

Relationship between the age of *Vespa velutina* workers and their defensive behaviour established from colonies maintained in the laboratory

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Abstract As the structural bases of insect societies are essential to colony survival, nests must be protected from predation. Nest defence behaviours are among the most important roles assigned to worker members. However, in hornet societies, temporal polyethism (age-dependent division of labour among workers) is assumed to be weak. Few studies have investigated this phenomenon, probably because hornet nests are aggressively defended and dangerous to approach. In the present study, we propose a method for rearing nests of *Vespa velutina*, a species newly introduced into Europe. This method enables the handling of hornets, and thus the design of experiments. By marking all newly emerged hornets, we recorded aggressiveness in workers of different ages from three captive colonies. We observed that nest defence behaviour in *V. velutina* depends

on the age of the workers. Nest defence appears to be mediated by the queen, probably through pheromones that promote nest organization. We also identified a previously unreported but important behaviour in *V. velutina* that workers are aggressive towards male hornets. This behaviour might be a strategy to avoid inbreeding. Collectively, our results provide new research perspectives for the management of social hymenopteran predators.

Keywords Division of labour · Inbreeding · Queen control · Social insects · Temporal polyethism · Vespidae · Yellow-legged hornet

Introduction

Insect societies are often regarded as superorganisms founded on caste hierarchies and the division of labour (Wilson, 1971; Robinson, 1992; Hölldobler and Wilson, 2008). In a superorganism (insect colony), the somatic (workers) and reproductive (gynes and males) cells are compartmentalized into functional organs (castes), the whole inhabiting a unique skeleton and skin structure (the nest) (Starr, 1990; Hölldobler and Wilson, 2008). As the structural basis of the colony, the nest must be protected to ensure colony survival. Predation, in particular, is regarded as a major cause of colony mortality (Strassmann, 1981; Starr, 1985, 1990). Consequently, nest defence behaviour is one of the most important roles assigned to workers.

Partition of labour among workers may arise from performance variability related to differences in size and/or shape (morphological polyethism) or age (temporal polyethism) (Wilson, 1971; Robinson, 1992; Beshers and Fewell, 2001; Hölldobler and Wilson, 2008). Young individuals usually remain within the nest while their seniors

Because of the risks engendered by the aggressive and invasive nature of *V. velutina*, handling rules must be respected. Collecting nests in the field and their manipulation in the laboratory require appropriate protection (complete body protection) to avoid stings that could provoke an anaphylactic reaction in people allergic to Hymenoptera venom. Handlers and observers should not stay alone in the vicinity of the cage, and unauthorized persons should keep away from the experimental room. We disclaim all responsibility for people who do not adhere to these instructions.

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attend to outside tasks (Matsuura, 1984; Jeanne et al., 1992; Robinson, 1992; Hurd et al., 2007). Temporal polyethism is widespread among social hymenopterans but is most common in bees and wasps (Hölldobler and Wilson, 2008). While extensively studied in honeybees (reviewed in Calderone, 1998; Johnson, 2010), this phenomenon has been little investigated in social wasps (Dew and Michener, 1981; Jeanne et al., 1988; Jeanne, 1991; Hurd et al., 2007; Kim et al., 2012) and particularly in hornet species (but see Matsuura, 1984; Volynchik et al., 2009) probably because hornet nests are less easily handled and observed than hives (Archer, 2010).

The yellow-legged hornet, *Vespa velutina*, is an alien Vespidae recently introduced into Europe from eastern China (Beggs et al., 2011; Roy et al., 2011). Its invasion has exerted a massive impact on beekeeping. Indeed, *V. velutina* hunt not only the domestic honeybee, *Apis mellifera*, but also other pollinators, to feed their larvae. Given that pollinators are already declining (Brown and Paxton, 2009; Potts et al., 2010), *V. velutina* predation imposes additional stress on honeybee colonies, which must be urgently reduced. Nevertheless, as in most biological invasions, efficient management plans require an accurate knowledge of the invader behaviour (Roitberg, 2007). Thus, the behaviours that ensure *V. velutina* colony survival are of major relevance. Unfortunately, to date, *V. velutina* behaviour has been largely neglected by researchers, probably because this species is considered particularly aggressive in its native area, and will attack with little provocation (Edwards, 1980; Starr, 1992; Martin, 1995). *V. velutina* nests are often cryptic and not easily detected, most of them being observed as leaves fall. Collecting behavioural data from the nest is therefore problematic. Video recordings will minimize risk but do not allow hornet manipulation while behavioural observations and individual handling are rendered possible by collecting and maintaining nests in captivity.

