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Daily and Seasonal Extranidal Behaviour Variations in the Invasive Yellow-Legged Hornet, *Vespa velutina* Lepeletier (Hymenoptera: Vespidae)

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Abstract In eusocial insect species, the nest represents the fundamental element of the colony. Extranidal activities (foraging, nest maintenance, defence) are fundamental for the development and the survival of the colony. Therefore, they may represent interesting targets to disrupt to limit their expansion in case of pest species such as *Vespa velutina*, an alien predator of domestic honeybees in Europe. An accurate knowledge of the pattern of activity of this pest's colonies is therefore required. Due to the highly defensive nature of this hornet, a video monitoring was realized on two colonies during their growth from August to November. Three major behaviours were monitored: nest maintenance, patrolling on the nest and foraging flights. Although of different size and monitored during different years, the two colonies exhibited similar patterns of daily and seasonal variation. This work is a first step in the study of this pest especially in view of control program.

Keywords Activity · foraging · invasive species · nest maintenance · vespidae

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Introduction

Insect societies are defined on the existence of castes (reproductives vs. workers) and the division of labour, organized around the fundamental element, the nest, which represents both the skeleton and the skin of the colony (Wilson 1971; Starr 1990; Robinson 1992; Hölldobler and Wilson 2008). The division of labour among the workers is either based on morphological differentiation (morphological polyethism) or age-dependent (temporal polyethism) (Wilson 1971; Robinson 1992; Beshers and Fewell 2001; Hölldobler and Wilson 2008). Whatever the source polyethism is, the task sharing is one factor keying the ecological success of social insect species (Robinson 1992; Moller 1996).

In social wasps, no obvious morphological difference exists in workers and the division of labour is age-related (Dew and Michener 1981; Matsuura 1984; Jeanne et al. 1988; Jeanne 1991; Hurd et al. 2007; Volynchik et al. 2009; Kim et al. 2012; Monceau et al. 2013a). Basically, young and inexperienced individuals stay inside the nest while the older and more experienced ones realize extranidal activities. Extranidal activities mainly include foraging for feeding the colony (carbohydrates, proteins, and water), collecting nest materials, maintaining nest integrity and obviously defending against natural enemies (Matsuura and Yamane 1990) and are all fundamental for the development and the survival of the colony.

The yellow-legged hornet, *Vespa velutina*, is a recently introduced alien species in Europe imported from eastern China and observed for the first time in Europe in 2004 close to Agen (France) (Arca et al. 2015). Then, it has rapidly spread through Europe, invading Spain, Portugal, Italy (see Monceau et al. 2014 for a review) and Germany (Witt 2015). In September 2016, a nest was also destroyed in Gloucestershire (UK National Bee Unit 2016), suggesting that the UK was also invaded. This hornet species is mostly known for its predation of domestic honeybees in Asia (see Matsuura and Yamane 1990; Abrol 1994). Indeed, to feed the brood, hornet workers hunt honeybees at the hive entrance. As the colony grows during summer and autumn, predation pressure on honeybee hives dramatically increases until the death of the queen, workers and males in late November-early December (Monceau et al. 2013b, c, 2015). Although previous observations of hornet activity at the nest were performed (see Perrard et al. 2009), no information on daily and seasonal extranidal activities (nest maintenance, patrolling on the nest and foraging for food) are available during the period of colony growth, i.e., from late July-early August to the end of the colony in late November (Monceau et al. 2013b, c). To a wider extent, the daily and seasonal activities at the nest are poorly investigated in hornet species (but see Matsuura and Yamane 1990).

In the last decade, *V. velutina* has become an additional but probably a major source of stress for honeybee colonies in the current context of pollinator decline (Goulson et al. 2015). An accurate knowledge of the basic behaviour and colony dynamics at the nest especially during the period of intense predation on honeybee hives is therefore required to propose efficient management strategies (Roitberg 2007). For example, the development of an efficient trapping strategy suggests that a substantial part of the workers contribute to foraging. For this purpose, two wild colonies of *V. velutina* were video monitored continuously from August to

November. These videos allowed quantifying the extranidal activities of *V. velutina* workers during the growth of the colony. We expected that the different activities increased until the end of the colony in November similarly to predation pressure (see Monceau et al. 2013b).

