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Evaluation of competition between a native and an invasive hornet species: do seasonal phenologies overlap?

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Abstract

One common dogma in ecology is based on the competitive exclusion principle. Hence, competition is often considered to be one of the primary determinants of the structure and functioning of ecosystems. In this paper, we investigate how the native *Vespa crabro* and the recently introduced *Vespa velutina* show some degree of niche differentiation that potentially minimizes their interspecific competition, the two dimensions investigated here being seasonal activity patterns and preferences for food. These two species share common characteristics: they are closely related, live in the same areas, belong to the same guild (predators), exploit the same kind of food sources, and exhibit a similar annual life cycle. Considering all these similarities, interspecific competition may occur if the two species exhibit identical seasonal phenologies. Our data show that their seasonal phenologies overlap to some extent probably due to biological constraints common to Vespinae. The shifts in time observed here allow the hornet species to not directly compete for food sources at the same time. It does not however exclude indirect competition, especially in a 'first-come, first-served' fashion.

Keywords: interspecific competition, predator facilitation, synergistic predation, temporal niche overlap, Vespinae

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Introduction

One fundamental and common dogma in ecology is based on the competitive exclusion principle (Hardin, 1960): species exploiting very similar niches cannot share it for an extended period of time. In such a way, it predicts that the more efficient species will 'competitively exclude' the less efficient species. Hence, interspecific competition has received considerable interest especially in understanding how it contributes to community assemblages although its role is controversial (Wiens, 1977; Connell, 1983; Schoener, 1983; Goldberg & Barton, 1992; Gurevitch *et al.*, 1992; Niemelä, 1993). Basically, interspecific competition is divided in two mechanisms: exploitation and interference (Reitz & Trumble, 2002; Duyck *et al.*, 2004). Exploitation occurs when individuals from different species exploit the same resource. In this case, individuals do not compete directly contrarily to interference in which individuals compete by direct contact. To reduce interspecific competition, the less competitive individuals may avoid their higher competitors temporally or spatially for example (Razgour *et al.*, 2011; Ronconi & Burger, 2011). In the most severe cases, interspecific competition may however conduct to the complete displacement (i.e., exclusion) of the less competitive species from the ecological niche (Reitz & Trumble, 2002).

According to Reitz & Trumble (2002), 78% of the displacements of insect and arachnid species are due to the introduction of alien species and biological invasions are known to be

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one of the major threats to biodiversity (Vitousek *et al.*, 1997; Chapin *et al.*, 2000; Clavero *et al.*, 2009). Especially, alien predators may impact the ecosystem at least at two levels: in preying upon native prey species and in interfering with native predators (Zaret & Paine, 1973; Bourdeau *et al.*, 2011; Snyder & Evans, 2006). Competition represents an important threat for native species sometimes leading to their decline although its effect are less often acknowledged than the effect of predation on native prey species. An example of such effect is provided by the proliferation of the invasive Asian ladybird *Harmonia axyridis*, which threatens native European ladybird species (Brown *et al.*, 2011; Roy *et al.*, 2012; Katsanis *et al.*, 2013).

In Western Europe, a single species of hornet occurred, the European hornet (*Vespa crabro*), until the accidental introduction of the yellow-legged hornet (*Vespa velutina*) from eastern China (Monceau *et al.*, 2014*a*). Observed for the first time in France in 2004, *V. velutina* extended its range to several European countries (see Ibáñez-Justicia & Loomans, 2011; Villemant *et al.*, 2011). Like other Vespinae, *V. crabro* and *V. velutina* prey on a wide range of arthropods (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990). Especially, they are well known by beekeepers to attack honeybees in apiaries (Matsuura & Yamane, 1990; Baracchi *et al.*, 2010; Monceau *et al.*, 2013*a*, *b*, 2014*b*). Indeed, beehives represent a valuable food source, getting proteins (larva and adult honeybees) for feeding hornet brood and carbohydrates (mainly honey storage) for adult hornets, the two kinds of resources used by vespine wasps (Raveret Richter, 2000). Additionally, *V. crabro* and *V. velutina* exhibit similar annual colony life cycle which can be divided in three major phases: (i) the foundation of the colonies following the emergence of foundresses from overwintering, (ii) the increase of the colony size and (iii) the emergence of sexuals for mating and the death of the colony. These three phases in the hornet life cycle can be monitored through their food preference because the nutritional requirements differ between adults and larvae, adult vespids mainly feeding on carbohydrates and larvae on proteins (Raveret Richter, 2000; Monceau *et al.*, 2014*a*). Although a part of the carbohydrate intakes can be obtained from the larvae (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990; Archer, 2012), three main peaks of foraging activity on carbohydrate sources are thus supposed to occur, roughly in spring, summer and autumn, each corresponding to the three phases of the hornet life cycle. Additionally, gathering proteins mainly occurs through summer and autumn with the colony growth. Protein requirements are even more important during the rearing of sexuals because they require more food, especially for gynes, and should thus raise a maximal consumption before the mating period in autumn (Spradbery, 1973; Edwards, 1980).

