All-day activity of a *Vespula vulgaris* (Linnaeus, 1758) (Hymenoptera, Vespidae) colony in Central Finland

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In social insects, colony activity varies over season and day. We studied the all-day flight activity of a natural colony of a social vespine wasp *Vespula vulgaris* (Linnaeus, 1758) in its native range in boreal Finland. Ingoing wasps were monitored at one-second resolution non-stop for a full day, starting before sunrise and ending after sunset. Shorter monitoring was carried out before and after the full-day monitoring. The colony was active about an hour before sunrise and 40 minutes after sunset. Activity was at its peak at 07:00–10:00 in the morning, which corroborates many previous studies. Activity declined after the early morning peak, until the evening peak 18:30 onwards. Activity was not related to ambient temperature. Throughout the day, activity showed irregular cycles at the scale of a few minutes. Our study provides novel, fine-scale information about flight activity of *V. vulgaris*.

Key words: Nest activity, social wasps, traffic rate, Vespinae, *Vespula vulgaris* (Linnaeus, 1758), yellowjackets.

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Introduction

In social vespid wasps (Vespinae), colony activity (measured as number of ingoing and/or outgoing wasps) varies during a day. This variation in activity is linked to local environmental conditions and workers' allocation of time to different activities, such as food and pulp collection and nest maintenance (Brian & Brian 1952, Archer 2000, 2004, Kasper *et al.* 2008). There is some evidence that colony activity is taxon-specific and roughly similar in different colonies of a given species, even in different biomes (Archer 2012); recently, however, this view has been questioned (Kasper *et al.* 2008, Komonen & Torniainen 2022).

Detailed patterns of all-day activity are poorly known, since they can only be established by combining a full-day monitoring with fine-scale resolution, which was deemed nearly impossible by Archer (2004). Thus, the extant studies have followed colony activity only on limited and/or discontinuous time during a day (Gaul 1952, Potter 1964, Akre *et al.* 1982, Archer 2000, 2004, Kasper 2004), and thus cannot capture the detailed dynamics. In many research articles, it is unclear whether transits were recorded at the resolution of seconds, minutes or hours (see Gaul 1952, Potter

1964, Vetter & Visscher 1995, Archer 2000, 2004), and thus whether the mean traffic rate has been interpolated or extrapolated.

Most studies on colony activities of Vespinae have focused on *Vespula* in temperate and tropical regions (Archer 2012), partly due to the global invasion of *V. vulgaris* (Linnaeus, 1758) and *V. germanica* (Fabricius, 1793) (Kasper *et al.* 2008, Lester *et al.* 2017). Activities of *Vespula* in the boreal region have been poorly studied (but see Pallett & Plowright 1979). Boreal region differs from temperate and tropical region in terms of macroclimate and duration of daylight, which both affect colony activity (Gaul 1952, Potter 1964, Kasper *et al.* 2008). Another important difference between temperate and boreal colonies vs. tropical colonies is that the former is annual and the latter perennial. This influences colony size and seasonal dynamics, possibly also within-day dynamics (Beggs *et al.* 2011). Also, predation, parasitism and pathogen pressure may differ in different regions (Field & Darby 1991, Gambino 1995, Rose *et al.* 1999). Many studies on nest activity have been done with laboratory or seminatural colonies of *Vespula* (Gaul 1952, Potter 1964, Roland & Horel 1976, Vetter & Visscher 1995), which again may lead to false generalisation to natural colonies.

We monitored the all-day activity of a natural colony of a social vespine wasp *Vespula vulgaris* in the native range of the species in boreal Finland with one-second resolution. We also analysed the relationship between activity and ambient temperature.

Materials and Methods

Study area and nest

The study was conducted in Jyväskylä (WGS84: 62° 13' 43,365"; 25° 45' 5,566"), Central Finland, which belongs to the middle boreal zone. The nest of *V. vulgaris* was underground in open wasteland (Figure 1). Daily air temperature was always clearly above 2°C, which is the threshold necessary for foraging activity of *Vespula* (Blackith 1958, Potter 1964).