Materials and Methods

Nest Description and Video Recording

Two undamaged nests were collected in southwest France and placed inside a building with a free and unlimited outside access at Sergeac (Dordogne, France, GPS: 45°00′11.3″N, 1°07′09.0″E, altitude: 88 m). *Vespa velutina* nesting sites are diverse (see Monceau et al. 2014), including natural supports (tree, shrubs) and human-made constructions (building, sheds). Nest A was monitored in 2008 and nest B in 2009. Although these nests were monitored at similar periods, nest B was larger than nest A, probably because colony B was more advanced in its development. In each case, nests were video recorded from August to November using a video camera Dragonfly Point Grey, 640 × 480 resolution, 100 FPS) connected to a computer (for video storage). *Vespa velutina* being diurnal, video recording was programmed with Numeriscope software (Viewpoint, France) to begin at sunrise and to stop at sunset. Only the side including nest entrance was filmed.

Video Analysis

Video recordings were analysed using VLC software (v. 2.0.0) and by a single person (AT) to avoid any experimenter effect. The video analysis began on the 8th of August for both nests but we did not have any information about the history of the colony (date of foundation for instance). From this date, one sample day was analysed every 5 ± 1 days. For nest A, the analysis finished on the 25th of November when the activity of the colony completely ceased, thus resulting in 23 sample days. For nest B, the analysis stopped on the 11th of December, resulting in 22 sample days. For each sample day, sample points were taken at the beginning of each hour, every hour for 5 min during daylight accordingly with season variations (max: 08:00 to 20:00). Our total sample for the whole observation period consisted in 195 and 215 sample points for nest A and B respectively.

Hornets leaving and entering the nests were counted and individual activity was categorized into three major activities: (*i*) working at nest maintenance, noted "nest maintenance", (*ii*) getting out the nest, walking on the nest then returning inside the nest without any other activity (no nest maintenance, no flight), noted "patrolling" and (*iii*) flying to or out the nest, noted "foraging flight". For hornets returning to the nest, it was almost impossible to determine if they came back with food for feeding larvae or with nest materials. Behaviours such as nest defence, nest-mate recognition or marking (excretion outside the nest) were also punctually observed but not included in the subsequent analyses.

Statistical Analysis

The number of hornets followed a negative binomial distribution as expected in case of count data (see Sileshi 2006), thus nonparametric tests were used. The congruence between the number of entrances and exits was tested using Spearman's rank correlation test. Negative Binomial Generalized Linear Models (NBGLM) were used to: (*i*) compare the number of hornets dedicated to each activity (namely "nest maintenance", "patrolling" and "foraging flight") and (*ii*) then, to analyse daily and seasonal variation in the number of hornets dedicated to each activity. The hour (daily variation) and the date (seasonal effect) of the sample points were included both as simple and quadratic effects to account for potential cyclic activities (see Monceau et al. 2013b). We also controlled for potential differences between hornet colonies by including the nest identity in our model. For each NBGLM, the statistical significance of each parameter included in the model was tested with likelihood ratio-based χ^2-statistics for unbalanced design (Fox and Weisberg 2011). The NBGLM was associated with post hoc Wilcoxon pairwise multiple comparison tests implemented with the Benjamini and Hochberg's correction (Benjamini and Hochberg 1995).

All statistics were computed using R software (v. 3.1.2, R Core Team 2014).

Results

Over the study period, in both nests, entrances and exists were highly related (Spearman's rank correlation test: nest A: $\rho = 0.85$, $P < 0.0001$, nest B: $\rho = 0.96$, $P < 0.0001$). Only the number of exits was therefore considered in our subsequent analyses.