Although the introduction of *V. velutina* represents an important threat to honeybees and beekeeping, it may also threaten *V. crabro*, which is protected in some areas within its native range (e.g., in Germany since 1987). Indeed, these two species share common characteristics: they are closely related, live in the same environment, belong to the same guild (predators), exploit the same kind of food sources and exhibit a similar annual life cycle. Considering all these similarities, interspecific competition may occur if the two species exhibit similar seasonal phenologies. The goals of this study were thus to characterize *V. crabro* and *V. velutina* seasonal phenologies by following the trapping yields of the two species on their two food requirements (carbohydrate and protein baits) in the course of time. We then compared the seasonal phenologies of each species to evaluate the extent of their temporal overlap. Therefore, the degree of overlap between *V. crabro* and *V. velutina* may provide a first assessment of the occurrence of interspecific competition between these two hornet species.

Materials and methods

Experimental design

Vespa crabro and *V. velutina* populations were monitored at two apiaries in the vicinity of Bordeaux (invaded by *V. velutina* in 2005): an apiary belonging to a professional beekeeper located in Artigues-près-Bordeaux (GPS: N44°51′37.20″ W0°28′43.28″, thereafter noted ART) and an experimental apiary of our research institute located in Villenave d'Ornon (GPS: N44°47′27.05″ W0°34′38.35″, thereafter noted VIL). These two apiaries were previously monitored to study *V. velutina* population dynamics in 2008 (see Monceau *et al.*, 2013*a*).

Seasonal phenologies of adult hornets were monitored with funnel traps composed of a glass jar (Le Parfait®, 1500 g, Ø 11 cm) equipped with a washable stainless steel funnel on the top (Supplementary fig. 1). In each apiary, four traps were positioned in between the hives (at ca. 1 m distance) and placed 50 cm above the ground on supports with a roof to protect from rainfalls (Supplementary fig. 1). For each site, two devices were baited with carbohydrate-based bait (40% apple concentrate in 250 ml of pure water) and two with protein-based bait (60 g of blended fresh fillets of farmed brown trout sexuals, *Salmo trutta*, provided by INRA St Pée-sur-Nivelle, in 250 ml of pure water).

All traps of ART and VIL were monitored weekly, at the same date (±1 day) from the 25th/24th of March to the 18th/17th of November in 2009 and 2010, respectively. Traps and baits were changed every week and the number of captured hornets was noted and pooled per bait, site and date.

Statistics

Poisson generalized linear models (GLMs) corrected for overdispersion were used to describe the variation in the number of hornet caught (trapping yields) depending on baits, sites, years and dates for each species separately. All predictors were standardized (Gelman, 2008) for model selection procedure generating all possible combinations of variables, except those including models containing interactions without their respective main effects. Models were then ranked using Akaike Information Criterion scores corrected for small sample sizes (AICc). The models displaying less than 2ΔAICc of difference with the best models were kept for model averaging procedure to obtain an average model (see Supplementary table 1) and predictors estimates assorted with their unconditional standard errors (SE), 95% confidence interval (95% CI), z statistic and relative importance (RI) (Burnham & Anderson, 2002). *Vespa crabro* and *V. velutina* densities based on trapping yields were compared within and between site and year using χ^2 tests. Finally, the deviation from random pattern of temporal activity overlap (i.e., whether a temporal niche overlap/segregation exist or not) was investigated using TimeOverlap program (v. 1.0, available at: http://hydrodictyon.eeb.uconn.edu/people/willig/Research/activity%20pattern.html, see Castro-Arellano *et al.*, 2010 for details) based on Rosario randomization algorithm to compute Pianka's and

Czechanowski's indices (Pianka, 1973; Feinsinger *et al.*, 1981). These indices range from 0 (no temporal overlap) to 1 (complete temporal overlap). Bilateral tests based on 10,000 randomizations were performed and *P*-values were calculated as twice the proportion of the lowest score of either (i) the number of randomizations that have an overlap that is equal to or greater than the observed overlap value or (ii) the number of randomizations that have an overlap that is equal to or less than the observed overlap value. This analysis was first performed on the trapping yields obtained for each bait by sites and years separately and then in pooling the yields by baits to obtain a global comparison.

