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Foraging niche separation of social wasps in an invaded area: Implications for their management

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Abstract

Foraging niche separation may be a mechanism to promote coexistence of two competing species by concentrating intraspecific competition relative to interspecific competition. The present study investigated foraging behaviour and microhabitat use of two coexisting species of invasive social wasps, *Vespula germanica* and *Vespula vulgaris*, when foraging for two different food resources. Also, we tested the attractiveness of traps baited with a synthetic lure for those two species. We found that *V. germanica* wasps prefer to forage at ground level regardless of the resource, while *V. vulgaris* prefers protein resources at the shrubland level given a choice between a protein bait at ground or at shrubland level. However, when baited with the synthetic lure, the species caught was not affected by the height at which traps were placed. That is, in a no choice scenario, the traps were sufficiently attractive to lure both species of wasps to both microhabitats (ground and shrubland levels). Thus, our results support the existence of spatial niche differentiation at least in protein foraging and suggest that the synthetic lure evaluated could be used to trap both species of *Vespula* wasps present in Argentina. These results could help to improve management strategies of these social wasps in an invaded area.

KEYWORDS

attractant lure, control strategy, foraging behaviour, spatial ecological niche, *Vespula germanica*, *Vespula vulgaris*

1 | INTRODUCTION

According to coexistence theory, the stable coexistence of species is understood as an interaction between two opposing forces: fitness differences between species, which should drive the best-adapted species to exclude others within a particular ecological niche, and stabilizing mechanisms, which maintain diversity (Chesson, 2000). Stabilizing mechanisms promote coexistence by concentrating intraspecific competition relative to interspecific competition and include niche differentiation (Chesson, 2000).

Vespula germanica and *Vespula vulgaris* are eusocial hymenopterans, native to Eurasia and Northern Africa. In the past decades, these species have invaded many parts of the world including Australia, New Zealand, South of Africa and the Americas (Beggs et al., 2011). The first record of *V. germanica* in Argentina was in 1980, while *V. vulgaris* was first detected in 2010 (Masciocchi, Beggs, Carpenter, & Corley, 2010; Willink, 1980). In all invaded areas, these wasps cause negative impact on industries, natural environment and to human activities due to their venomous sting, aggressive behaviour and efficient foraging abilities (Beggs et al., 2011; Clapperton, Alspach, Moller, & Matheson, 1989; MacIntyre & Hellstrom, 2015; Yeruham, Schwimmer, & Brami, 2002). However, currently, direct destruction of nests or toxic baits are the only tools available for its management and its success is often variable (Beggs et al., 2011; Edwards, Toft, Joice, & Westbrooke, 2017).

Both *Vespula* wasps coexist in their native range as well as in invaded areas such as Argentina and New Zealand (Archer, 1978; Harris, Thomas, & Moller, 1991; Pereira, Pirk, & Corley, 2016).

Interestingly, these two species are very similar in their morphology and biology and show a considerable overlap in their distribution, although *V. germanica* has a narrower altitudinal foraging range than *V. vulgaris*. Both species are defined as opportunistic and carrion predators, feeding on a variety of insects and dead animals (Akre & MacDonald, 1986; Barr, Moller, Christmas, Lyver, & Beggs, 1996). Adults feed on carbohydrate sources and carry protein food sources to the nest to feed their larvae (Spradbery, 1973). According to Harris and Oliver (1993), Diptera was the most abundant prey component for both species. However, some differentiation was observed, with *V. germanica* foraging more Diptera and less Araneae, Hemiptera and Lepidoptera than *V. vulgaris*.

It is widely accepted that niche differentiation plays a key role in coexistence of competing species, on relatively small scales (Tang & Zhou, 2011). Since *V. germanica* and *V. vulgaris* present temporal overlap as well as a high degree of diet overlap, the coexistence could be facilitated at least in part by foraging niche partitioning (Harris et al., 1991). Previous studies suggested that both species have spatial resource partitioning in New Zealand *Nothofagus* honeydew beech forest, where *V. vulgaris* were found foraging in the shrubland level while *V. germanica* were on the ground (Harris et al., 1991). However, no previous studies have looked in depth at this spatial separation or in other habitats. Beech forests offer a unique situation of a high abundance of carbohydrates where *V. vulgaris* has successfully displaced *V. germanica* (Beggs, Karl, Wardle, & Bonner, 2005; Harris et al., 1991). The term honeydew beech forest refers to beech forests infested by *Ultracoelostoma assimile* and *Ultracoelostoma brittini*, scale insects abundant in certain areas of New Zealand (Harris et al., 1991). The scale insects secrete droplets of honeydew that contains various carbohydrates (Grant & Beggs, 1989), which the wasps collect (Moller & Tilley, 1989). It was suggested that *V. vulgaris* is more efficient at harvesting this particular carbohydrate resource (Harris, Moller, & Winterbourn, 1994), which would explain why it outcompetes *V. germanica* in the forests that are infested by scale insects.

