calling for regular monitoring.

Our goal was to study the annual and seasonal population dynamics of social wasps (Vespinae) in south-central Finland using a standardized sampling with beer traps. Annual wasp dynamics are poorly known in the boreal zone, and seasonal dynamics have rarely been studied over many years. We asked (1) how much the worker populations fluctuate annually and are the fluctuations cyclic; (2) are the annual fluctuations spatially consistent; and (3) are the seasonal fluctuations spatially and annually consistent. We focus on the two most common species, *Vespula vulgaris* and *Dolichovespula media*.

Material and methods

Study sites

The study was conducted in south-central Finland. The main study site (Jyväskylä) was sampled for six years (2019–2024). To evaluate generality of the wasp dynamics, less intensive trapping was conducted in Hyytiälä and Lammi for four years (2019–2022) and Kuopio for five years (2017–2021) (Appendix 1); the data from Turku (2008–2014) were largely published in Sorvari (2018) so we used it only when comparing wasp density and occupancy, as well as occupancy dynamics among sites. The southernmost site Turku is 390 km SW from the northernmost site Kuopio. Traps (*see* Sorvari 2013: fig. 2) were hung in trees or bushes 1.5 to 2 m aboveground. Each trap was filled with 2 dl of beer and a hint of brown sugar and dry yeast (*see* Dvorak 2007, Sorvari 2013). The mean daily temperature and precipitation from April to August near the main study site are listed in Appendix 2. Individuals were identified to species using Douwes *et al*. (2012).

Trapping

At the main study site, we studied worker wasp dynamics during six years. Traps were kept in the same locations except for two traps which had to be moved 80 m and 100 m, respectively, in 2022. Traps were set for somewhat variable periods during the peak flight season of worker wasps from July to September (Appendix 1). Annual fluctuations were studied with 28 traps, of which 22 were operating for 11 days from mid-July and 11 days from mid-August onwards, and 6 traps were operating continuously and those were emptied and refilled once a week. In case of the continuously operating traps, we used the data from a 14-day periods in mid-July and in mid-August to match the sampling period of the other traps; this was also done in Hyytiälä and Lammi, where only continuously operating traps (n = 3 in each) were used. In Kuopio and Turku, 20 traps were operating for a week, starting from mid-August (Appendix 1). Seasonal fluctuations were studied with continuously operating traps, which generally were used from the second week of July to late September/early October in Jyväskylä, and to mid-September at other sites. Over the six years and all the study sites, only 0.03% of the trapping periods (= time between set up and emptying of a single trap) included damaged and dried traps. If the dried traps contained no wasps (n = 14 trapping periods), they were excluded from the data for that trapping period; if they contained wasps (n = 5), they were included.

Statistical analyses

Annual fluctuations were analysed separately for *V. vulgaris* and *D. media*, using statistical tests and visual interpretation of graphs. Statistical analyses were conducted only for Jyväskylä and Kuopio, as they had sufficient data. Both sites were analysed separately due to different trapping years. Because of some damaged traps and variation in trapping times, wasp abundance was standardized to mean number of individuals per trap day for each trapping period (i.e. 7, 11 or 14-day period depending on the analysis).

Differences in the numbers of individuals among years were analysed with generalized linear mixed models (GLMM), as implemented in IBM SPSS Statistics ver. 28. Trap (random factor) was considered a subject and Year and Month (fixed factors) repeated measures; an interaction between Year and Month was included. The normal distribution with an identity link, and diagonal as the repeated covariance structure, were used, as it gave the smallest AICc-value and/or best model fit, as judged by residuals. We also modelled the response with the Poisson and negative binomial distributions using counts of individuals without standardization but with an offset variable controlling for the difference in trapping times. These models did not fit the data as well as did the chosen model, yet they all provided qualitatively similar results, which indicated that the statistical analyses were robust. For post-estimation settings, degrees of freedom were estimated using the Satterthwaite method, and the tests of fixed effects and coefficients were estimated using robust covariances. Estimated means were compared using pairwise contrasts, and the sequential Bonferroni was used to adjust for multiple comparisons. Based on the visual inspection of the residual plots, residuals were adequately normally distributed and homoscedastic.