All other statistics were calculated using R software (v. 3.0.1; R Development Core Team, 2013) implemented with the following packages: *epicalc* for overdispersion detection, *dispmod* for fitting overdispersed Poisson log-linear GLMs, *arm* for variable standardization and *MuMIn* for model selection.

Results

Seasonal phenologies

Vespa crabro

Capture yields for *V. crabro* varied between baits and sites (table 1, Supplementary table 1). There were more *V. crabro* caught (i) with carbohydrate than with protein bait (see table 2 for details) and (ii) in ART than in VIL (160 and 59, respectively). The numbers of *V. crabro* caught were similar in 2009 and 2010. The overall dynamics could be summarized in three series: (i) in April, (ii) from mid-June to late September and (iii) in October (fig. 1). This dynamics was similar for carbohydrate and protein baits (fig. 2).

Vespa velutina

Capture yields for *V. velutina* differed between baits (table 3, Supplementary table 1): more hornets were caught with protein than with carbohydrate bait (see table 2 for details). Trapping yields also varied from March to November (fig. 1) with differences between baits and sites. This trend was consistent between years. For the carbohydrate bait, three series of captures could be observed: (i) from March to early June, (ii) from July to mid-September and (iii) from mid-September to November (fig. 2a). For the protein bait, a single wave was observed from mid-July to mid-November (fig. 2b). Additionally, dynamics differed between sites (table 3). The captures in spring ended later in ART than in VIL (ART: March to mid-June, VIL: March to April) and captures in VIL were more spread out than in ART during summer (Supplementary fig. 2).

Vespa crabro vs. Vespa velutina

Density

A general characteristic in both sites was the predominance of *V. velutina* in traps (table 2). In ART, the ratio between *V. crabro* and *V. velutina* was consistent over years (χ^2-square test: $\chi^2_1 = 3.00$, $P = 0.08$) and was in average 1: 21 (table 2). In VIL, this ratio was not consistent over years ($\chi^2_1 = 4.90$, $P = 0.03$) with a larger proportion of *V. crabro* in 2010 than in 2009 (1:70 in 2009 vs. 1:37 in 2010, table 2). The average ratio in VIL was 1: 50 which is two times less than in ART ($\chi^2_1 = 51.62$, $P < 0.0001$, table 2).

Table 1. Analysis of *V. crabro* capture yields according to the baits, sites, dates and years.

	β	SE	95% CI	*z*	*P*	RI
Intercept	−0.93	0.15	[−1.23; −0.63]	6.02	<0.0001	–
Bait	**−1.41**	**0.29**	**[−1.98; −0.85]**	**4.90**	**<0.0001**	**1.00**
Date	**1.88**	**0.29**	**[1.31; 2.46]**	**6.41**	**<0.0001**	**1.00**
Site	**−0.97**	**0.27**	**[−1.51; −0.43]**	**3.53**	**<0.001**	**1.00**
Bait : Date	−0.42	0.60	[−1.60; 0.76]	0.69	0.49	0.20
Bait : Site	0.34	0.56	[−0.76; 1.45]	0.61	0.54	0.19
Year	0.09	0.27	[−0.43; 0.62]	0.35	0.73	0.17

Each predictor selected in the best models are presented with its estimate (β) assorted with unconditional standard errors (SE), 95% confidence interval (95% CI), the *z*-test statistic (*z*) and associated *P*-value (*P*) and the relative importance of the parameter (RI). Significant predictors are in bold.

Table 2. Trapping yields for *V. crabro* and *V. velutina* per sites and years with the total number of both species.

	Vespa crabro			*Vespa velutina*		
	CB	PB	CB + PB	CB	PB	CB + PB
ART						
2009	73	16	89	142	1467	1609
2010	57	14	71	213	1510	1723
2009 + 2010	130	30	160	355	2977	3332
VIL						
2009	16	6	22	186	1365	1551
2010	30	7	37	277	1116	1393
2009 + 2010	46	13	59	463	2481	2944
Overall	176	43	219	818	5458	6276

CB, carbohydrate bait; PB, protein bait.