In Patagonian Argentina, an area dominated by *Nothofagus* forest where the abundance of carbohydrates resources is scarce, as infestations of scale insects have neither been observed nor reported, little is known about the interaction between *V. vulgaris* and *V. germanica*, in spite of both species have coexisted there for over 10 years at least (Pereira et al., 2016). The fact that *V. germanica* promotes local enhancement by attracting conspecifics to food resources suggests that intraspecific competition is not avoided in this species. Thus, we hypothesize that niche differentiation acts as a stabilizing mechanism which allows coexistence of these two species.

For this purpose, we investigated foraging patterns and microhabitat use to determine whether *V. germanica* and *V. vulgaris* exhibit habitat partitioning while foraging for protein and carbohydrate resources in Patagonian forests, with the aim to develop management strategies for these two invasive wasps. We assessed the attractiveness of both species to food baits placed on forest litter as well as in the shrubland level. Moreover, we assessed the efficacy of a synthetic bait comprised of compounds from different phylogenetical sources (i.e., from plants, fungi and animals) to determine its efficacy for both species and at both types of foraging microhabitats. Unelius, Suckling, Brown, Josvaid, and El-Sayed (2015) have tested this bait with success in New Zealand *Nothofagus* beech forest, where *V. vulgaris* had displaced *V. germanica* and thus 98% of the wasps caught were *V. vulgaris*. Thus, testing trap captures in an area where both species coexist would provide further information on the effectiveness of the bait towards *V. germanica*. We compared trap captures of each species at shrubland level height as well as at ground level to determine whether there is an effect of height on the type of species captured. A better understanding of the mechanisms involved in the foraging behaviour of *Vespula* species is necessary to improve management strategies for these problematic species.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted around San Carlos de Bariloche (41°S, 71°W), Río Negro, Argentina. All experiments were carried out under natural conditions in forest sites along the Gutierrez, Moreno and Nahuel Huapi Lakes where *V. vulgaris* and *V. germanica* are abundant. The flora of the sites varies with latitude and topographic position. In the undergrowth (shrubland level), the most characteristic species are the Colihue Cane (*Chusquea culeou*), Notro (*Embothrium coccineum*), the Aljaba (*Fuchsia magellanica*) and other species of the *Berberis* genus. Parasitic and climbing plants, mosses, lichens, ferns and fungi are also present. The higher level is dominated by forest of *Austrocedrus chilensis*, with some other woody plant species such as *Nothofagus dombeyi* and *Fitzroya cupressoides*. The Andean-Patagonian forest also includes Arrayán (*Luma apiculata*), Maitén (*Maytenus boaria*) and Radal (*Lomatia hirsuta*). Experiments were conducted during February and March of 2018 and 2019, on sunny and still days, to minimize the effect of weather, and when wasps are typically most active.

2.2 | Preference tests to assess foraging height

Choice preference tests were conducted to compare the behaviour of *V. germanica* and *V. vulgaris* wasps when foraging for two different food baits (i.e., protein or carbohydrate) located at different heights (i.e., ground level or 1.5 m from the ground, from here on called shrubland level). Four choice experiments were conducted to compare the foraging height preference of each species: (a) preferred height for *V. germanica* when foraging for carbohydrates; (b) preferred height by *V. germanica* when foraging for proteins; (c) preferred height for *V. vulgaris* when foraging for carbohydrates; and (d) preferred height by *V. vulgaris* when foraging for proteins. As protein bait, we used ground cow meat, sardine cat food and sliced ham, while as carbohydrate bait we used honey and fruit. Different resources were used in each bait based on previous studies demonstrating that combination of different compound classes increases the attractiveness of the bait (Unelius et al., 2015), and preliminary studies which showed that ground cow meat is not a very attractive