Interspecific differences in annual and seasonal abundance and fluctuations were analysed statistically, but also evaluated visually. Interspecific differences in the total number of trapped individuals each year were tested with a χ^2-test (df = 1), using exact p values that were Bonferroni adjusted within each site. Coefficient of variation (CV) was used to quantify and compare annual variation in abundance at different sites and species over a comparable period in August. In Jyväskylä, CV was also used to quantify the magnitude of seasonal (weekly) variation for each species (11 to 16 trapping weeks each year in 2019–2024; n = 6 continuously operated traps); interspecific differences in CV were analysed with a t-test (Sokal & Brauman 1980). To find out if the weekly abundances of *V. vulgaris* and *D. media* fluctuated in synchrony, we correlated the first differences in the six-year time series; the first difference being the change in

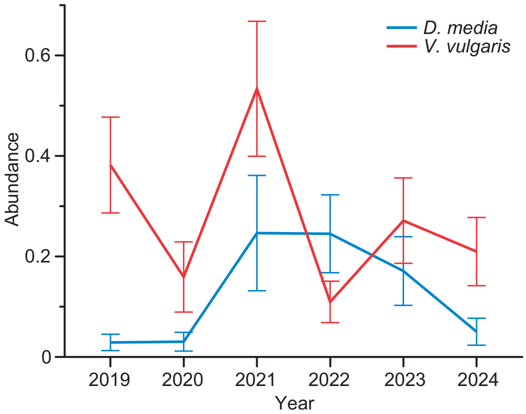

Fig. 1. Mean ± 95%CI numbers of *Vespula vulgaris* and *Dolichovespula media* workers per trap-day in Jyväskylä 2019–2024; traps (n = 28) operated each year for about two weeks from mid-July and mid-August onwards.

value from a point in the time series to the next point. Significant correlation would indicate that the weekly abundances covary.

Results

At the main study site (Jyväskylä), the mean number of *V. vulgaris* individuals per trap day varied among years (GLMM: $F_{11,59}$ = 8.71, p < 0.001; Table 1 and Appendix 3) and among trap locations (random effect Z = 2.54, p = 0.01). There was also some tendency for annual cyclicity (Fig. 1). The mean number of individuals did not differ consistently between July and August (contrast estimate = 0.025; Table 1 and Fig. 2). The mean number of *D. media* individuals per trap day varied among years, as well as between July and August (GLMM: $F_{11,66}$ = 10.98, p < 0.001; Table 1 and Appendix 3) and among trap locations (Z = 2.09, p = 0.036), and there was no indication of annual cyclicity (Fig. 1). The mean number of individuals was higher in July than in August (contrast estimate = 0.046; Table 1 and Fig. 2). The total number of trapped *V. vulgaris* individuals was each year greater than that of *D. media* (χ^2 > 13.9, p < 0.01; Appendix 1). Coeffi-

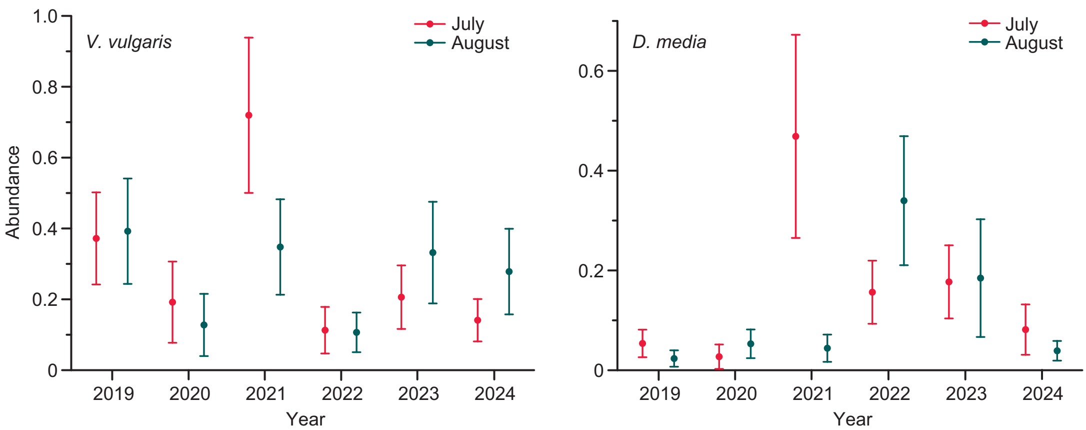

Fig. 2. Mean ± 95%CI numbers of *Vespula vulgaris* and *Dolichovespula media* workers per trap day in July and August in Jyväskylä 2019–2024. Traps (n = 28) operated for about two weeks from mid-July and mid-August onwards each year.