Temporal niche overlap analyses

Temporal niche overlap analyses between *V. crabro* and *V. velutina* gives congruent results in using either Pianka's or Czechanowski's indices. Overall, these indices suggest that temporal pattern of activity in *V. crabro* and *V. velutina* partially overlapped (Pianka index range 0.53–0.86; Czechanowski index range: 0.41–0.70) but not more than expected by chance (all comparisons being non-significant, table 4).

Discussion

Invasive alien species are one of the major threats to biodiversity (Vitousek *et al.*, 1997; Chapin *et al.*, 2000; Clavero *et al.*, 2009). Especially, alien generalist predators often greatly impact the whole ecosystem by preying on native naïve prey, displacing and excluding intra-guild competitors and most of the time without any regulation by natural enemies (Zaret & Paine, 1973; Snyder & Evans, 2006; Bourdeau *et al.*, 2011; Perdereau *et al.*, 2011; Haddaway *et al.*, 2012; Roy *et al.*, 2012). To date, *V. velutina* is mainly known for its predation on honeybees but its effect on *V. crabro*, which belong to the same guild remains completely unknown (Monceau *et al.*, 2014*a*). Our study is thus the first relating a potential impact of *V. velutina* on its direct competitor *V. crabro* in Europe (see

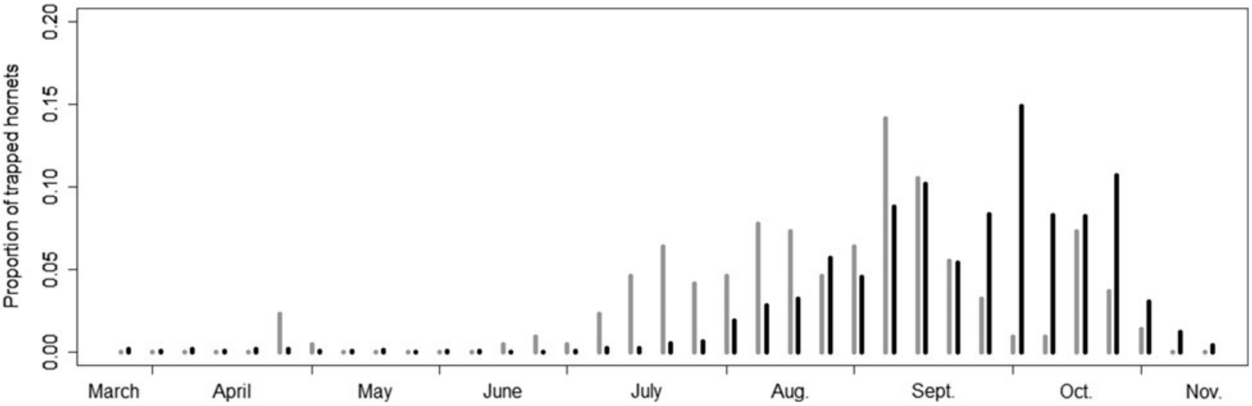

Fig. 1. Overall trapping yields of *V. crabro* (grey bars, $N_{VC} = 219$) and *V. velutina* (black bars, $N_{VV} = 6276$), from March to November represented as a proportion of the total number of each hornet species (data pooled for 2009 and 2010, carbohydrate and protein baits, and ART and VIL).