In the present study, we first describe our methodology for collecting, caging and rearing *V. velutina* nests in the laboratory. We also describe the first behavioural experiment on this species under such conditions. Three colonies were obtained from the wild, and were caged and reared in the laboratory for several weeks. To assess the extent to which nest defence behaviour is related to the age of *V. velutina* workers, each colony was subjected to experimentally simulated nest attacks.

Materials and methods

Nest collection, caging procedure and rearing

Because *V. velutina* is a diurnal insect, the nest is most safely approached at night or during the early morning. We

selected the early morning period to collect the nests, when light and hornet activity are still low (Perrard et al., 2009). Nests can be found in diverse localities, attached to walls or branches. Any threatening signals, such as vibrations and light sources, induce a noisy reaction of the colony and the rapid exit of individuals from the nest. The nests were collected by extricating them from the wall or by cutting the support (branch) on which they were built. The detached nests were placed in individual boxes that were sealed once all the individuals flying in the nest vicinity had returned to the nest. Minor nest damage introduced by handling was rapidly repaired by workers within 2–3 days of captivity. During this procedure, the occurrence of eggs and capped and uncapped larvae was noted.

Before transferring the nests into the laboratory rearing cages, hornets were anaesthetized by placing them in a cold chamber (4 °C controlled atmosphere for 2 h). In both cases, the nests were transferred from the travelling box to the cage within 5 min, because hornets recover rapidly from both anaesthesia and cooling. Nests built on branches were placed into the cage intact, while those removed from structures such as walls were placed on a support. Prior to caging, all individuals were marked with a uniquely coloured weather-proof acrylic pencil brush (Marabu GmbH and Co. KG, Tamm, Germany) to distinguish them from later-emerging individuals. Paint dot was chosen as a classical insect marker (Edwards, 1980; Hagler and Jackson, 2001).

The 0.216-m³ cubic cages (60 × 60 × 60 cm), wood framed with Plexiglas and stainless steel wire mesh sides (Fig. 1; Online Resource 1), were placed in an experimental room at room temperature. The door of the cage was equipped with an airlock opening (mesh sleeve) for easy cleaning and insect handling. The bottom of the cage

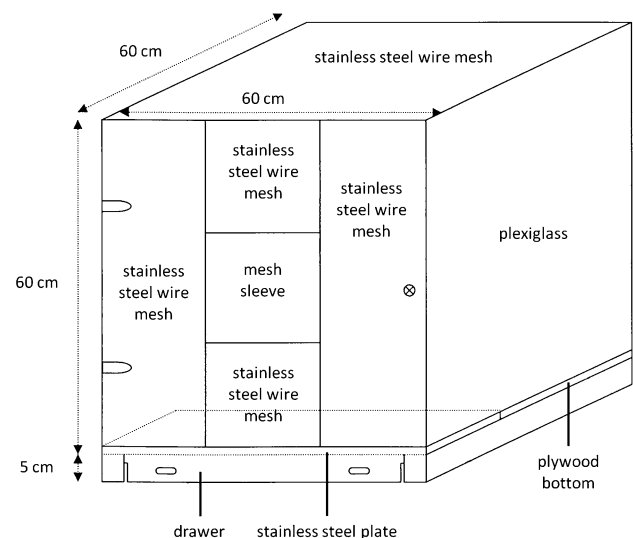


Fig. 1 Cage for *Vespa velutina* nest rearing

Table 1 Population composition of the three *Vespa velutina* nests reared in laboratory conditions

	Nest 1	Nest 2	Nest 3
Origin (GPS coordinate)	N44°54'56.55" W0°28'35.57"	N44°33'52.36" W0°20'44.79"	N44°51'48.56" W0°29'28.26"
Date of caging	15/06/2011	17/06/2011	03/07/2012
At caging			
Number of queens	0	1	1
Number of workers	7	19	13
Number of males	0	0	0
Eggs and larvae	Yes	Yes	Yes
Captivity duration (days)	41	41	24
Emergences of males	No	Yes	No

comprised a mobile drawer for feeding the hornets, sealable with a stainless steel plate (Fig. 1; Online Resource 1). Wasps require carbohydrate liquids (mainly ingested by adults) and protein solids (consumed by larvae) (Spradbery, 1973; Edwards, 1980; Matsuura and Yamane, 1990; Matsuura, 1991). Adults were fed with honey or blackcurrant syrup, while larvae were fed with either standard commercial wet cat food (11 % proteins, 78 % water) or fresh fish (fillets of farmed brown trout reproducers, *Salmo trutta*, provided by St Pée-sur-Nivelle Inra research centre). Food and water were provided ad libitum in Petri dishes.