Table 1. GLMM summary of the standardized number of *V. vulgaris* and *D. media* workers in beer traps in Jyväskylä in July and August 2019–2024.

Term	*Vespula vulgaris*				*Dolichovespula media*			
	F	df_1	df_2	p	F	df_1	df_2	p
Year	12.58	5	49	< 0.001	8.16	5	44	< 0.001
Month	0.45	1	17	0.510	7.46	1	68	0.008
Year × Month	6.30	5	55	< 0.001	9.70	5	59	< 0.001

cients of variation across the years were 121% and 210% for *V. vulgaris* and *D. media*, respectively. For both species the mean number of individuals and trap occupancy showed rather synchronous annual fluctuations (Fig. 1 and Appendix 4).

In Kuopio, the mean number of *V. vulgaris* individuals per trap day varied among years (GLMM: $F_{4,43} = 15.65$, $p < 0.001$; Appendix 3) but not among trap locations ($Z = 0.84$, $p = 0.40$). There was also a tendency for annual cyclicity (Fig. 3). The mean number of *D. media* individuals per trap day varied among years but or among trap locations (GLMM: $F_{4,34} = 3.02$, $p = 0.031$; $Z = 1.14$, $p = 0.25$; Appendix 3), and there was no indication of annual cyclicity (Fig. 3). The total number of trapped *V. vulgaris* individuals was each year larger than that of *D. media* ($\chi^2 > 21.6$, $p < 0.01$). Coefficients of variation across the years were 73% and 98% for *V. vulgaris* and *D. media*, respectively. For both species the mean number of individuals and trap occupancy showed rather synchronous annual fluctuations (Fig. 3 and Appendix 4).

The patterns at other sites were partly similar. In Turku, the total number of trapped *V. vulgaris* individuals was each year greater than that of *D. media* ($\chi^2 > 11.8$, $p < 0.01$; Appendix 3), except in 2017 and 2013, respectively, when no difference was observed. Coefficients of variation across the years were 97% and 82% for *V. vulgaris* and *D. media*, respectively. For both species the mean number of individuals and trap occupancy showed rather synchronous annual fluctuations (Appendix 4; Sorvari 2018). In Hyytiälä, *D. media* was more abundant in 2021 and 2022 ($\chi^2 > 19.8$, $p < 0.01$; Appendix 3) but no difference was observed in 2019 and 2020 (Fig. 4). In Lammi, *V. vulgaris* was more abundant in 2019 and 2022 ($\chi^2 > 8.6$, $p < 0.05$; Appendix 3), *D. media* in 2021 ($\chi^2 = 14.8$, $p = 0.004$) and no difference was found in 2020 (Fig. 4). Compared with those in Jyväskylä, fluctuations in Kuopio were partly asynchronous, and those in Lammi and Hyytiälä partly synchronous; in Turku, trapping years did not overlap with those at the other sites.

Seasonal dynamics were variable. In Jyväskylä, the magnitude of variation (measured as CV) in the number of individuals was similar for *V. vulgaris* and *D. media* each year ($t = 0.16$–1.13, df = 20–40, $p > 0.10$). Weekly abundance fluctuations of the two species were not correlated (r between the first differences = 0.04, $n = 83$, $p = 0.7$; Appendix 5). *Dolichovespula media* had a single peak, generally during the weeks 30 and 31, whereas *V. vulgaris* either lacked a clear, single peak or had a few peaks (Fig. 5), and also flew later in the season and had a longer flight period. Seasonal dynamics in Hyytiälä and Lammi were highly variable (Appendix 6), but because there were only three traps at these sites, the pattern was sensitive to random fluctuations. The abundance peak of *V. vulgaris*, and especially that of *D. media*, was about two to three weeks earlier in 2021 than in the other years.