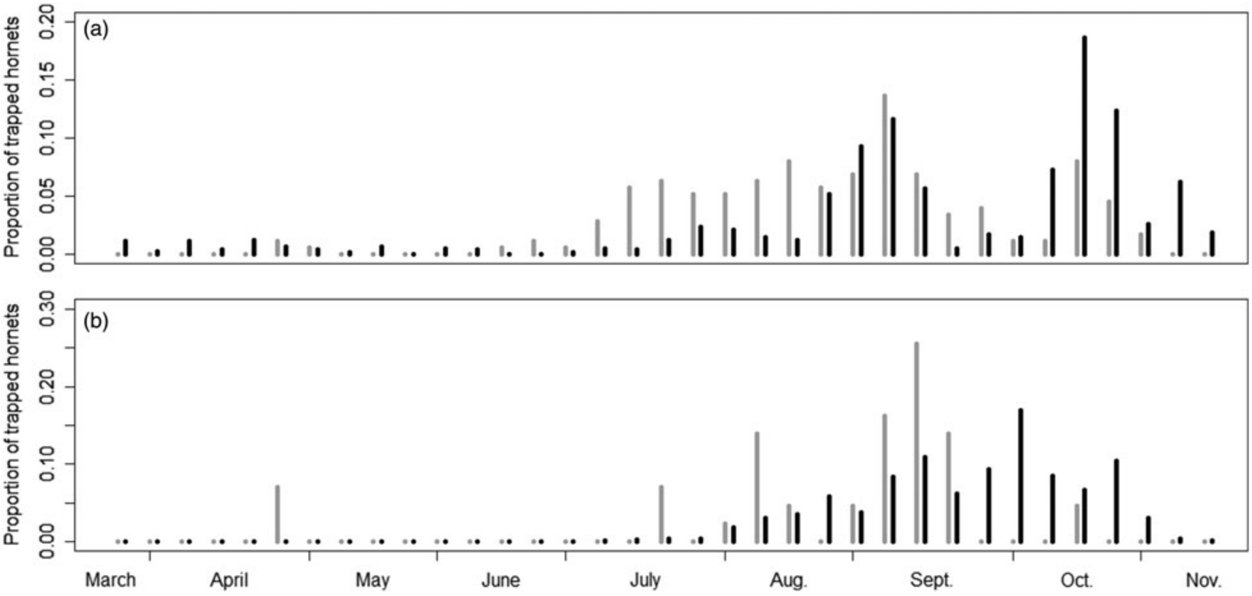

Fig. 2. Trapping yields of *V. crabro* (grey bars) and *V. velutina* (black bars) from March to November represented as a proportion of the total number of each hornet species caught with (a) carbohydrate bait ($N_{VC} = 176$ and $N_{VV} = 818$) and (b) protein bait ($N_{VC} = 43$ and $N_{VV} = 5458$) (data pooled for 2009 and 2010, and ART and VIL).

Choi *et al.*, 2012 in Korea) and it suggests that the two species show some degree of niche differentiation that potentially minimizes their interspecific competition.

In spring, *V. velutina* foundresses are the first to regain activity and their period of flight is longer than *V. crabro* (March to mid-June and late April to early May, respectively). This difference is expected to be the result of variation in overwintering duration, which is documented as a bet-hedging strategy to adapt to novel environments (Gourbière & Menu, 2009). Contrarily to *V. velutina* (Monceau *et al.*, 2012, 2013*a*), the present data for *V. crabro* differs from previous observations in which the foundresses were found to fly from mid-April to early-July (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990). However, these data were acquired in a different area and consequently, such variability in flying period cannot be clearly attributed to the presence of *V. velutina*. During summer, foraging activity on carbohydrates begins earlier and is slightly longer in *V. crabro* than in *V. velutina* (from mid-June to late September and from early July to mid-September, respectively). *Vespa velutina* seasonal phenology has already been monitored in 2008 (the year before the present study), in the same locations using carbohydrate baits during summer and autumn (Monceau *et al.*, 2013*a*). We overall find common trends between these different surveys: a first slight increase in early-July to mid-August followed by a drastic increase of the foraging activity from mid-August to mid-September and then a slow down before the emergence of sexuals. Finally, in the last part of the cycle (when sexuals need carbohydrates before mating), the foraging activity on carbohydrates begins earlier and is longer

Table 3. Analysis of *Vespa velutina* capture yields according to the baits, sites, dates and years.

	β	SE	95% CI	z	*P*	RI
Intercept	1.39	0.10	[1.19; 1.59]	13.44	<0.0001	–
Bait	**0.54**	**0.20**	**[0.14; 0.95]**	**2.65**	**<0.01**	**1.00**
Date	**4.34**	**0.22**	**[3.91; 4.77]**	**19.66**	**<0.0001**	**1.00**
Site	−0.27	0.20	[−0.66; 0.13]	1.32	0.18822	1.00
Bait : Date	**4.23**	**0.44**	**[3.37; 5.09]**	**9.64**	**<0.0001**	**1.00**
Date : Site	**1.19**	**0.43**	**[0.35; 2.03]**	**2.78**	**<0.01**	**1.00**
Year	0.29	0.20	[−0.10; 0.66]	1.44	0.14981	0.90
Bait : Year	−0.73	0.38	[−1.47; 0.01]	1.93	0.05319	0.80
Site : Year	0.43	0.38	[−0.30; 1.17]	1.15	0.24870	0.28
Date : Year	−0.46	0.43	[−1.30; 0.39]	1.06	0.28817	0.26
Bait : Site	0.20	0.38	[−0.55; 0.94]	0.52	0.60478	0.10

Each predictor selected in the best models are presented with its estimate (β) assorted with unconditional standard errors (SE), 95% confidence interval (95% CI), the *z*-test statistic (*z*) and associated *P*-value (*P*) and the relative importance of the parameter (RI). Significant predictors are in bold.