TABLE 1 Number of replicates for the preference tests by species and bait in each microhabitat

Bait	Carbohydrate						Protein					
Site	1		2		3		1		2		3	
Sp./Microhabitat	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL	GL	SL
Vespula germanica	17	17	30	30	20	20	38	38	25	25	28	28
Vespula vulgaris	16	16	23	23	14	14	15	15	17	17	30	30

Abbreviations: GL, ground level; SL, shrubland level.

bait for *V. vulgaris* wasps in Argentina (unpublished data). Each bait consisted of a plastic dish (diameter = 5 cm) with 10 g of fresh ground cow meat, 10 g of sliced ham and 10 g of sardine cat food or 10 g of 30% w/v solution of honey in water and a piece of apple of 10 g. To evaluate the preference of individual wasps, in each experiment, one proteinaceous or carbohydrate bait was simultaneously placed at ground level and one at shrubland level, 1.5 m from the ground. The experiment started when the first wasp arrived at the bait and the total number of wasps landing on each baited dish at the different heights was recorded for 10 min. The wasps that landed on it were sucked with a wasp aspirator to avoid counting it again and to prevent attraction or interference to conspecifics (D'Adamo, Corley, Sackmann, & Lozada, 2000). The experiment was replicated at three different sites: Gutierrez, Moreno and Nahuel Huapi, with a separation of more than 5 km between sites. To get independent data from each replicate within each site, the wasps captured were kept in the aspirator until the end of the day, the minimum distance between sampling sites was 70 m and each sampling site was not resampled. Replicates within each site were randomly positioned to minimize potential position effects, and the number varied by site according to the availability of areas with coexistence of both species (Table 1). Non-parametric tests were used to analyse the data. A *Kruskal–Wallis* test was performed to analyse the effect of the site on the total number of wasps caught. Then, non-parametric *Wilcoxon*-matched pairs test comparisons were performed to test the effect of height on wasp preference for each wasp species, for each type of bait. That is, the paired comparisons were done by species and by type of bait.

2.3 | Wasp trapping with a synthetic lure

Another trial was done to confirm the attraction of the lure identified by Unelius et al. (2015) (from here on called *synthetic lure*) towards both species of *Vespula* present in Argentina. Also, we aimed to identify whether there was a foraging height preference in a no choice scenario when we used a synthetic lure as attractant. The trapping trials were operated at the same months (February to March of 2018 and 2019) in the same three sites: Gutierrez, Moreno and Nahuel Huapi. Orange delta sticky traps, which have limited attraction to non-target species, were used (Unelius et al., 2015). The traps were placed in the forest (within 100–200 m of the forest edge), at three different sites (n = 3) separated by >5 km. Treatments consisted of two different heights: ground level or 1.5 m from the ground. Ten treated and two blank or control traps per site were placed randomly, >70 m apart from each other. This distance would ensure that the wasps would not be perceiving the odour of two traps simultaneously providing a no choice scenario for the wasps. Traps were assigned to a treatment randomly, and two control traps (i.e., one on the ground and one at 1.5 m) were randomly interspersed at each site. Only two blank traps were used, as the objective was to corroborate the attractiveness of the synthetic lure at each site (i.e., negative control). The total numbers of wasps captured by trap were counted after 15 days.

2.3.1 | Chemicals

Lures used were comprised by compounds found to be attractive by Unelius et al. (2015), which were purchased (all of ≥98% purity) from Aldrich/SAFC. These compounds were (a) putative wasp pheromone heptyl butanoate, CAS nr: 5870-93-9 (Buteler et al., 2018; Unelius et al., 2014); (b) from fermented brown sugar: 3-methylbut-1-yl acetate, CAS nr: 123-92-2, 2-methyl-1-butanol, CAS nr: 137-32-6 (Unelius et al., 2015); (c) from beech forest honeydew (Brown, El-Sayed, Unelius, Beggs, & Suckling, 2015): methyl phenylacetate, CAS nr: 101-41-7; (d) from green-lipped mussel: 1-octen-3-ol, CAS nr: 3391-86-4, 3-octanone, CAS Number: 106-68-3 (Unelius et al., 2014); compounds with stereocenters were tested as racemates.

