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BRIEF REPORT

Nest visitors of *Vespula* wasps and their potential use for biological control in an invaded range

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Abstract

The common and the German wasp, *Vespula vulgaris* and *V. germanica,* have proved to be prolific invasive species capable of degrading local ecosystems and costing invaded countries millions of dollars annually. Despite clear incentive, control strategies are yet to have any significant deleterious impact on invasive populations. Several species of arthropods are known to inhabit *Vespula* nests and feed upon developing larvae as either parasitoids or predators. Recent control strategies propose the use of such parasitoids as agents of biocontrol against invasive wasps (*Volucella inanis* in particular). Despite a general understanding of parasitoid ecology, some aspects such as prevalence, distribution, and behaviour remain limited. Here, we surveyed natural enemy prevalence in wasp nests over the period of three years and we tested larvae prey preference of two *Volucella* species, *V. inanis* and *V. zonaria* towards *Vespula* wasps. We find *V. inanis* to be the most prevalent of four prominent candidates for Vespid biocontrol—*V. inanis, V. zonaria, Sphecophaga vesparum,* and *Metoecus paradoxus*. Using two-choice assays, we find larvae of *V. inanis* to have slight yet significant prey preference for *V. vulgaris* larvae over *V. germanica* larvae, whilst *V. zonaria* display no preference. Furthermore, *V. inanis* were not averse to still predating upon *V. germanica*, doing so in 41% of trials. Prior exposure has no effect on the prey-preference. Our work provides experimental evidence that *V. inanis* is a promising candidate for biocontrol of invasive *Vespula* wasps, as the larvae predate on both target species of *Vespula* and display no exclusive preference among them.

Keywords *Vespula vulgaris* · *Vespula germanica* · *Volucella inanis* · *Volucella zonaria* · Wasps

Introduction

Social wasps (Vespidae), native to Eurasia and Northern Africa, have proved to be prolific invasive species, establishing introduced populations in North and South America, as well as southern Africa and Oceania (Lester and Beggs 2019). The generalist lifestyle of *Vespula* species, coupled with strong behavioural plasticity, enables invasive wasps to predate upon native insect populations whilst also directly competing with them for food resources, rapidly impacting all trophic levels (Yamane and Yamane 2020). Consequently, *Vespula* have had significant deleterious impacts on invaded regions, with both environmental and economic consequences (Lester et al. 2014; Cook 2019; Lester and Beggs 2019). For example, in New Zealand, invasive *V. vulgaris* (common wasp) and *V. germanica* (German wasp) populations have established in native ecosystems and significantly altered resource flow (Lester et al. 2013; MacIntyre and Hellstrom 2015). With a particular influence on the apiculture and pastoral farming industry, their impact is estimated to cost the New Zealand economy up to $130 million per annum (Clapperton et al. 1989; MacIntyre and Hellstrom 2015). Environmentally, *Vespula's* capacity to cause large-scale ecosystem degradation represents one of New Zealand's greatest invasive threats and is deemed responsible for the degradation of the honeydew beech forest ecosystems

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of the South Island (Clapperton et al. 1989; Moller and Tilley 1989; Beggs 2001). Such negative impacts are not unique to New Zealand, and are observed in other *Vespula* invaded regions (e.g. in Argentina Sackmann et al. 2001 or in Australia Wood et al. 2006). In response, strategies have been employed in attempts to control *Vespula sp.* populations, for example the release of the parasitoid *Sphecophaga* (Donovan and Read 1987; Donovan et al. 2002), and the use of insecticidal baits (e.g. Vespex) (Edwards et al. 2017), but so far these have proven to be financially and environmentally impractical (Lester et al. 2014; Lester and Beggs 2019; Palmer et al. 2021). For instance, the effectiveness of *Sphecophaga* was shown to be reduced after a year in the field (e.g. fewer brachypterous adults produced, Beggs et al. 2008) and the use of Vespex, whilst effective after the application, can allow for recolonisation by queens in following years (Lester and Beggs 2019).