Table 4. Summary of the tests for temporal niche overlap between *V. crabro* and *V. velutina* based on Pianka and Czechanowski indices and associated *P*-values (based on 10,000 randomizations).

		Pianka index	*P*	Czechanowski index	*P*
ART					
CB	2009	0.79	0.44	0.63	0.35
	2010	0.73	0.43	0.60	0.34
PB	2009	0.70	0.44	0.46	0.45
	2010	0.57	0.59	0.42	0.55
CB + PB	2009	0.78	0.31	0.64	0.34
	2010	0.67	0.51	0.49	0.55
VIL					
CB	2009	0.53	0.56	0.41	0.67
	2010	0.86	0.34	0.70	0.26
PB	2009	0.82	0.24	0.50	0.21
	2010	0.61	0.40	0.53	0.46
CB + PB	2009	0.82	0.15	0.61	0.22
	2010	0.77	0.27	0.64	0.45

ART, Artigues-près-Bordeaux; VIL, Villenave d'Ornon; CB, carbohydrate bait; PB, protein bait.

in *V. velutina* than in *V. crabro* (from mid-September to late November and only during October, respectively).

Concerning the foraging activity on protein sources, the discrepancy between species is clearer. It begins earlier and is shorter in *V. crabro* than in *V. velutina* (mid-July to mid-November and early July to late November, respectively). Interestingly, this peak occurs between the two peaks of foraging activity for carbohydrates in *V. crabro* and *V. velutina* (mid- and late September, respectively). At the advent of gyne emergence, the ratio larva/worker is at its lowest and the productivity of the colony is at its maximum (Matsuura & Yamane, 1990). Although most of the foraging activity for proteins is concentrated in summer and autumn, a few individuals were also trapped in spring using protein bait (late April 2010 in ART: three *V. crabro* and three *V. velutina* in the same trap). In early spring, just at the exit from overwintering, foundresses are not supposed to feed on proteins. Thus, this single event could solely be an artefact.

Our data show that temporal patterns of activity of *V. crabro* and *V. velutina* overlap, which suggests competition, but most of the dynamics do not differ from expected in random events. This partial overlap probably results from the biological constraints of the Vespinae, hornet species exhibiting similar life-cycle timing (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990). The fact that the overlap is not total suggests that they do not probably compete directly for food sources at the same time. It does not however exclude indirect competition, especially in a 'first-come, first-served' fashion. Indeed, *V. velutina* foundresses emerge first from overwintering and are also more active, explorative and bolder than *V. crabro* (Monceau *et al.*, in press). They can consequently monopolize the best food sources before *V. crabro* foundresses. After this phase, considered the most critical (Spradbery, 1973), *V. crabro* takes advantage and seems to complete its life cycle quicker than *V. velutina*, suggesting that the 'initial dominance' of *V. velutina* is reversed. It should however be considered here that the populations of the two species greatly differ in number. The numerical dominance of *V. velutina* on *V. crabro* obviously depends on the number of nests in the vicinity of the experimental sites. Nonetheless, the localization of hornet colonies is often realized *a posteriori*, nests being usually cryptic. Most importantly, the difference in population size can be explained by their respective colony size. Indeed, *V. crabro* forms medium-sized colonies containing ca. 500–4500 cells (in average ca. 1100 adult produced), occupied by 300–400 workers at the maximum colony activity and produce in average 200 gynes and 350 males (Edwards, 1980; Matsuura & Yamane, 1990; Archer, 1993; Hoffmann *et al.*, 2000). *Vespa velutina* can build larger nests containing more than 10,000 cells (in average ca. 6000 adults produced), occupied by more than one thousand workers at time and produce in average 350 gynes and 900 males (Martin, 1995; Nakamura & Sonthichai, 2004; Monceau *et al.*, 2014*a*). The difference in sexual production is also visible with the last peak of foraging activity on carbohydrates, which is higher in *V. velutina* than in *V. crabro* in regards to the rest of the cycle.