After colony collapse, the nest was removed on September 23 and its characteristics were recorded. There were five combs and 1711 cells, of which 370 were large and 1341 small; large cells were all in the latest, outermost combs. It is not unambiguous to estimate the total worker numbers by cell numbers, since worker mortality can be high and cells are reused (Archer 2012). The colony produced both males and queens, and only five closed cells were recorded, so the colony can be considered successful. The nest was parasitised by the beetle *Metoecus paradoxus* (Linnaeus, 1761) (Coleoptera: Rhipiphoridae). We observed 38 adults emerging from the nest during the monitoring and other visits. After the nest was excavated, 87 cells with larval or pupal remains were recorded, which we interpreted to indicate the presence of *Metoecus*. Thus, the overall parasitism rate was 2.2%.

Monitoring

Altogether, we monitored the colony for 26 hours and 51 minutes (17 August to 19 September 2020). We did one non-stop, full-day monitoring starting about at sunrise (05:33) and ending after sunset (22:15) on the 18 August 2020, i.e. at peak season (Figure 2). Because the flight started earlier than we expected, we monitored the early morning activity (04:00–05:32) on the 20 August and combined it with the data from the 18 August. Monitoring was done visually with a stopwatch, each observer taking two-hour turns, except for two hours when video recording was used. Colony activity was measured as the number of individuals returning per minute to the nest (hereinafter *traffic rate*). During monitoring weather was rainless and varied from cloudy to sunny. Ambient temperature was recorded every half an hour a few meters from the nest, 1.5 meters above ground, using a digital thermometer, which was at the same place for the entire day.

Statistics

Traffic rates are expressed and analysed as individuals per minute, or per 5 minute for illustrative purposes; in the latter case, activity is also illustrated using centered moving averages, calculated over seven 5-min periods.

To analyse the relationship between temper-

FIGURE 1. The studied *Vespula vulgaris* nest in Central Finland was underground in open wasteland. Monitoring was done visually, but a video camera was used for two hours.

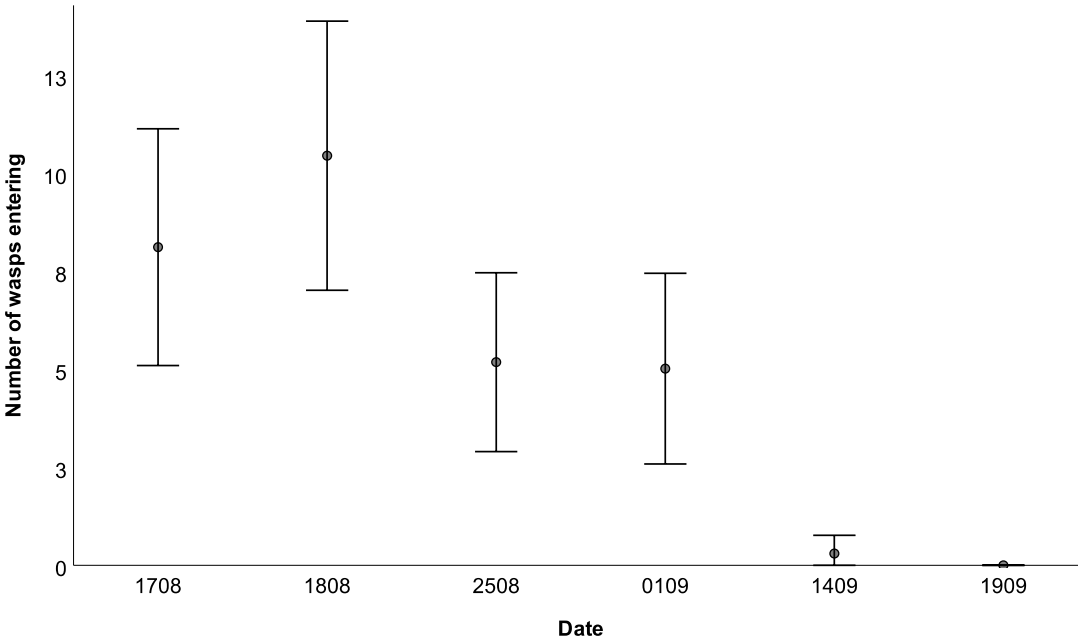

FIGURE 2. Change in the mean (± SD) number of *Vespula vulgaris* entering the nest per minute in Central Finland during August–September 2020. The mean is for 10–11 AM, except 11:13–12:13 on August 17, 13:36–14:06 on September 14 and 12:40–13:10 on September 19.

ature and traffic rate (i.e. the broad variation in mean traffic rate over day), we used the Expert Modeler option in SPSS, which automatically identifies and estimates the best-fitting ARIMA or exponential smoothing models. Because temperature was measured at 30-min intervals, we made it continuous by replacing missing values using linear interpolation. In the Expert Modeler, the final model only includes those independent variables, which have a significant relationship with the dependent series. Model fit was judged by the non-significance of the Ljung-Box statistic and visual judgement of the residual autocorrelation plots. No transformation was used. Analyses were conducted with IBM Statistics SPSS 26.0.