The understanding of natural enemies of social wasps can prove very valuable in controlling pest species, in both agricultural and "natural" environments (Lester and Beggs 2019; Palmer et al. 2021). In the native ranges of *Vespula vulgaris* and *V. germanica* several parasitoid, predatory, and scavenging species exploit the protected and protein-rich environment of *Vespula* nests (Ward 2013). Species from diverse taxonomic groups are known to inhabit wasp nests including mites, hoverflies, a beetle and as well as at least one parasitoid wasp (Rupp 1989; Oi et al. 2020), and these insect associates are often collectively referred to as 'guests', or 'sphecophiles' (Parmentier 2019). Despite their implied negative impact on host colonies, the distribution and prevalence of *Vespula* sphecophiles within host ranges remains uncertain. Given this void in understanding, and the capability for natural enemies to reduce populations of Vespid wasps, investigations into general parasitoid ecology are important and can lead potentially into the discovery of new or more efficient methods to control invasive *Vespula* wasps.

Specifically, three species within *Volucella* (Diptera: Syrphidae), a genus of broad-bodied hoverflies found commonly across Europe (Ball and Morris 2015), have specialised larvae that are obligate sphecophiles of *Vespula* nests (Speight 2014). The adults of *Volucella zonaria*, *V. pellucens* and *V. inanis* infiltrate *Vespula* nests and oviposit on the nest-encasing paper envelope. The eggs then hatch and enter the nest cavity to begin foraging (Rupp 1989). Larvae of *V. zonaria* and *V. pellucens* migrate to the bottom of the nest and develop in the nest litter, feeding on detritus from the colony above (Rotheray and Gilbert 1998; Speight 2014). Whilst mostly living as scavengers, *V. zonaria* and *V. pellucens* larvae can also crawl up into the combs and predate upon live *Vespula* larvae (Rotheray and Gilbert 1998). Larvae of *V. inanis*, however, are obligate *Vespula* ectoparasites (Rotheray and Gilbert 1998; Parmentier 2019) and reside permanently in the nest brood chambers (until ready to pupate); to facilitate this, *V. inanis* larvae have specialised, dorsoventrally flattened bodies that enable them to enter larval cells alongside *Vespula* larvae to feed on them (Rupp 1989; Ward 2013). During development, each *V. inanis* larva consumes multiple *Vespula* larvae before going to the bottom of the nest to pupate (Rupp 1989; Brown 2021a, b). *Volucella* females are thought to lay between 60 and 300 eggs in each oviposition (Rupp 1989), and hence infestation by *Volucella* may impose a substantial impact on *Vespula* colony development.

Considering the propensity for *V. zonaria*, *V. pellucens* and *V. inanis* to predate *Vespula* larvae, either being facultative or obligate entomophages (Rotheray and Gilbert 1998), the *Volucella* genus has been identified as a potential agent of biocontrol against invasive *Vespula* populations (Ward 2013). Biocontrol research in New Zealand has considered that the release of large numbers of *Volucella* into native ecosystems could provide suppression of wasp numbers across very large areas and help reduce their invasive impact, without bringing their own deleterious effects (Brown 2021a, b). Of the three aforementioned *Volucella* species that inhabit *Vespula* nests, *Volucella inanis* has been recognised as the best candidate (Brown 2021a, b). Firstly, as the sole obligate ectoparasite (Rotheray and Gilbert 1998), each *V. inanis* larva is thought to cause more significant and consistent damage to the host wasp nest, as each *V. inanis* must consume at least two wasp larvae to grow (Brown 2021a, b). Secondly, the more specialised nature of *V. inanis*'s niche reduces the threat of opportunistic predation of non-target species—trials have shown *V. inanis* to refuse to parasitise the brood of buff-tailed bumblebees (*Bombus terrestris audax*; considered the most likely non-target species present in New Zealand), even under no-choice conditions (Brown 2021a, b). Conversely, the more generalist, scavenging niche of *V. zonaria* and *V. pellucens*, coupled with reported sightings in non-*Vespula* nests (Ball and Morris 2004), has driven hypotheses that they are less *Vespula*-specific than their close relative *V. inanis*; however, this requires further investigation (Lester et al. 2013). Having been approved by authorities, researchers in New Zealand have begun attempts at introducing *V. inanis* into *Vespula* nests in contained trials to assess its efficacy as a biocontrol agent, *in situ* (Brown 2021a, b). If proven effective, similar biocontrol could be initiated in other invaded regions, both within and beyond New Zealand. However, despite the identification of the potential for *Volucella inanis* as a biocontrol agent and the commencement of live trials, there are still significant gaps in the understanding of *Volucella* ecology.