Several Vespine wasps have already colonized different areas worldwide (see Beggs *et al.*, 2011 for review), including *V. crabro* in North America (Akre *et al.*, 1980; Buck *et al.*, 2008; Kimsey & Carpenter, 2012). In the present case, *V. velutina* largely surpasses *V. crabro* in term of colony size/productivity. Interestingly, the overall ratios between *V. crabro* and *V. velutina* are consistent between 2009 and 2010, although there were slightly more *V. crabro* relative to *V. velutina* in VIL in 2010. This consistency through two consecutive years suggests that less than 4 years after the colonization of this area (the first *V. velutina* was first observed in 2005 in this area), the co-occurrence of the native and the invading hornet species could be considered stabilized. To some extent, it seems like the native hornet species may take advantage from the presence of this alien species, although we cannot exclude that *V. crabro* population may have previously suffered from the introduction of *V. velutina*. These two hornet species are known to prey on domestic honeybees (Matsuura & Yamane, 1990; Baracchi *et al.*, 2010; Monceau *et al.*, 2014*a*). Some beekeepers in the invaded areas have observed an increase in the number of *V. crabro* in their apiaries since the introduction of *V. velutina* (Monceau *et al.*, 2014*a*). This suggests that *V. crabro* may benefit from the presence of *V. velutina* in apiaries. Indeed, *V. velutina* exerts a strong predation pressure and weakens honeybee colonies (Monceau *et al.*, 2013*b*). *Vespa crabro* may take advantage of the situation to chase on weakened colonies, which are less defended and/or scavenge on leftover dead bee bodies by *V. velutina* (N. Maher, personal observation). Predator facilitation (Charnov *et al.*, 1976, also known as synergistic predation) may thus occur in this newly established association (Losey & Denno, 1999). If so, this may be seriously considered because synergistic predation often results in an overall higher rate of prey consumption than if predator species would have occurred separately (Soluk & Collins, 1988; Kotler *et al.*, 1992).

Conclusions and perspectives

The present data show that the seasonal phenologies of *V. crabro* and *V. velutina* partially overlap probably due to biological constraint common to Vespine wasps. It is impossible to conclude on the effect of *V. velutina* on *V. crabro* without any measurement of the seasonal phenology of the native species without its putative competitor (Colwell & Futuyma, 1971). However, in the present case of *V. crabro*, rather little population dynamics studies were done which do not allow comparisons before and after the introduction of *V. velutina*. Also, any removal of the alien hornet by eradicative methods is now impossible which do not allow any further study on *V. crabro* alone.

Although the invasive species is largely more numerous than the native one, a few years after the beginning of the invasion, these two species seem to be quite stable. *Vespa crabro* does not seem to be threatened by *V. velutina*, and we even suspect that the native could take advantage of the massive attack exerted by the alien hornet species on honeybee colonies. This would have however to be tested at a larger geographical scale in further studies.

Interspecific competition between *V. crabro* and *V. velutina* should also consider another dimension that is competition for nesting sites (Spradbery, 1973; Edwards, 1980; Matsuura & Yamane, 1990; Matsuura, 1991; Gamboa *et al.*, 2002, 2004; Liebert *et al.*, 2006; Choi *et al.*, 2012). Even though the known cases of interspecific competition are rather rare or underreported in Vespids, Matsuura & Yamane (1990) give the example of five *Vespa* species (*Vespa analis*, *Vespa crabro*, *Vespa mandarinia*, *Vespa tropica* and *Vespa simillima*) nesting in South-western Honshu (Japan). Although they all live in the same area, they either differ for their nesting habit or for their timing of nest initiation thus limiting to a certain extent potential competition. In the case of *V. crabro* and *V. velutina*, the timing of nest initiation could be problematic since *V. velutina* foundresses emerge from overwintering before *V. crabro*. Moreover, a recent study on the behaviour of foundresses shows that *V. velutina* is also more active, explorative and bolder than *V. crabro* potentially giving to the invasive hornet species an advantage when searching a convenient nesting site (Monceau *et al.*, in press). Thus, it would be interesting to focus on this part of the hornet life cycle to fully understand the extent of *V. velutina* impact on *V. crabro*. Such information is crucial since it can help understand how *V. velutina* may have invaded and spread through Europe, foundresses being accountable for the invasion of new areas.

Supplementary Material

The supplementary material for this article can be found at http://www.journals.cambridge.org/BER

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