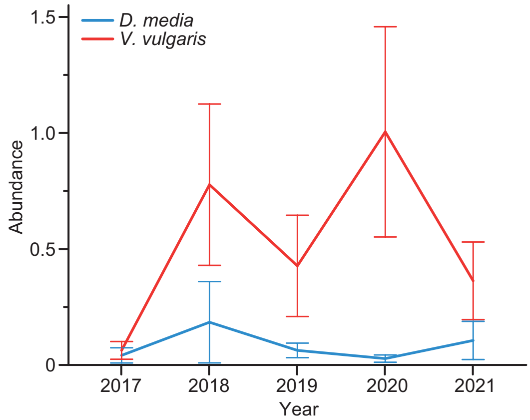

Fig. 3. Mean ± 95%CI numbers of *Vespula vulgaris* and *Dolichovespula media* workers per trap day in Kuopio 2017–2021; traps (n = 20) operated for one week from mid-August onwards each year.

In 2021, the mean daily temperature in Jyväskylä in June and July was about 1 and 2 °C higher, respectively, than in the next warmest year, and the average daily precipitation was below the six-year average during both months (Appendix 2).

Discussion

The abundances of *V. vulgaris* and *D. media* varied greatly among sites and years, as well as within season. This is a general phenomenon and has been shown with different methods, such as observing foraging adults and counting nests, as well as using malaise, suction and bait traps (Akre & Reed 1981, Pawlikowski

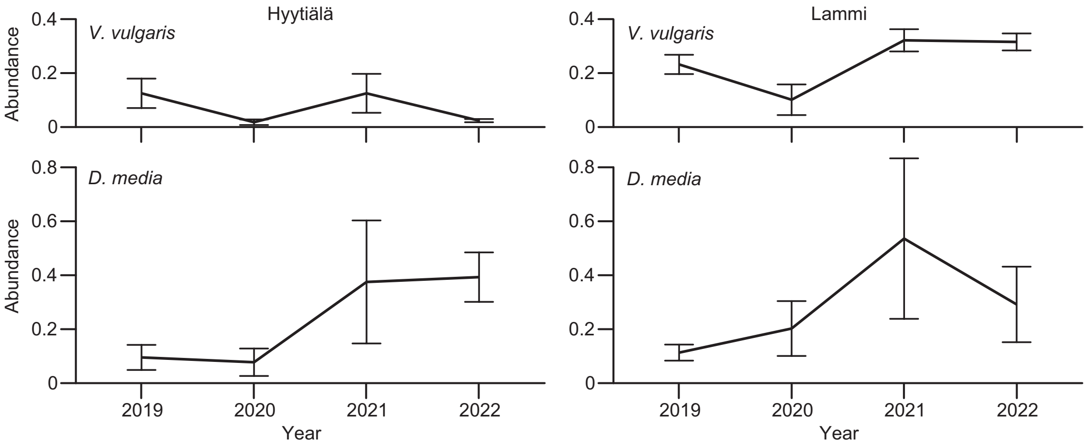

Fig. 4. Mean ± SE numbers of *Vespula vulgaris* and *Dolichovespula media* workers per trap day in Hyytiälä and Lammi 2019–2022 (three traps ran for 56 days from mid-July onwards each year in both sites).

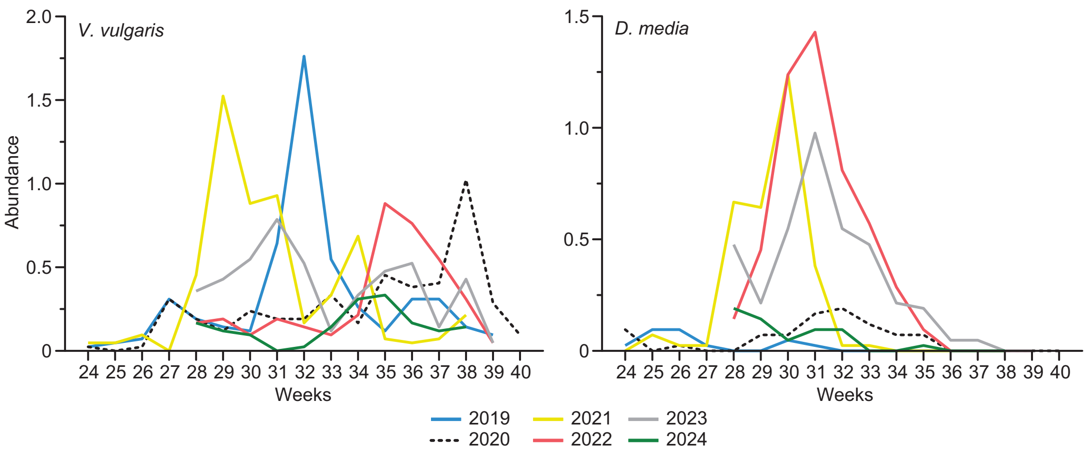

Fig. 5. Mean numbers of *Vespula vulgaris* and *Dolichovespula media* workers per trap day (n = 6 traps) in Jyväskylä 2019–2024.