2.3.2 | Dispensers

Polyethylene bags of 4 × 5 cm (80 µm, O. Möllerström AB) with a surface area at 3 × 5 cm, containing 3.5 × 1.3 cm pieces of felt (100% viscose, Ernst Textil), were made in the laboratory using a Quick Seal (Quick Seal 200, O. Möllerström AB). Using a pipette, 100 µl of each of the six compounds were distributed onto the felt in each dispenser bag. Lures were made up before the bags were sealed using the Quick Seal and then placed in aluminium bags (O. Möllerström AB) and sent to Argentina by express courier. The baits were kept in the freezer until they were used for experimentations. The dispensers were found to release an even rate of 20–30 mg/day at 20°C, for 15 days. An untreated felt strip in a polyethylene bag in an orange delta sticky trap was used as negative control (n = 2).

Non-parametric *Wilcoxon* signed-rank tests were performed to test whether the height at which the traps baited with synthetic lures are placed and impact the type of species caught. Additionally, the relationship between the number of *V. germanica* and *V. vulgaris* wasps captured in traps was analysed using linear regression. All

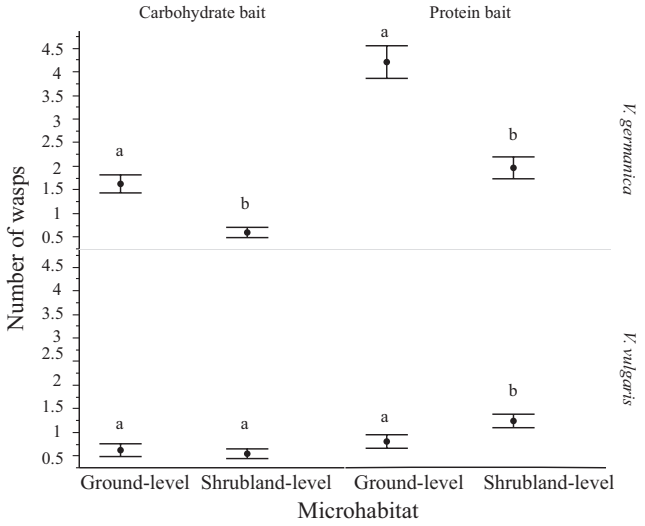

FIGURE 1 Numbers of *Vespula germanica* and *Vespula vulgaris* wasps in ground level and shrubland level by each bait. *Vespula germanica* prefers to forage at ground level regardless of the resource; while *V. vulgaris* wasps prefers to forage at shrubland level for protein but show no microhabitat preference for carbohydrates. Non-parametric *Wilcoxon*-matched pairs test comparisons were made for each bait by species. The point indicates the median value and horizontal lines indicated the standard errors. Bars with different letters within species and microhabitat are significantly different (Wilcoxon test: $p < .05$, *n V. germanica*-carbohydrate = 67, *n V. germanica*-protein = 91, *n V. vulgaris*-carbohydrate = 53, *n V. vulgaris*-protein = 62)

statistical analyses were carried out using the R software (version 3.3.2, the R foundation for statistical computing).

3 | RESULTS

3.1 | Preference tests to assess foraging height

There was no site effect in the total number of wasps landing on the baits ($\chi^2 = 3.54$, $df = 2$, $p = .17$), so site was not included as a factor in the analysis. There were significant differences in the number of wasps foraging in the different microhabitats depending on the species and bait. The number of *V. germanica* wasp foraging at ground level was greater than the number foraging in the shrubland level for carbohydrates ($\chi^2 = 33.39$, $df = 1$, $p < .001$) as well as for protein baits ($\chi^2 = 48.11$, $df = 1$, $p < .001$; Figure 1; FigureS1). On the other hand, *V. vulgaris* showed no differences in the number of wasp foraging at ground and shrubland level when carbohydrate baits were tested ($\chi^2 = 0.01$, $df = 1$, $p = .92$; Figure 1; Figure S1). However, *V. vulgaris* preferred to forage in the shrubland level when the resource was a protein bait ($\chi^2 = 6.61$, $df = 1$, $p < .05$; Figure 1; Figure S1).