Repartition of the Hornets in the Different Activities

The two nests differed greatly in the number of hornets realizing extranidal activities: they were more numerous in nest B than in nest A (GLM Negative Binomial family: $\chi^2 = 825.82$, df = 1, $P < 0.0001$, Fig. 1). The number of hornets dedicated to each tasks also differed ($\chi^2 = 1140.26$, df = 2, $P < 0.0001$, Fig. 1) with more hornets leaving the nest in flight compared to those who inspected or maintained the nest (post hoc tests: $P < 0.0001$ in both cases). The numbers of hornets involved in patrolling and nest maintenance were different in nest A and B ($\chi^2 = 135.07$, df = 2, $P < 0.0001$, Fig. 1): no difference was found for nest A between the two tasks ($P = 0.52$), while in nest B, more individuals were involved in the nest maintenance than in patrolling ($P < 0.0001$).

Daily and Seasonal Variation of Extranidal Activities

Nest Maintenance

Nest maintenance activity varied across the day but similarly in the two nests (Table 1, Fig. 2): the number of hornets working on the nest increased through the morning until 14:00 and then decreased during the afternoon. This activity also varied during the season: it increased during summer to reach a peak in late September and then

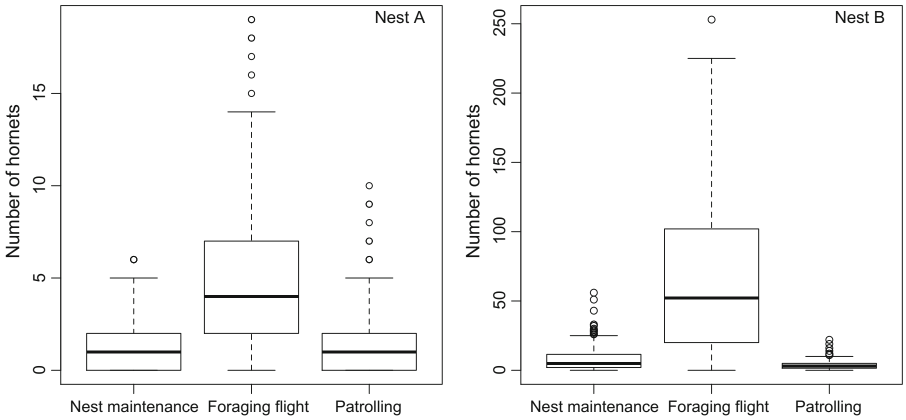

Fig. 1 Number of hornets observed during each 5 min of observation dedicated to nest maintenance, patrolling on the nest and foraging flight. Boxes, plain line, dashed lines, and open circles represent 50% of all values, medians, 1.5 interquartile range and extreme values respectively

decreased during autumn (Table 1, Fig. 2). The difference between nests (Table 1) was due to the fact that the peak for this activity was reached a little bit sooner in nest B than in nest A (Online Resource 1).

Patrolling on the Nest

Patrolling activity varied across the day: it increased through the morning until midday and then decreased through the afternoon (Table 2, Fig. 3). This pattern was however slightly shifted in time for nest A and B (Table 2, Online Resource 2). This activity also varied during the season with an increase through the summer and autumn (Fig. 3). It was also different between nests (Table 2, Online Resource 3). In nest A, it reached a peak in early October and then decreased while in nest B, the number of hornets inspecting the nest increased through the season until late November and then decreased.

Table 1 Summary of the NBGLM analysing the daily (hour and hour^2) and seasonal (date and date^2) variations in the number of hornets dedicated to nest maintenance activity in colony A and B based on likelihood ratio-based χ^2-statistics and associated *P*-values. Significant effects are in bold. The seasonal and diurnal effects appear as both linear (Date and Hour) and quadratic effect (Date^2 and Hour^2)

	χ^2	df	*P*
Date	155.07	1	< 0.0001
Date^2	242.04	1	< 0.0001
Hour	8.93	1	< 0.01
Hour^2	8.53	1	< 0.01
Nest	393.95	1	< 0.0001
Date: Nest	4.84	1	< 0.05
Date^2: Nest	7.56	1	< 0.01
Hour: Nest	0.14	1	0.71
Hour^2: Nest	0.09	1	0.76