& Pawlikowski 2006, Sorvari 2013, Masciocchi *et al*. 2016, Lester *et al*. 2017). At the two northernmost sites, Jyväskylä and Kuopio, and the southernmost site Turku, *V. vulgaris* was clearly more numerous than *D. media*, whereas in Hyytiälä and Lammi there was more variation annually. Low abundance of *D. media* in Kuopio and Turku can be partly explained by the fact that traps operated in August, which is generally after the peak flight time of the species, as shown here. Magnitude of population fluctuations of both species varied among locations, but there was no consistent interspecific difference.

While some annual fluctuation cyclicity was observed in *Vespula vulgaris*, this was not the case in *D. media*. Annually cyclic fluctuations have been documented for *Vespula* species in Europe (Archer 2001, Sorvari 2013, 2018), yet the amplitude of the cycles tends to vary. For example, in southern Finland the abundance of *V. vulgaris* and *V. germanica* fluctuates annually, but occasionally there are years of extreme abundances (Sorvari 2018, this study). Our results also support the lack of annual cyclicity in *D. media* in Finland and, interestingly, two bad years were followed by three good years exactly as in Sorvari (2013). Whether this is a coincidence or indicates more complex dynamics than in *V. vulgaris*, requires further long-term studies. The reasons for different dynamics of *D. media* and *V. vulgaris* (or more generally of *Dolichovespula* and *Vespula*) are not known but the occasional mass migrations of *D. media* queens can play some role (Mikkola *et al*. 2007, Sorvari 2013). Both genera have different parasitoids (Komonen 2022, Komonen 2023) and vertebrate predators (Archer 2012), which could cause differences in cyclicity (pathogens of vespines are poorly known). The challenge for researchers is that detecting population regulation with a high probability requires decades of data (Woiwod & Hanski 1992).

Seasonal dynamics were predictable overall: the number of workers increased from spring and reached peak abundance in late summer. Generally, worker abundance started to increase around the last week of July but the timing of the abundance peak varied annually. Over the six years, the abundance of *V. vulgaris* did not differ between mid-July and mid-August, whereas *D. media* was slightly more abundant in mid-July. Yet, in any given year, both species can reach the peak abundance in July or August, most likely depending on the spring and summer weather (Akre & Reed 1981, Pawlikowski & Pawlikowski 2006, Sorvari 2018; but *see* Fox-Wilson 1946). There was some difference in the timing of abundance peaks between *V. vulgaris* and *D. media* in Jyväskylä: the former had more variation in the timing than the latter, and the weekly abundances did not covary. Some of the variation in the number and timing of abundance peaks could be explained by weather. For example, in the year 2021, the abundances of both species were exceptionally high, and the timing of the peak abundance was up to three weeks earlier than in the other years. High wasp abundances and early peaks could be explained by the warm and dry summer of 2021, especially in June and July. However, also the year 2024 was very warm from May to August, yet wasp catches were poor. Thus, the causal relationship between weather and wasp abundance is not straightforward, and its reliable documentation would require much longer time series than the present six years (*see* Woiwod & Hanski 1992).

Large variation in wasp abundance among trap locations is expected, since social wasps live in colonies; thus, traps that are near nests can attract considerable number of individuals. Conspecific attraction and learning can contribute to the clumped distribution of workers in food resources and traps (Reid *et al*. 1995, Lozada & D'Adamo 2011). Foraging distances are generally some hundreds of meters around the nest but vary depending on wasp species, location and availability of food sources (Archer 2012). Because beer traps are generally lethal thus preventing wasps from returning to nest, wasps are unlike to share information about the food source (*see* Santoro *et al*. 2015). Thus, lethal traps could give a more accurate picture of the abundance of certain wasp species in an area than non-lethal methods, unless individuals are marked. It may also be useful to accompany any trapping scheme with direct, systematic observation of foraging wasps, but the relationship between trap catches and direct observations should be studied. Although only three traps operated in Hyytiälä and Lammi, yet their catches roughly reflected the abundance of *V. vulgaris* and *D. media* in Jyväskylä, which was extensively sampled. Thus, although the more traps the better, smaller number of traps can be partly compensated with longer trapping periods. Longer sampling periods are also encouraged due to the intra- and interspecific variation in the seasonal peak abundance.