3.2 | Wasp trapping with a synthetic lure

There were significant differences in the number of wasps caught between treated and control traps for *V. germanica* ($\chi^2 = 9.72$, $df = 1$, $p < .005$) and *V. vulgaris* ($\chi^2 = 13.42$, $df = 1$, $p < .005$). Control traps practically did not catch any wasps. When a synthetic lure was used as bait, the numbers of wasps caught at the different forage microhabitats (ground level vs. shrubland level) were similar ($\chi^2 = 2.72$, $df = 1$, $p = .1$). Within each species, the average number of *V. germanica* and *V. vulgaris* wasps foraging at each height, when wasps were baited with synthetic lures, was also similar (*V. germanica*: $\chi^2 = 1.54$, $df = 1$, $p = .21$; *V. vulgaris*: $\chi^2 = 1.09$, $df = 1$, $p = .29$; Figure 2; Figure S2).

Furthermore, we determined a positive correlation between species in the trap captures (Number of *V. germanica*/trap = 2.02 + 0.79 * Number of *V. vulgaris*; $R^2 = .28$; $p = .001$; Figure 3; Figure S3).

4 | DISCUSSION

Our results suggest that *V. germanica* wasps prefer to forage at ground level regardless of the resource (carbohydrate and protein), while *V. vulgaris* prefers protein resources at the shrubland level when given a choice between a protein bait at ground level or at shrubland level. When traps were left out for 15 days and were baited with an attractive synthetic lure (i.e., comprised of compounds from protein as well as carbohydrate sources), the height at which they were placed did not have an effect on the species caught. This means that, in a no choice scenario, traps can catch both species of wasps in both microhabitats (ground and shrubland levels). *Vespula vulgaris* and *V. germanica* coexist in their native range (Archer, 1978), and the current study corroborates that they coexist in the Argentine Patagonia, as previous studies suggested (Pereira et al., 2016). Given their similarity in biology, and overlap in nesting sites and diet, these species may have developed strategies to avoid or reduce competition for limiting resources. Interestingly, Pereira et al. (2016) found that *V. germanica* significantly avoids *V. vulgaris* visual and odour cues in bioassays with free-flying wasps arriving to protein baits and Harris et al. (1991) observed foraging spatial niche differentiation in beech forests.

The results support the existence of some kind of spatial niche differentiation at least in protein foraging and show that *V. germanica* foraged at the ground while *V. vulgaris* forages equally at ground level as well as in the forest shrubland level. Previous sampling studies conducted in New Zealand also found a prevalence of *V. vulgaris* above the ground at shrubland level using sweep nets/swatting wasps, suggesting niche partitioning also in New Zealand beech forests (Harris et al., 1991). The current study determined the active foraging preference of wasps for a given microhabitat, depending on the type of resource. We found that foraging location (ground or shrubland level) may depend on species as well as the type of resource, as *V. vulgaris* occurred at ground level in similar numbers as in the shrubland level when foraging for carbohydrates.

With regard to protein food, which in our study was represented by the "meat baits," we observed some degree of spatial differentiation which could be related to the fact that these wasps species vary slightly in the types of prey they collect (Harris & Oliver, 1993), which may be occurring at different microhabitats within the forest or that

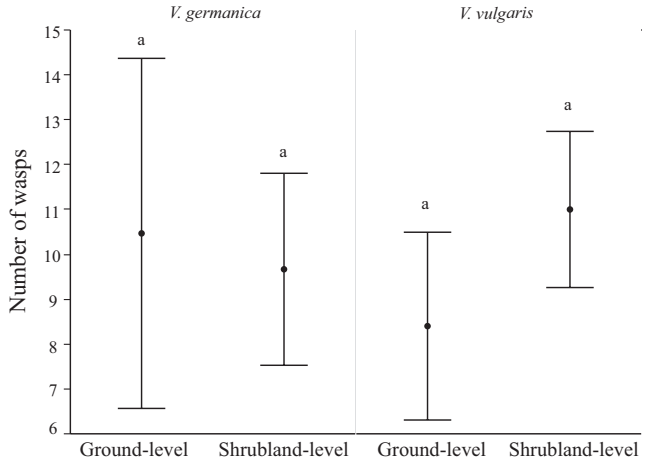

FIGURE 2 Numbers of *Vespula* wasps per trap in ground and shrubland levels. *Vespula germanica* and *Vespula vulgaris* did not show differences in the foraging microhabitat when the synthetic lure was used as bait. Non-parametric *Wilcoxon*-matched pairs test comparisons were made for each species. The point indicates the median value, and horizontal lines indicated the standard errors. Same letters indicate not significantly differences from each other (Wilcoxon test: $p > .1$, $n = 36$)