Three nests were collected in the field (numbered 1–3 according to the date of arrival; see Table 1 for details). During captivity, the queen was observed in nests 2 and 3 but was absent from nest 1. This absence was later confirmed when the nest was destroyed. In nest 1, none of the original workers survived to the end of captivity. In nest 2, the queen alone survived while in nest 3, the queen and five workers survived. Because of the large number of emerging hornets from all nests, some individuals (randomly chosen at each age) were removed from the cage to prevent overcrowding.

Behavioural experiment

Regularly (typically every 2 or 3 days), all individuals were caught and transferred from the cage to individual small plastic pots with aeration holes. This was achieved by introducing large tweezers to the front of the nest through the airlock opening. The tweezers were slightly moved towards hornets and the nests, mimicking an intruder into the nest and thus inciting an attack. Hornet defence behaviour was usually displayed as bite and sting attempts to the tweezers. The hornets were removed from the cage in the order in which they advanced to attack the tweezers, hereafter called *rank of defence*. In parallel, each newly emerged hornet was marked as previously explained. Each new cohort emerging at a specific date was marked with a unique colour, allowing the age of the adults to be

estimated. Age was expressed as the mean of the maximum and minimum possible ages of the hornets (the ages of those that hatched shortly after the previous marking event and those that hatched immediately before the current marking event, respectively). As an illustrative example, consider two marking events performed on 08/07/2011 and 12/07/2011. A hornet marked as newly emerged on the latter date cannot be older than 4 days or younger than 0 days, and is thus classified as '2 days old'. All individuals in the nest were considered marked when (1) no hornets apparently remained in the nest or (2) when no internal noise was detected in response to cage vibration (the sound information was used only at the end of the experiment). The hornets were then released into their native cage in reverse order, assuming that the individuals exiting the cage later were less aggressive than those first aroused. The entire procedure (capture, mark, release) was completed in around 30 min to 1 h.

Based on the few available data recorded by Matsuura (1984), guarding behaviour is infrequently displayed by hornets younger than 1 week old. To ensure the existence of week-old adults in our sampled colonies, we conducted four consecutive behavioural experiments (hereafter referred to as sessions) spanning more than 15 days after caging (see Tables 1, 2). During these sessions, individuals' rank of defence and age were recorded (excluding queens and male hornets who do not contribute to defence). Queens were usually the last individuals to exit the nest, but on two occasions (see Table 2 for details), one hornet was left unmarked because it could not be captured without damaging the nest. In both cases, the individual concerned was excluded from analysis.

Statistical analysis

To account for differences in colony size among nests, the individual ranks of defence were first divided by the number of workers in the colony. The relationship between age and rank was then analyzed using a generalized linear model

Table 2 Summary of colony size (before some workers were removed) and composition during the four experimental sessions

	Session 1	Session 2	Session 3	Session 4
Nest 1				
Session date	04/07/2011	06/07/2011	08/07/2011	12/07/2011
Colony size (total)	42	44	43	37
Queens	0	0	0	0
Workers	42	44	43 ^a	37
Males	0	0	0	0
Number of workers removed	0	0	0	0
Mean worker age range (days)	2–15.5	1–17.5	1–19.5	2–23.5
Median worker age (days)	7.5	9.5	11.5	10
Nest 2				
Session date	05/07/2011	07/07/2011	11/07/2011	13/07/2011
Colony size (total)	28	31	32	36
Queens	1	1	1	1
Workers	26	28 ^a	28	20
Males	1	2	3	15
Number of workers removed	2	1	0	0
Mean worker age range (days)	2–18	1–17.5	1–21.5	1–23.5
Median worker age (days)	7	8	11	10
Nest 3				
Session date	18/07/2012	20/07/2012	23/07/2012	25/07/2012
Colony size (total)	46	46	53	51
Queens	1	1	1	1
Workers	45	45	52	50
Males	0	0	0	0
Number of workers removed	5	0	5	0
Mean worker mean age range (days)	1–15	1–17	1.5–20	1–22
Median worker age (days)	8	10	11	13

^a Excluding one unmarked individual

(GLM), accounting for nest effect. The four replicates were introduced into the model as a within-nest nested effect. The statistical significance of each parameter was assessed by *F*-ratio statistics for unbalanced design (Fox and Weisberg, 2011). This procedure was separately performed for the nest with queen absent (nest 1) and the nests with queens present (nests 2 and 3). By default, the workers present at caging were regarded as 1 day old on this date. Statistical analyses were performed by R software (v. 2.12.1, R Development Core Team, 2008) implemented with the *car* package.