Results

The flight started 59 minutes before sunrise and ended 39 minutes after sunset. During the full-day monitoring we observed 8801 wasps entering the nest between sunrise and sunset (9408 wasps during the entire day, including the August 20 morning). The sunrise to sunset traffic rate varied from 0 to 23 min^{-1} (mean = 9.26, SD = 3.50; CV% = 38), i.e. the mean time between wasps entered the nest was 7 seconds. Traffic rate varied throughout the day overall and from one 5-min period to another (Figure 3); the peak was between 7:00 to 10:00 in the morning. The lows of the 5-min periods were 31% and the lows for 35-min moving average were 42% of the peak (Figure 3). The activity was modelled best by a simple seasonal time series model (stationary r^2 = 0.76, Ljung-Box Q = 19.9, df = 16, p = 0.27). Because temperature was not included in the final model, this suggests no relationship between traffic rate and ambient temperature (see also Figure 3). There was also irregular cyclicity at the scale of minutes (Figure 4).

Discussion

Colony activity varied over day. Wasps were active about an hour before sunrise and 40 minutes after sunset, which is typical for vespids (Gaul 1952, Potter 1964, Archer 2004, Kasper *et al.* 2008, Heinrich 1984, Komonen & Torniainen 2022). Overall, there was a small early morning (5:00) activity peak, followed by decline and then the daily peak at 7:00. After 8:30 activity decreased until the evening peak at 19:30. Early morning and evening peaks have been repeatedly observed for *Vespula* (Potter 1964, Heinrich 1984, Archer 2004), but they are not a universal pattern (Kasper *et al.* 2008). It has been suggested that between- and within-days variation in activity is linked to different activities carried out by the workers (Archer 2000), yet some research indicates that this variation is caused by weather (Potter 1964, Kasper *et al.* 2008).

Traffic rate showed cycles over a few minutes. This pattern is not idiosyncratic for the studied colony, since similar cyclicity was documented for all the studied colonies of *Dolichovespula saxonica* (Fabricius, 1793) (Komonen & Torniainen 2022). For a particular colony, the foraging and pulp collecting trip times, as well as the in-nest times, are typically rather constant, even for individuals carrying out different activities (Archer 2012). The reason might be that wasps tend to revisit good foraging sites and might be capable of information sharing (Santoro *et al.* 2015), or local enhancement (D'Adamo *et al.* 2000), regarding food sources. This could maintain similar trip times for workers of a particular colony and enhance cyclicity in activities. Among colonies, constancy in trip times would indicate that the availability of food and pulp sources do not vary markedly. This is a reasonable expectation, since vespids are generalist foragers.

Colony activity was not related to ambient temperature. This was not surprising, since monitoring was done during good weather: wind was calm, the sky clear or half cloudy, and the temperature outside the nest over +6.3°C, which is clearly more than the threshold for vespid activity (Blackith 1958, Potter 1964). Many older studies have not accounted for autocorrelation in the activity time series. Because ambient temperature increases in the morning and decreases in the evening, simple regression of activity against temperature does not indicate causal relationships. Furthermore, discontinuous monitoring is not