Our study shows that different social vespine wasp species have different annual and seasonal dynamics. These differences should be considered in developing monitoring schemes for research or environmental change. Given the high variability in wasp abundance, even among nearby traps, spatio-temporally extensive trapping is needed to get reliable species-specific national or regional data over years. Despite its limitations, long-term standardized monitoring of social vespine wasps is easy to conduct and increases our knowledge about insect population fluctuations.

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Appendix 1. Trapping period and effort by site and year, and the number of trapped wasp individuals as well as that of the two most numerous species. Sites are ordered from the south to the north.

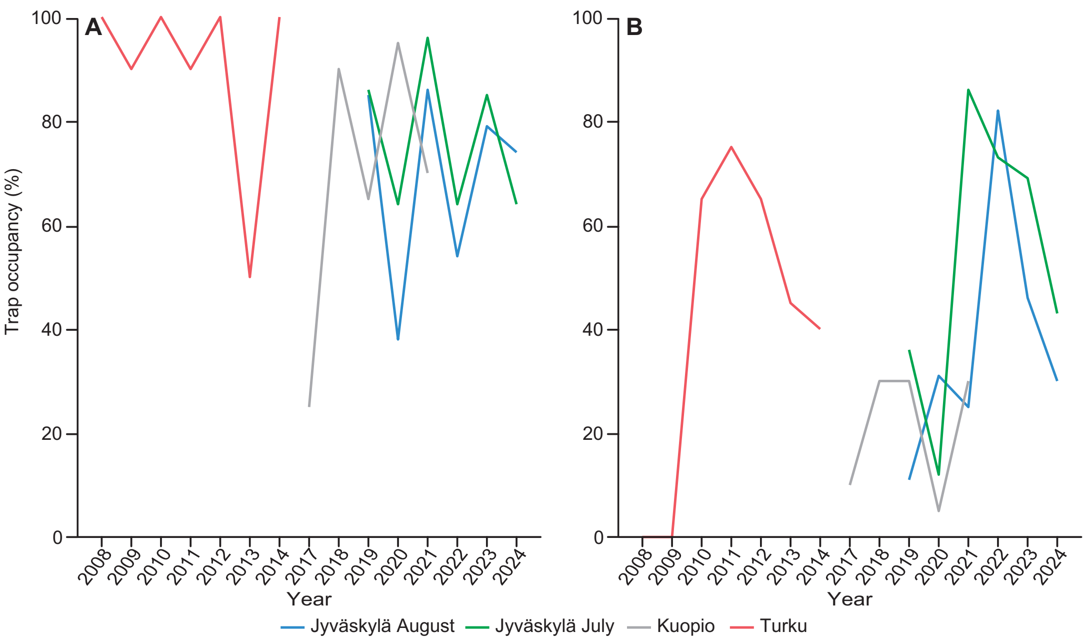
Site and year	Trapping period	Traps	Cumulative trapping days	Total number of wasps	*Vespula vulgaris*	*Dolichovespula media*
Turku 2008	13–20 Aug.	20	140	505	208	0
Turku 2009	1–8 Aug.	20	140	65	45	0
Turku 2010	30 July–6 Aug.	20	140	602	429	39
Turku 2011	4–11 Aug.	20	140	119	73	37
Turku 2012	7–14 Aug.	20	140	422	189	50
Turku 2013	5–12 Aug.	20	140	41	20	19
Turku 2014	8–15 Aug.	20	140	922	605	20
Lammi 2019	16 May–26 Sep.	3	405	93	59	30
Lammi 2020	6 July–14 Sep.	3	213	55	18	36
Lammi 2021	15 July–16 Sep.	3	192	154	54	102
Lammi 2022	11 July–12 Sep.	3	192	136	84	50
Hyytiälä 2019	1 July–2 Sep.	3	192	56	24	23
Hyytiälä 2020	6 July–14 Sep.	3	213	25	7	13
Hyytiälä 2021	12 July–13 Sep.	3	192	85	22	63
Hyytiälä 2022	11 July–12 Sep.	3	192	75	7	66
Jyväskylä A 2019	13 July–30 Sep.	6	846	250	223	16
Jyväskylä A 2020	11 May–4 Oct. (7 Oct.)	6	891	237	188	37
Jyväskylä A 2021	13 May (17 May)–30 Sep.	6	815	377	229	129
Jyväskylä A 2022	11 July–2 Oct. (3 Oct.)	6	507	364	154	210
Jyväskylä A 2023	12 July (13 July)-31 Aug. (4 Oct.)	6	405	322	162	150
Jyväskylä A 2024	12 July–27 Sep.	6	462	97	67	25
Jyväskylä B 2019	15–26 July & 12–23 Aug.	22	517	226	196	16
Jyväskylä B 2020	13–24 July & 13–24 Aug.	22	473	71	61	6
Jyväskylä B 2021	12–23 July & 9–20 Aug.	22	528	366	247	103
Jyväskylä B 2022	11–22 July & 8–19 Aug.	22	484	123	43	75
Jyväskylä B 2023	13–24 July & 11–22 Aug.	22	506	167	114	45
Jyväskylä B 2024	12–23 July & 12–23 Aug.	22	528	140	115	16
Kuopio 2017	16–23 Aug.	20	140	11	6	3
Kuopio 2018	6–13 Aug.	20	140	129	106	23
Kuopio 2019	12–19 Aug.	20	140	63	57	6
Kuopio 2020	9–16 Aug.	20	140	134	131	1
Kuopio 2021	9–16 Aug.	20	140	62	48	12