Results

Noticeable behavioural observations

In nest 2, 44 % of the adults that emerged during captivity were males, the first being recorded 3 days after caging. These males behaved very differently from their worker nestmates; in particular, they showed no apparent parti-

cipation in nest tasks (feeding larvae and nest construction). Instead, they habitually occupied the walls of the cage, as though trying to escape its confines. We also observed several instances of agonistic behaviour by workers towards males (i.e. stinging and biting). The workers attacked active males walking on the cage wall. Typically, a worker would pounce on a male, attempt to bite his head/thorax junction, and then attempt to sting him. Although the targeted male frequently fell to the bottom of the cage, in most instances, they successfully evaded the worker and returned to the cage wall. In all three nests, sections of hornets (heads, thoraxes and abdomens) were found in the cage, but the sex of the dissected individuals could not be identified. Thus, we cannot determine the status of the individuals killed by such aggressive behaviour.

Nest defence and worker age

Individual rank of defence was overall related to worker age, but this relationship differed among nests (Table 3).

Table 3 Summary of the GLM test for assessing the relationship between rank of defence and worker age of four replicates in each of three nests

	<i>df</i>	<i>F</i>	<i>P</i>
Age	1	75.81	<0.0001
Nest	2	0.17	0.84
Nest × replicate	9	0.79	0.62
Age × nest	2	18.55	<0.0001
Age × nest × replicate	9	1.01	0.43
Residuals	436		

Since the within-nest replicates did not vary significantly, the data could be pooled in subsequent analyses. In nest 1, no relation emerged between rank of defence and hornet age (GLM: $F = 0.03$, $df = 1$, $P = 0.87$, Fig. 1a) while in nests 2 and 3, the earliest attacking individuals were the oldest ones (GLM: $F = 122.16$, $df = 1$, $P < 0.0001$, Fig. 1b). A similar behaviour was observed in colonies (nest effect: $F = 0.14$, $df = 1$, $P = 0.70$ and interaction age × nest: $F = 0.06$, $df = 1$, $P = 0.80$).

Discussion

Janet (1895) concluded that *V. crabro* could not be reared in captivity, but this notion was later contradicted by Hoffmann et al. (2000). The present study shows that *V. velutina* nests may be captured for a few weeks, sufficiently long to realize observations and experiments.

Although caging is a valuable method for collecting data, it is limited in several ways. Our captive colonies collapsed more rapidly than field colonies and the number of emergences decreased throughout the experiment, suggesting that the queens stopped producing eggs after caging (Bonnard et al., 2012). Such a decline could be attributed to stress caused by nest collection and/or missing nutrients or plant materials that might be required to regulate the colony or maintain its health (e.g. plant-produced antibiotics such as propolis, which is gathered by bees). Indeed, various Vespidae are known to cannibalize their larvae when proteins become scarce (Spradbery, 1973; Matsuura and Yamane, 1990). Although protein food was provided ad libitum, the caged hornets cannibalized not only their larvae but also other adults. Therefore, determining the optimal conditions for prolonged captivity would be a useful future study.

Limitations aside, laboratory environments ensure uniform and thus convenient conditions for experiments. The central methodology of the present experiment is the marking of all hornets in the colony, which could not have been achieved in the field. In particular, by rearing a hornet

colony in the laboratory, we have observed unusual or at least under-reported behaviours in *V. velutina*, such as the aggression of workers towards males. Laboratory rearing has also enabled investigation of one of the most crucial organized behaviours in insect societies; namely, nest defence. To our knowledge, this is the first report of such behaviour in *Vespa* species.