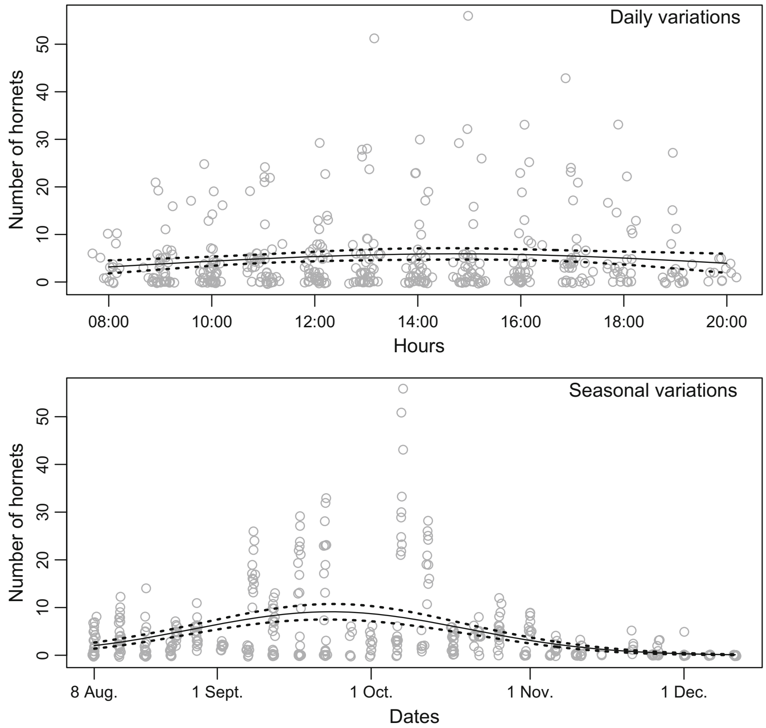

Fig. 2 Number of hornets working at the maintenance of the envelope of the nest during the day (*above*) and the season (*below*). Data are pooled nest A and B. Predicted values fitted with the GLM model (plain line) with 95% confidence interval (*dash lines*)

Foraging Flight

As in patrolling behaviour, the number of hornets flying out the nest varied across the day (Table 3, Fig. 4). In both cases, the number of hornets working on the nest increased through the morning, reaching a peak at mid-day and then decreasing during the afternoon. However, the peaks for the two nests were slightly shifted in time: 14:00

Table 2 Summary of the NBGLM analysing the daily (hour and hour^2) and seasonal (date and date^2) variations in the number of hornets dedicated to patrolling activity in nest A and B based on likelihood ratio-based χ^2-statistics and associated *P*-values. Significant effects are in bold. The seasonal and diurnal effects appear as both linear (Date and Hour) and quadratic effect (Date^2 and Hour^2)

	χ^2	df	*P*
Date	39.45	1	< 0.0001
Date^2	19.06	1	< 0.0001
Hour	6.04	1	< 0.05
Hour^2	5.78	1	< 0.05
Nest	76.67	1	< 0.0001
Date: Nest	10.62	1	< 0.01
Date^2: Nest	13.08	1	< 0.001
Hour: Nest	5.12	1	< 0.05
Hour^2: Nest	3.96	1	< 0.05