Appendix 2. Spring and summer weather (mean daily temperature and precipitation) at the Jyväskylä airport during the trapping years 2019–2024 (data: Finnish Meteorological Institute, www.ilmatieteenlaitos.fi; the weather station is located 17 km north of the study area).

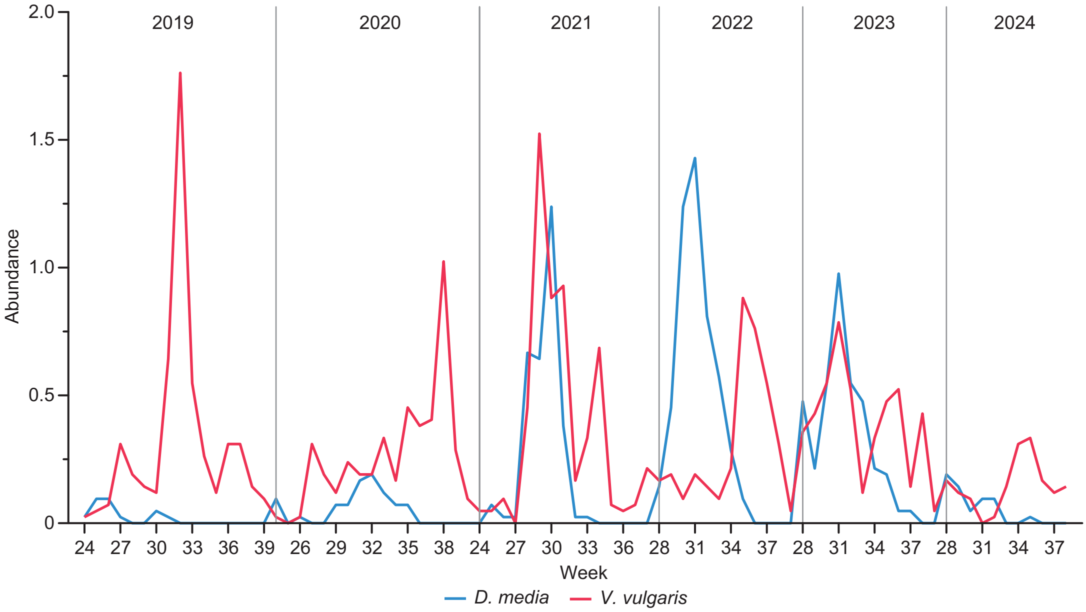
	Temperature (°C)						Precipitation (mm)					
	2019	2020	2021	2022	2023	2024	2019	2020	2021	2022	2023	2024
April	4.7	1.7	2.8	1.5	2.5	0.9	1.8	0.8	1.7	1.7	0.9	1.1
May	8.8	7.6	9.2	9.0	10.0	12.7	2.7	0.6	2.8	1.1	1.1	0.5
June	16.1	17.9	18.6	15.6	15.4	16.5	1.3	1.9	1.5	2.3	2.5	2.1
July	15.7	15.1	19.6	16.8	15.9	17.8	0.3	2.7	1.5	3.9	5.3	2.3
August	14.6	14.8	14.0	16.8	16.0	16.2	2.2	0.6	4.8	1.8	3.6	2.5