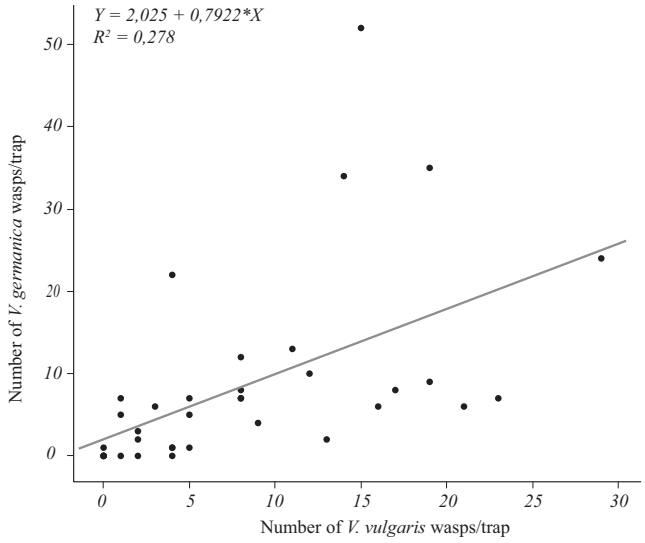

FIGURE 3 Numbers of *Vespula germanica* wasps in relation to the numbers of *Vespula vulgaris* wasps captured in traps baited with the synthetic lure (modified from Unelius et al., 2015). Each point represents the number of captured wasps of each species in each Delta trap ($R^2 = .28$, $p = .001$)

spatial niche differentiation could be an adaptation to reduce competition as there is high overlap in their diet. We do not know whether these food resources are limiting, so this hypothesis remains untested.

With regard to carbohydrate resources, previous studies found that *V. vulgaris* was more efficient at harvesting carbohydrate resources based on feeding time and observations of wasps returning to the nest (Harris et al., 1994). *Vespula vulgaris* wasps fed at a faster rate and returned to the nest with the crop full of sugar while a lot of *V. germanica* wasps returned empty (Harris et al., 1994). These results point to a better competitive ability of *V. vulgaris* which could explain why it outcompetes *V. germanica* in beech forests. According to our results, *V. vulgaris* forages for carbohydrate resources at shrubland level as well as ground level while *V. germanica* does it mainly at ground level. Typically, carbohydrate resources are going to occur at the foliage, sapling and branches level, and in a habitat where the carbohydrate resources are more abundant (i.e., *Nothofagus* beech forest of New Zealand) *V. vulgaris* would be able to take advantage of it more effectively than *V. germanica*.

Improving our understanding of foraging behaviour of invasive species may help to develop alternative techniques for managing undesired social wasp populations. The current results corroborated that the synthetic lure is equally attractive to *V. vulgaris* and *V. germanica* as traps caught similar numbers of individuals of each species. Lures have previously been tested in an environment where almost no *V. germanica* were present (Unelius et al., 2015). However, the total numbers of wasps caught per trap were strikingly lower in the current study than that reported by Unelius et al. (2015). This was expected based on the high densities of wasps attained in *Nothofagus* beech forest in comparison with other habitats. The density of nests, in Argentina, is on average four nests per hectare depending on the species and site (Sackmann, Rabinovich, & Corley, 2001), while in New Zealand one can find up to twelve nests per hectare (Barlow, Beggs, & Barron, 2002).

The synthetic lure used in the present study is comprised of odours from protein as well as carbohydrate sources. Our results suggest that this synthetic bait could be an environmentally friendly alternative for the capture of both species of wasps in those environments where they coexist. Given that the synthetic lure used contains numerous and high quantities of six compounds of different phylogenetic origin, it should be effective throughout the season with the changing preference for different food types (Spradbery, 1973). That is, at the beginning of the season, when wasp density is still relatively low and wasps are not as attracted to the toxic protein baits, this lure could help reduce the population density of both species. Future studies should test the attractiveness of the lure throughout the season and whether early season trapping could affect wasp density later in the season.