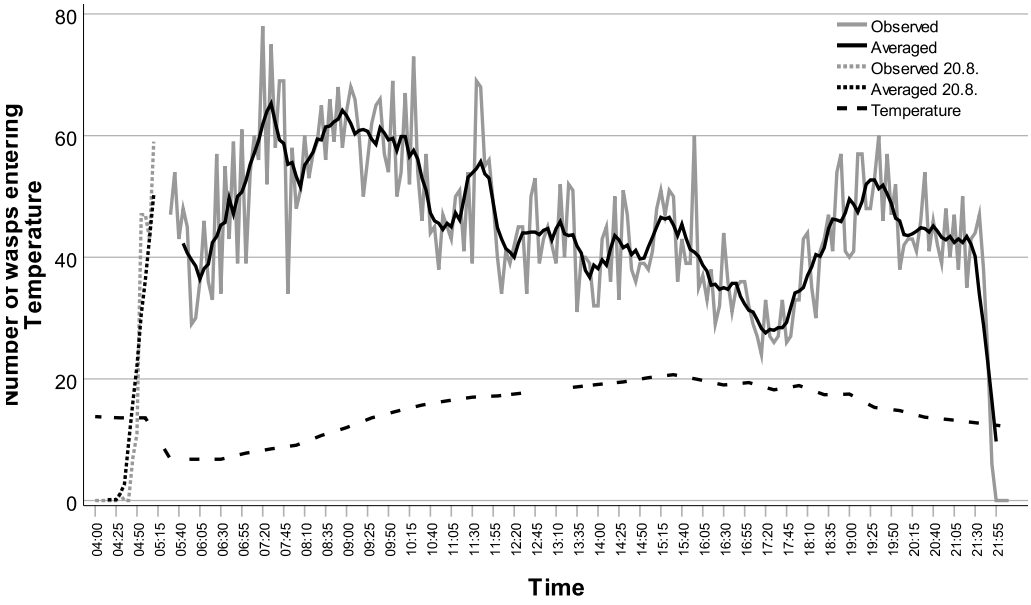

FIGURE 3. Observed number of *Vespula vulgaris* individuals entering the nest per 5 minute, the 35-min centered moving average and ambient temperature (°C) starting from 04:00 and ending at 22:30 on 18 August 2020 (04:00–05:30 is from the morning of 20 August). Note the small break in temperature recordings.

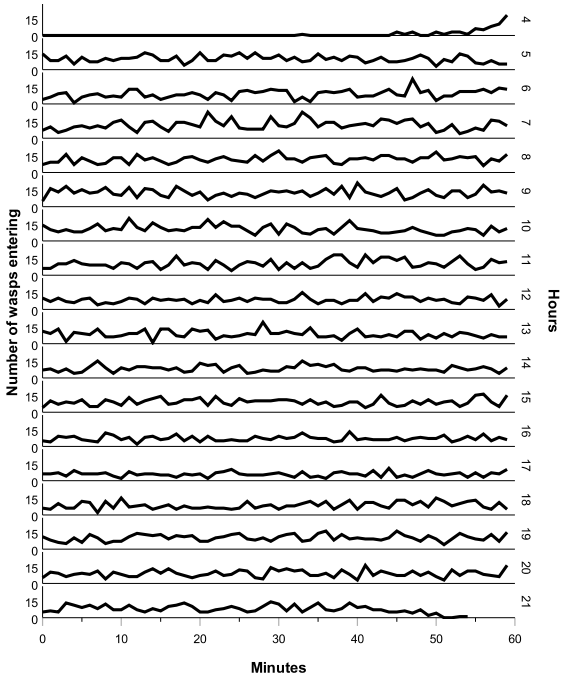

FIGURE 4. Minute-to-minute variation in the observed number of *Vespula vulgaris* individuals entering the nest per minute, starting from 04:00 and ending at 22:30 (the last individual entered the nest 21:54) on 18 August 2020 (04:00–05:30 is from the morning of 20 August). Sunrise was at 5:32 and sunset at 21:15.

optimal for detecting the effect of temperature on activity, and do not allow detailed time series analyses of activity. Our results also show that ambient temperature cannot explain the observed fine-scale, minute-to-minute variation in activity, since ambient temperature was rather constant during the day and changed gradually (see also Komonen & Torniainen 2022).

The large within-day variation in activity has implications for monitoring *Vespula* colonies. In order to estimate worker numbers, Malham *et al.* (1991) suggested a 10-min count, which seems to work well for invasive, perennial *Vespula* colonies. The desired precision and accuracy of the estimate depends on the purpose, but our study suggests that even a half-an-hour monitoring may produce biased estimates (see also Komonen & Torniainen 2022). Thus, we encourage longer monitoring times (at least an hour) divided in (at least) two discrete time periods, one before noon and one afternoon.

Our study provides novel, fine-scale information about the flight activity of a natural colony of *Vespula vulgaris* in the native range of the species in the boreal biome. Many important and interesting questions about wasps' activity patterns can only be answered with such continuous and high-resolution data. Our study is the first to demonstrate the irregular fine-scale cyclicity in the all-day activity of *Vespula*. This fine scale pattern and the underlying causal factors needs further verification with more nests, and in different geographical locations.

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