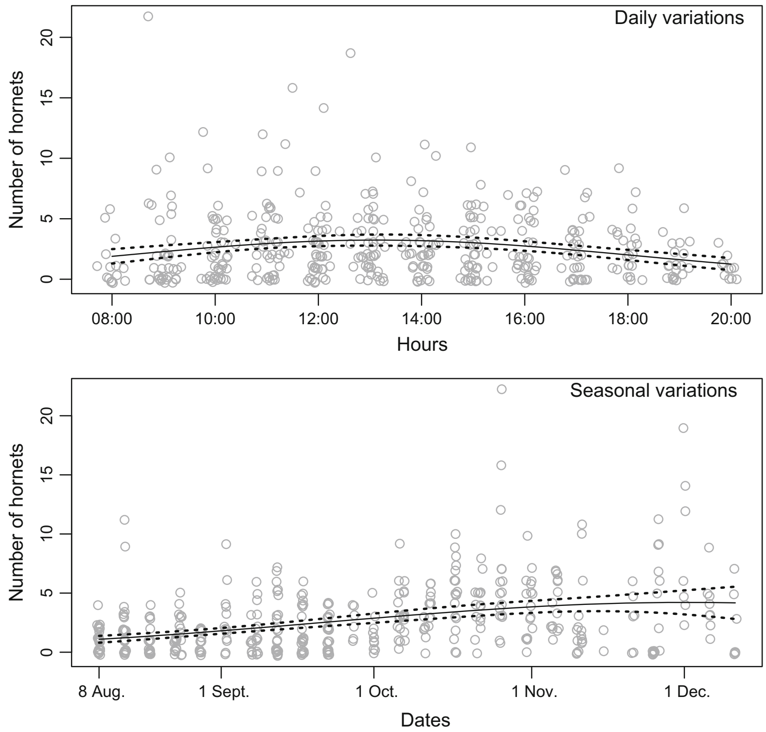

Fig. 3 Number of hornets patrolling on the nest during the day (*above*) and the season (*below*). Data are pooled nest A and B. Predicted values fitted with the GLM model (*plain line*) with 95% confidence interval (*dash lines*)

for nest A and 13:00 for nest B (Online Resource 4). This activity also varied during the season with an increase during the summer to reach a maximum in October (Fig. 4). Nest A and B were however slightly shifted in time; the peak was reached earlier in nest A than in nest B (Online Resource 5).

Discussion

This study is the first one attempting to monitor the dynamics of *V. velutina* activity at the nest during colony growth to the end of its life cycle. Three activities were studied: nest maintenance, patrolling on the nest and foraging flight. The two nests mainly differed in the size of their colonies; colony B was larger than colony A.

Despite the fact that they were of different size and monitored in two consecutive years, colony A and B showed similar patterns of activity although slight shifts in time could be observed, probably due to environment (seasonal) variation in weather conditions. Overall, all activities increased through the summer, reaching a peak in early autumn and then decreased until the end of the colony. For both nests, the number of hornets dedicated to the maintenance of the nest started decreasing in late September but the patrolling behaviour continued through November in nest B. This could be attributed either to late emerging individuals (workers and sexuals). Overall, this

Table 3 Summary of the NBGLM analysing the daily (hour and hour^2) and seasonal (date and date^2) variations in the number of hornets flying out nest A and B based on likelihood ratio-based χ^2-statistics and associated *P*-values. Significant effects are in bold. The seasonal and diurnal effects appear as both linear (Date and Hour) and quadratic effect (Date^2 and Hour^2)

	χ^2	df	*P*
Date	894.04	1	< 0.0001
Date^2	710.47	1	< 0.0001
Hour	25.84	1	< 0.0001
Hour^2	28.4	1	< 0.0001
Nest	2504.27	1	< 0.0001
Date: Nest	35.37	1	< 0.0001
Date^2: Nest	15.07	1	< 0.001
Hour: Nest	6.11	1	< 0.05
Hour^2: Nest	5.72	1	< 0.05

seasonal pattern corresponds to the annual life cycle of the hornets, that is colony growth until the emergence and departure of the sexuals in autumn and then the collapse of the colony.

At a daily time scale, hornet activities exhibited similar profiles; overall activity increased during the morning to reach a maximum at midday and then declined through