We provide evidence that spatial resource partitioning may be another plausible explanation as to why *V. vulgaris* wasps take better advantage of carbohydrate resources than *V. germanica* wasps, it may be worthwhile to test the hypothesis in the forests of New Zealand where scale insects provide such a rich carbohydrate source in the shrubland level of the trees. Moreover, our discovery of a lure that is attractive for South American *Vespula* wasps allows for investigations of the expansion range of these species in other Latin American environments.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

MB, MM and CRU conceived research and secured funding. MM and MB conducted experiments. CRU provided all the lures used. All authors participated in the writing of the manuscript and have approved the submitted version.

DATA AVAILABILITY STATEMENT

We confirm that the data supporting the findings of this study are available within the article and its supporting information.

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REFERENCES

Akre, R. D., & MacDonald, J. F. (1986). Biology, economic importance and control of yellowjackets. In S. B. Vinson (Ed.), *Economic impact and control of social insects* (p. 421). New York, NY: Praeger.

Archer, M. E. (1978). *Provisional atlas of the insects of the British Isles. Part 9: Hymenoptera, Vespidae*. Huntingdon, UK: Biological Records Centre.

Barlow, N. D., Beggs, J. R., & Barron, M. C. (2002). Dynamics of common wasps in New Zealand beech forests: A model with density dependence and weather. *Journal of Animal Ecology*, *71*, 663–671. https://doi.org/10.1046/j.1365-2656.2002.00630.x

Barr, K., Moller, H., Christmas, E., Lyver, P., & Beggs, J. (1996). Impacts of introduced common wasps (*Vespula vulgaris*) on experimentally placed mealworms in a New Zealand beech forest. *Oecologia*, *105*, 266–270. https://doi.org/10.1007/BF00328556

Beggs, J. R., Brockerhoff, E. G., Corley, J. C., Kenis, M., Masciocchi, M., Muller, F., … & Villemant, C. (2011). Ecological effects and management of invasive alien Vespidae. *BioControl*, *56*, 505–526. https://doi.org/10.1007/s10526-011-9389-z

Beggs, J. R., Karl, B. J., Wardle, D. A., & Bonner, K. I. (2005). Soluble carbon production by honeydew scale insects in a New Zealand beech forest. *New Zealand Journal of Ecology*, *29*, 105–115.

Brown, R. L., El-Sayed, A., Unelius, C. R., Beggs, J., & Suckling, D. M. (2015). Invasive *Vespula* wasps utilize kairomones to exploit honeydew produced by Sooty Scale Insects, *Ultracoelostoma*. *Journal of Chemical Ecology*, *41*, 1018–1027. https://doi.org/10.1007/s10886-015-0635-1

Buteler, M., Fernandez, P. C., Stadler, T., Weaver, D. K., Yossen, M. B., & Lozada, M. (2018). Heptyl butyrate, a putative pheromone involved in social communication of *Vespula germanica* wasps. *Insectes Sociaux*, *65*, 95–101. https://doi.org/10.1007/s00040-017-0591-6

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*(1), 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Clapperton, B. K., Alspach, P. A., Moller, H., & Matheson, A. G. (1989). The impact of common and German wasps (Hymenoptera: Vespidae) on the New Zealand beekeeping industry. *New Zealand Journal of Zoology*, *16*, 325–332. https://doi.org/10.1080/03014223.1989.10422897

D'Adamo, P., Corley, J. C., Sackmann, P., & Lozada, M. (2000). Local enhancement in the wasp *Vespula germanica*. Are visual cues all that matter? *Insectes Sociaux*, *47*, 289–291. https://doi.org/10.1007/PL00001717

Davis, M. A. (2009). *Invasion biology*. Oxford, UK: Oxford University Press on Demand.