Worker behaviour towards males

Males are thought to be mainly produced in autumn in synchrony with the new queens (Villemant et al., 2011). We show here that a large number of males may be produced earlier; in particular, males comprised 44 % of the total emergences from nest 2. These observations corroborate previous data from field surveys (Monceau et al., 2013a), but here we cannot conclude whether the emerging males were produced by the queen or by workers. The first male emerged 3 days after the caging of the nest. Considering that larval development during the queen colony phase in *Vespa* sp. ranges from 27 to 51 days depending on climatic conditions, with 48.1 days for *V. velutina* (Archer, 2010), the emergence of males throughout the survey cannot be attributed to captivity. The agonistic behaviour exhibited by workers towards males has been previously reported in *V. simillima* (Matsuura and Yamane, 1990) but has never been suspected in *V. velutina*. In this context, forced dispersal might be a strategy by which the wasps limit inbreeding (Tabadkani et al., 2012). This behaviour should receive full consideration because inbreeding (through the Allee effect; Courchamp et al., 1999) may effectively manage the population expansion of *V. velutina* in the future (Liebhold and Tobin, 2008; Tobin et al., 2011).

Age-dependent nest defence behaviour

To date, the division of labour in hornet species has received limited attention. The very few existing studies have focussed on either a single nest or on a restricted set of individuals (Matsuura, 1984; Volynchik et al., 2009). To our knowledge, this study presents the first experimental analysis of the relationship between worker age and nest defence behaviour in a hornet species, although similar results have been reported for certain eusocial wasps (Jeanne et al., 1992; Togni and Giannotti, 2010). For example, Jeanne et al. (1992) showed that defence behaviour in the wasp *Polybia occidentalis* is linked to worker age in a step-function fashion. However, the behavioural patterns of *P. occidentalis* reported by Jeanne and colleagues are not directly comparable to the behaviours we observed in *V. velutina*, because the former study measured the number of attacks, whereas we have reported the rank of defence.

Different hypotheses have been proposed to explain why older workers invest more time in nest defence. First, older workers may become the first line of defence against predators, because potential injuries are less costly (when weighted against life expectancy) to aged individuals than to younger individuals (Wakano et al., 1998). Second, younger hornets may have lower investment in the nest than their seniors, and consequently, less interest in nest defence (Judd, 2000). Third, according to age polyethism (Wilson, 1971; Robinson, 1992; Beshers and Fewell, 2001; Hölldobler and Wilson, 2008), older individuals may identify and react more rapidly than younger individuals to potential predator aggression; that is, their experience renders them more efficient in nest defence. This hypothesis is feasible since Vespidae demonstrate elaborate cognitive processes (see for example Toh and Okamura, 2003; Weiss et al., 2004; Warkentin et al., 2006; Moreyra et al., 2012). Moreover, a previous study on *V. velutina* foraging behaviour suggests that the wasps gain efficacy from experience (Monceau et al., submitted), suggesting that age polyethism is also applicable to foraging behaviour. Although *V. velutina* may benefit from its novel European environment (Monceau et al., 2013b), its prey species are similarly well-organized insect societies with (presumably) equally well-developed strategies and experience. Defending the nest and feeding the brood are the most important tasks undertaken by *V. velutina*. Thus, do older workers forage and/or defend and how do colonies implement these dual activities? We may hypothesize that a recently introduced alien species with no obvious predator will relax its defence behaviour in favour of foraging behaviour. Such behaviour switching may underlie the high degree of plasticity displayed by invasive social insects (Moller, 1996).

Division of labour and queen control

Although this experiment should be repeated for confirmation, our results support previous observations of orphan *Vespa* sp. colonies (Matsuura, 1984). The disappearance of the queen in a colony with sufficient workers does not portend that the colony dies within a few hours. Instead, one worker may first express dominance and begins egg laying within few days (the unfertilized eggs ultimately become males, Matsuura 1984). In this way, the colony may survive until the last workers have disappeared (Matsuura, 1984).

The absence of relation between age and defence behaviour in the orphan colony may result from a cluster of older individuals which do not engage in defence (see Fig. 2a, the individuals of 20–23 days old in the upper right corner). These individuals may have undergone ovary development and thus could behave more queen-like than worker-like. However, we observed no dominance among *V. velutina* workers; no eggs were laid and no new males emerged from nest 1. Interestingly, however, this colony without a queen appeared to behave similarly to the queened colonies, suggesting that orphan *V. velutina* colonies may survive short term under minimal organization. Essentially, the queen is the colony pacemaker, but the extent of her control may depend on colony size (Robinson, 1992; Jeanne, 2003). In large Vespidae colonies such as those of *V. velutina*, the influence of the queen is presumed limited because she cannot directly interact with the entire nest population. Instead, she mediates the colony by secreting a pheromone (Spradbery, 1991; Jeanne, 2003). Our results suggest that the queen is fundamentally responsible for task organization in *V. velutina* colonies. If this is indeed the case, disrupting the queen pheromone, and therefore the