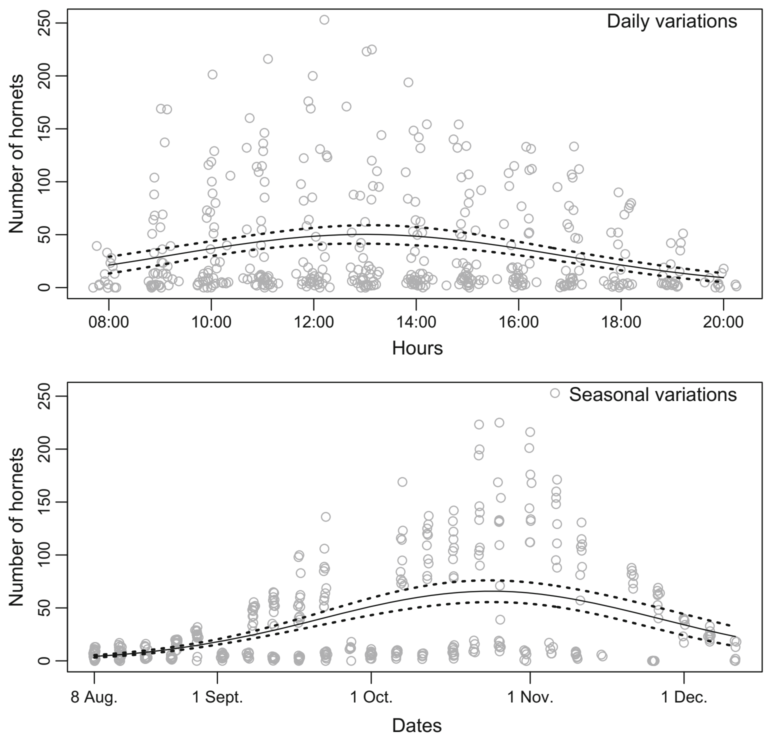

Fig. 4 Number of hornets leaving the nest during the day (*above*) and the season (*below*). Data are pooled nest A and B. Predicted values fitted with the GLM model (*plain line*) with 95% confidence interval (*dash lines*)

the afternoon. Vespidae activity is classically modulated by weather conditions (Cruz et al. 2006; da Rocha and Giannotti 2007; Kasper et al. 2008; Canevazzi and Noll, 2011; de Castro et al. 2011), which is the case for *V. velutina* hunting in apiaries (Monceau et al. 2013c). The higher activity at midday may correspond either to higher temperature or higher solar UVB irradiation effect. Indeed, in a close related species, *V. orientalis*, the cuticle has been shown to convert solar into metabolic energy similarly to photovoltaic cells, thus explaining higher activity at noon hours (Ishay 2004; Volynchik et al. 2008; Plotkin et al. 2010). To date, such a system has never been studied in *V. velutina*. These results however differ from the observations concerning predation pressure on honeybee hives. Indeed, the number of hornets preying at honeybee hives did not vary during this lapse of time (Monceau et al. 2013b). This suggests that a proportion of hornets leaving the nest, especially in the morning, were not all concerned by bee hunting and are probably diverted to other tasks such as gathering water, plant material for nest maintenance or supplementary food. The main foraging activity by workers concern prey harvest hunting but as they also forage for prey other than honeybees (Monceau et al. 2014), but harvesting fluids or plant material for nest maintenance is probably underestimated. However, it is almost impossible to determine in this study what hornets brought back to the nest without capturing them. Workers who left the nest could also be inexperienced leaving the nest for the first time in an orientation flight. Similarly to honeybees or bumblebees, hornets are central place foragers that need to learn spatial landmarks to locate their colony (Collett 1996; Capaldi and Dyer 1999). Because individuals were not individually marked the duration of their trip outside the nest could not be quantified.

Conclusions and Perspectives

Our results are consistent with previous findings on *V. velutina* for activity at a daily time scale, but the authors only realized observation during the early stage of the colony (June and July see Perrard et al. 2009). Our study is thus the first to provide information on colony activity during the most important part of the life cycle and especially the major growth of the colony that explains the substantial increase in predation on honeybees (Monceau et al. 2013c). We show that foraging is the major activity and could thus be the target of the management strategy. The use of a specific Trojan method associating with food baits could thus be promising. However, to date, bait attractiveness and specificity is still an unsolved problem (see Monceau et al. 2014).

Interestingly, although the two colonies were monitored in different years thus making extrapolation to the species-specific behaviour reasonably difficult to realise, the congruent pattern of activity suggests that colony dynamics is most probably driven by the internal biological clock of the colony and the pheromonal control of the queen. These observations are important and may represent a first step in our understanding of the activity of *V. velutina* colonies. Since nests are a major target in the management of *V. velutina* invasive populations, understanding how the regulation of the different tasks occurs is therefore of major interest. Previous work has already shown in captive colonies that nest defence was age-related (Monceau et al. 2013a). Further research is thus required in this way and also to understand the contribution of pheromones that could be used for nest disruption.

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