Edwards, E., Toft, R., Joice, N., & Westbrooke, I. (2017). The efficacy of Vespex® wasp bait to control *Vespula* species (Hymenoptera: Vespidae) in New Zealand. *International Journal of Pest Management*, *63*, 266–272. https://doi.org/10.1080/09670874.2017.1308581

Fridley, J. D., Stachowitcz, J. J., Naeem, S., Saex, D. F., Seabloom, E. W., Smith, M. D., … & Von Holle, B. (2007). The invasion paradox: Reconciling pattern and process in species invasions. *Ecology*, *88*, 3–17. https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

Grant, W. D., & Beggs, J. R. (1989). Carbohydrate analysis of beech honeydew. *New Zealand Journal of Zoology*, *16*, 283–288. https://doi.org/10.1080/03014223.1989.10422893

Harris, R. J., Moller, H., & Winterbourn, M. J. (1994). Competition for honeydew between two social wasps in South Island beech forests, New Zealand. *Insectes Sociaux*, *41*, 379–394. https://doi.org/10.1007/BF01240641

Harris, R. J., & Oliver, E. H. (1993). Prey diets and population densities of the wasps *Vespula vulgaris* and *V. germanica* in scrubland-pasture. *New Zealand Journal of Ecology*, *17*, 5–12.

Harris, R. J., Thomas, C. D., & Moller, H. (1991). The influence of habitat use and foraging on the replacement of one introduced wasp species by another in New Zealand. *Ecological Entomology*, *16*, 441–448. https://doi.org/10.1111/j.1365-2311.1991.tb00237.x

Kennedy, T. A., Naeem, S., Howe, K. M., Knops, J. M., Tilman, D., & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, *417*, 636–638. https://doi.org/10.1038/nature00776

MacIntyre, P., & Hellstrom, J. (2015). An evaluation of the costs of pest wasps (*Vespula* species) in New Zealand. *International Pest Control*, *57*, 162–163.

Masciocchi, M., Beggs, J. R., Carpenter, J. M., & Corley, J. C. (2010). Primer registro de *Vespula vulgaris* (Himenóptera: Vespidae) en la Argentina. *Revista Sociedad Entomológica Argentina*, *69*, 267–270.

Moller, H., & Tilley, J. A. V. (1989). Beech honeydew: Seasonal variation and use by wasps, honey bees, and other insects. *New Zealand Journal of Zoology*, *16*, 289–302. https://doi.org/10.1080/03014223.1989.10422894

Pereira, A. J., Pirk, G. I., & Corley, J. C. (2016). Foraging behavior interactions between two non-native social wasps, *Vespula germanica* and *V. vulgaris* (Hymenoptera: Vespidae): Implications for invasion success? *Journal of Insect Science*, *16*, 1–6. https://doi.org/10.1093/jisesa/iew058

Sackmann, P., Rabinovich, M., & Corley, J. C. (2001). Successful removal of German yellowjackets (Hymenoptera: Vespidae) by toxic baiting. *Journal of Economic Entomology*, *94*, 811–816. https://doi.org/10.1603/0022-0493-94.4.811

Spradbery, J. P. (1973). *Wasps: An account of the biology and natural history of solitary and social wasps*. Seattle, WA: University of Washington Press.

Tang, J., & Zhou, S. (2011). The importance of niche differentiation for coexistence on large scales. *Journal of Theoretical Biology*, *273*, 32–36. https://doi.org/10.1016/j.jtbi.2010.12.025

Unelius, C. R., El-Sayed, A. M., Twidle, A. M., Stringer, L. D., Manning, L. M., Sullivan, T. E., … & Noble, A. D. L. (2014). Volatiles from green-lipped mussel as a lead to Vespid wasp attractants. *Journal of Applied Entomology*, *138*, 87–95. https://doi.org/10.1111/jen.12103

Unelius, C. R., Suckling, M., Brown, R. L., Josvaid, J., & El-Sayed, A. M. (2015). Combining odours isolated from phylogenetically diverse sources yields a better lure for yellowjackets. *Pest Management Science*, *72*, 760–769. https://doi.org/10.1002/ps.4050

Willink, A. (1980). Sobre la presencia de *Vespula germanica* (Fabricius) en la Argentina (Hymenoptera: Vespidae). *Neotropical Entomology*, *26*, 205–206.

Yeruham, I., Schwimmer, A., & Brami, Y. (2002). Epidemiological and bacteriological aspects of mastitis associated with yellow-jacket wasps (*Vespula germanica*) in a dairy cattle herd. *Journal of Veterinary Medicine Series B*, *49*, 461–463. https://doi.org/10.1046/j.1439-0450.2002.00487.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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