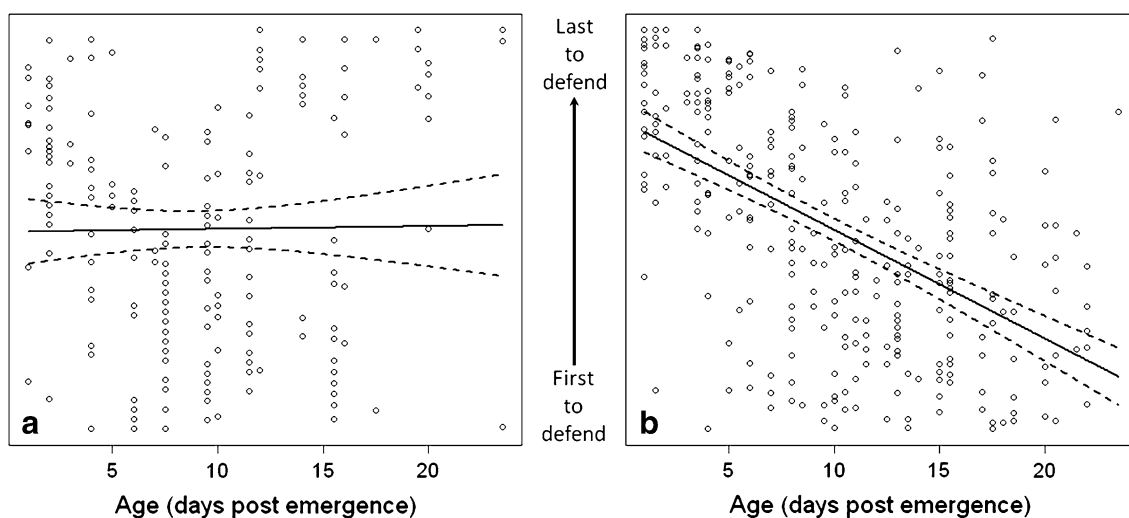


Fig. 2 Order in which *Vespa velutina* workers exited the cage as a function of their age; **a** nest 1 and **b** nests 2 and 3 (pooled data). Each point represents the rank of defence of an individual according to its

age at one experimental session. The data are pooled for the four replicates because they did not differ from each other. Solid line GLM predicted values, dashed lines 95 % confidence intervals

colony organization, may eventually be adopted as a pest management strategy.

Conclusions

Although investigations of captive colonies are of questionable long viability, this work has identified several behavioural traits that may be biologically important to *V. velutina*: (1) the early production of males and the agonistic behaviour of the workers towards them; (2) the possible survival of orphan colonies for several weeks; (3) the relationship between worker rank and age in nest defence, and finally (4) the role of the queen in the division of labour of the whole among the colony members. Such traits should now be investigated in field colonies of different sizes. Ultimately, they may provide useful insights into pest management and the evolution of sociality.