Appendix 3. Spatio-temporal variation in wasp abundance in roughly equal periods in mid-August (in Jyväskylä also mid-July). Given are the standardized mean number of individuals (density) per trap day (min–max) and percentage of occupied traps (min–max) for *Vespula vulgaris* and *Dolichovespula media* workers in beer traps. Occupancy is not shown for Hyytiälä and Lammi due to small number of traps.

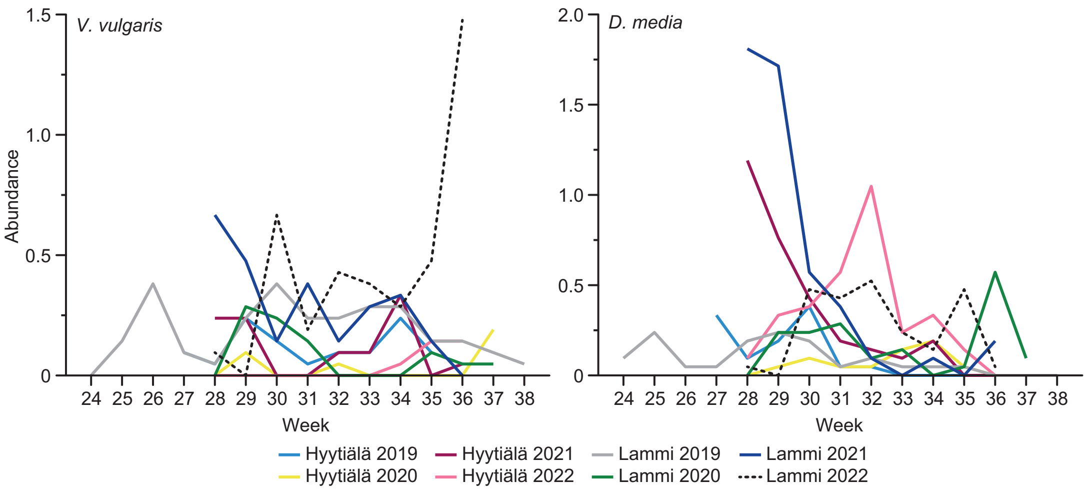
Site	Years	Density		Occupancy (%)	
		V. vulgaris	*D. media*	*V. vulgaris*	*D. media*
Jyväskylä July	2019–2024	0.29 (0.11–0.72)	0.15 (0.02–0.46)	76 (64–96)	53 (12–86)
Jyväskylä August	2019–2024	0.26 (0.11–0.39)	0.11 (0.01–0.33)	69 (38–86)	38 (11–82)
Kuopio	2017–2021	0.51 (0.04–0.98)	0.06 (0.01–0.16)	69 (25–95)	21 (5–30)
Turku	2008–2014	1.60 (0.14–4.32)	0.17 (0–0.36)	90 (50–100)	41 (0–75)
Lammi	2019–2022	0.23 (0–0.40)	0.14 (0.05–0.38)	na	na
Hyytiälä	2019–2022	0.07 (0–0.17)	0.23 (0–0.64)	na	na



Appendix 4. Percentage of traps occupied by (**A**) *Vespula vulgaris* and (**B**) *Dolichovespula media* workers in Jyväskylä (mid-July and mid-August 2019–2024; $n = 28$ traps), Kuopio (mid-August 2017–2021; $n = 20$ traps) and Turku (early to mid-August 2008–2014; $n = 20$ traps).



Appendix 5. Mean numbers of *Vespula vulgaris* and *Dolichovespula media* workers per trap day (n = 6 traps) in Jyväskylä in 2019–2024. Vertical lines indicate the first trapping week in each year. This figure is based on the same data as Fig. 5 but trapping periods arranged continuously to allow for easier interspecific comparison.



Appendix 6. Mean numbers of *Vespula vulgaris* and *Dolichovespula media* workers per trap day (n = 3 traps) in Hyytiälä and Lammi 2019–2022.