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References

- Archer M.E. 2010. The queen colony phase of vespine wasps (Hymenoptera, Vespidae). *Insect. Soc.* **57**: 33-145
- Beggs J.R., Brockerhoff E.G., Corley J.C., Kenis K., Masciocchi M., Muller F., Rome Q. and Villemant C. 2011. Ecological effects and management of invasive Vespidae. *BioControl* **56**: 505-526
- Beshers S.N. and Fewell J.H. 2001. Models of division of labor in social insects. *Annu. Rev. Entomol.* **46**: 413-440
- Bonnard O., Monceau K. and Thiéry D. 2012. Elevage de colonies de *Vespa velutina*, un prédateur d'abeilles domestiques récemment introduit en France. *Cah. Tech. Inra* **76**: 1-11. <http://www6.bordeaux-aquitaine.inra.fr/sante-agroecologie-vignoble/Publications/Articles-sans-comite-de-lecture>. Accessed on 28 May 2013
- Brown M.J.F. and Paxton R.J. 2009. The conservation of bees: a global perspective. *Apidologie* **40**: 410-416
- Calderone N.W. 1998. Proximate mechanisms of age polyethism in the honey bee, *Apis mellifera* L. *Apidologie* **29**: 127-158
- Courchamp F., Clutton-Brock T. and Grenfell B. 1999. Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**: 405-410
- Dew H.E. and Michener C.D. 1981. Division of labor among workers of *Polistes metricus* (Hymenoptera: Vespidae): laboratory foraging activities. *Insect. Soc.* **28**: 87-101
- Edwards R. 1980. *Social Wasps. Their Behaviour and Control*. Rentokil Limited, Sussex
- Fox J. and Weisberg S. 2011. *An R Companion to Applied Regression*, Second Edition. Sage Publications, Thousand Oaks
- Hagler J.R. and Jackson C.G. 2001. Methods for marking insects: current techniques and future prospects. *Annu. Rev. Entomol.* **46**: 511-543
- Hoffmann W.R.E., Neumann P. and Schmolz E. 2000. Technique for rearing the European hornet (*Vespa crabro*) through an entire colony life cycle in captivity. *Insect. Soc.* **47**: 351-353
- Hölldobler B. and Wilson E.O. 2008. *The Superorganism*. W.W. Norton & Company, New York
- Hurd C.R., Jeanne R.L. and Nordheim E.V. 2007. Temporal polyethism and worker specialization in the wasp, *Vespula germanica*. *J. Insect Sci.* **7**: 43. <http://www.insectscience.org/7.43/> Accessed on 28 May 2013
- Janet C. 1895. Etudes sur les fourmis, les guêpes et les abeilles. Neuvième note. Sur *Vespa crabro* L. Histoire d'un nid depuis son origine. *Mem. Soc. Zool. Fr.* **8**: 1-140
- Jeanne R.L. 1991. Polyethism. In: *The Social Biology of Wasps* (Ross K.G. and Matthews R.W., Eds), Cornell University Press, New York. pp 389-425
- Jeanne R.L. 2003. Social complexity in the Hymenoptera, with special attention to the wasps. In: *Behaviors and Evolution of Social Insects* (Kikuchi T., Azuma N. and Higashi S., Eds). Hokkaido University Press, Sapporo. pp 81-130
- Jeanne R.L., Downing H.A. and Post D.C. 1988. Age polyethism and individual variation in *Polybia occidentalis*, an advanced eusocial wasp. In: *Interindividual Behavioral Variability in the Social Insects* (Jeanne R.L., Ed). Westview Press, Boulder. pp 323-357
- Jeanne R.L., Williams N.M. and Yandell B.S. 1992. Age polyethism and defense in a tropical social wasp (Hymenoptera: Vespidae). *J. Insect Behav.* **5**: 211-227
- Johnson B.R. 2010. Division of labor in honeybees: form, function, and proximate mechanisms. *Behav. Ecol. Sociobiol.* **64**: 305-316
- Judd T.M. 2000. Division of labour in colony defence against vertebrate predators by the social wasp *Polistes fuscatus*. *Anim. Behav.* **60**: 55-61
- Kim B., Kim K.W. and Choe J.C. 2012. Temporal polyethism in Korean yellowjacket foragers, *Vespula koreensis* (Hymenoptera, Vespidae). *Insect. Soc.* **59**: 263-268
- Liebholt A.M. and Tobin P.C. 2008. Population ecology of insect invasions and their management. *Annu. Rev. Entomol.* **53**: 387-408
- Martin S.J. 1995. Hornets (Hymenoptera: Vespinae) of Malaysia. *Malay. Nat. J.* **49**: 71-82
- Matsuura M. 1984. Comparative biology of five Japanese species of the genus *Vespa* (Hymenoptera, Vespidae). *Bull. Fac. Agri., Mie Univ.* **69**: 1-131
- Matsuura M. 1991. *Vespa* and *Provespa*. In: *The Social Biology of Wasps* (Ross K.G. and Matthews R.W., Eds), Cornell University Press, Ithaca. pp 232-262
- Matsuura M. and Yamane S. 1990. *Biology of Vespine Wasps*. Springer-Verlag, Berlin
- Moller H. 1996. Lessons for invasion theory from social insects. *Biol. Conserv.* **78**: 125-142
- Monceau K., Arca M., Lepêtre L., Mougél F., Bonnard O., Silvain J.-F., Maher N., Arnold G. and Thiéry D. 2013b. Native prey and invasive predator patterns of foraging activity: the case of the yellow-legged hornet predation at European honeybee hives. *PLoS ONE* **8**: e66492
- Monceau K., Maher N., Bonnard O., Thiéry D. 2013a. Predation dynamics study of the recently introduced honeybee killer *Vespa velutina*: learning from the enemy. *Apidologie* **44**: 209-221
- Moreyra S., D'Adamo P. and Lozada M. 2012. Cognitive processes in *Vespula germanica* (Hymenoptera: Vespidae) when relocating a food source. *Ann. Entomol. Soc. Am.* **105**: 128-133
- Perrard A., Haxaire J., Rortais A., Villemant C. 2009. Observations on the colony activity of the Asian hornet *Vespa velutina* Lepelletier 1836 (Hymenoptera: Vespidae: Vespinae) in France. *Ann. Soc. Entomol. Fr.* **45**: 119-127
- Potts S.G., Biesmeijer J.C., Kremen C., Neumann P., Schweiger O. and Kunin W.E. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* **25**: 345-353

- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org>. Accessed on 28 May 2013
- Robinson G.E. 1992. Regulation of division of labor in insect societies. *Annu. Rev. Entomol.* **37**: 637-665
- Roitberg B.D. 2007. Why pest management needs behavioral ecology and vice versa. *Entomol. Res.* **37**: 14-18
- Roy H.E., Roy D.B. and Roques A. 2011. Inventory of terrestrial alien arthropod predators and parasites established in Europe. *BioControl* **56**: 477-504
- Spradbery J.P. 1973. *Wasps: An Account of the Biology and Natural History of Social and Solitary Wasps*. University of Washington Press, Seattle.
- Spradbery J.P. 1991. Evolution of queen number and queen control. In: *The Social Biology of Wasps* (Ross K.G. and Matthews R.W., Eds), New York, Cornell University Press. pp 336-388
- Starr C.K. 1985. Enabling mechanisms in the origin of the sociality in the Hymenoptera: the sting's on the thing. *Ann. Entomol. Soc. Am.* **78**: 836-840
- Starr C.K. 1990. Holding the fort: colony defense in some primitively social wasps. In: *Insect Defences. Adaptive Mechanisms and Strategies of Prey and Predators* (Evans D.L. and Schmidt J.O., Eds). State University of New York Press, Albany. pp 421-463
- Starr C.K. 1992. The social wasps (Hymenoptera: Vespidae) of Taiwan. *Bull. Natl. Mus. Nat. Sci.* **3**: 93-138
- Strassmann J.E. 1981. Parasitoids, predators, and group size in the paper wasp, *Polistes exclamans*. *Ecology* **62**: 1225-1233
- Tabadkani S.M., Nozari J. and Lihoreau M. 2012. Inbreeding and the evolution of sociality in arthropods. *Naturwissenschaften* **99**: 779-788
- Tobin P.C., Berek L. and Liebhold A.M. 2011. Exploiting Allee effects for managing biological invasions. *Ecol. Lett.* **14**:615-624
- Togni O.C. and Giannotti E. 2010. Colony defense behavior of the primitively eusocial wasp, *Mischocyttarus cerberus* is related to age. *J. Insect Sci.* **10**: 136. <http://www.insectscience.org/10.136/> Accessed 28 May 2013
- Toh Y. and Okamura J.-Y. 2003. Foraging navigation of hornets studied in natural habitats and laboratory experiments. *Zool. Sci.* **20**: 311-324
- Villemant C., Muller F., Haubois S., Perrard A., Darrouzet E. and Rome Q. 2011. Bilan des travaux (MNHN et IRBI) sur l'invasion en France de *Vespa velutina*, le frelon asiatique prédateur d'abeilles. In: Journée Scientifique Apicole (Barbançon J.-M. and L'Hostis M., Ed). Nantes, ONIRIS-FNOSAD. pp 3-12
- Volynchik S., Plotkin M., Bergman D.J. and Ishay J.S. 2009. Polyethism in an Oriental hornet (*Vespa orientalis*) colony. *Sch. Res. Exch.* doi:10.3814/2009/243436
- Wakano J.Y., Nakata K. and Yamamura N. 1998. Dynamic model of optimal age polyethism in social insects under stable and fluctuating environments. *J. Theor. Biol.* **193**: 153-165
- Warkentin K.M., Buckley C.R. and Metcalf K.A. 2006. Development of red-eyed treefrog eggs affects efficiency and choices of egg-foraging wasps. *Anim. Behav.* **71**: 417-425
- Weiss M.R., Wilson E.E. and Castellanos I. 2004. Predatory wasps learn to overcome the shelter defences of their larval prey. *Anim. Behav.* **68**: 45-54
- Wilson E.O. 1971. *The Insect Societies*. Cambridge, MA: Belknap/Harvard University Press