Whilst *Volucella* species are able to infest nests of both *Vespula* species that have invaded New Zealand (*V. vulgaris* and *V. germanica*) (Rotheray and Gilbert 1998), it is unknown whether they display any host preferences. Could it be that *Volucella* are predisposed to associate with one species over another, given equal opportunity for both? Additionally, prior exposure has been shown to be able to influence preference in parasitoid species, whereby females prefer to associate with more familiar hosts (Mandeville and Mullens 1990; Turlings et al. 1990; Cortesero et al. 1995; Lentz-Ronning and Kester 2013). Considering this, could *Volucella* preferentially choose to associate with larvae of the same species as their nest of origin? Knowing if *Volucella inanis* have a strong preference to the host species from which they were collected could significantly enhance the development of mass rearing methods en route to their releases as biological control agents. Since the two hoverfly species, *V. inanis* and *V. zonaria,* can commonly be found in nests of both *V. vul*garis and *V. germanica*, we hypothesised that *Volucella* larvae will have no preference for either *Vespula spp*, and that there will be no difference in host prey preference between the parasitoid species. We also hypothesised that *Volucella* preference will not be dependent on its origin.

Here, we firstly investigated the presence of arthropod parasites in *Vespula* nests collected in the UK over three years, providing the first exploration of brood parasite prevalence in *Vespula* nests in southeastern England. We then experimentally test our hypotheses regarding the host preferences of *Volucella* by conducting two-choice prey preference experiments in petri dish arenas. We compared larvae prey preference of two *Volucella* species, *V. inanis* and *V. zonaria.* Then, we scrutinised prey preference in *V. inanis*, considering the origin of the parasitic larvae to investigate whether the nest from which *V. inanis* was sourced (either *Vespula vulgaris* or *V. germanica*) had any effect on prey preference.

Material and methods

Vespula and brood parasite field collection

Nests of *Vespula vulgaris* and *V. germanica* were collected from the Wallingford area, Oxfordshire, UK, and from around Sutton, London, UK, in September to October of 2018, 2019 and 2021. A total 54 nests were collected (2018, *V. vulgaris* $N=16$, *V. germanica* $N=4$; 2019, *V. vulgaris* $N=8$, *V. germanica* $N=2$; 2021, *V. vulgaris* $N=21$, *V. germanica* $N=3$), whereby all nest material (including detritus that had accumulated at the bottom of the nest cavity) was gathered and brought back to the laboratory at CABI, Egham, UK (2018 and 2019) or UCL, London, UK (September to October 2021). To promote normal parasitoid movement and feeding, nest combs were kept as intact as possible and stacked on top of each other separated by slim foam spacers, and stored in well ventilated plastic cages (Exo Terra Breeding Box). Workers were sedated with CO_2 and removed from the combs regularly to avoid attacking the parasites. Cages were stored at room temperature under a natural light regime.

Parasite prevalence

Each nest was then rigorously searched for four species of social parasites: *Volucella inanis* and *V. zonaria* (all larval instars)*; Metoecus paradoxus* (adults, and larvae)*;* and *Sphecophaga vesparum* (both adults and cocoons). Searches were conducted by separating the combs of each nest and examining all cells under white light. The detritus from beneath each nest was also sifted through to identify any individuals that had been residing there, or that had been displaced there during nest extraction. Any parasites discovered were collected using soft forceps and identified, and the presence or absence of each of species was recorded for each nest.

Prey preference experiment

From nests collected in October 2021, we conducted prey preference experiments. Two-choice experiments were conducted to investigate prey preferences of the two hover fly species, *Volucella inanis* and *V. zonaria*. Each individual larva was tested 4 consecutive times, alternating the position of the two wasp species (right or left). Test arenas consisted of Petri dishes (9 cm diameter) positioned 50 cm below a LED lamp. All trials were conducted at room temperature under light to encourage movement and to standardise room conditions. Two *Vespula vulgaris* larvae (5th instar) were placed adjacent to each other at one pole of the arena, and two *V. germanica* larvae (5th instar) were placed at the opposite pole (Fig. 1). We used two larvae of *Vespula* to avoid locomotion. All *Vespula* larvae were placed simultaneously, immediately after removal from their parent nest, and each used in only one trial. The position that each host *Vespula* species was placed at (left or right pole) was alternated in each trial. A single *Volucella* second-instar larva (either *V. inanis* or *V. zonaria*) was then placed in the centre of the arena, equidistant from all *Vespula* larvae and orientated to face perpendicular to both *V. vulgaris* and *V. germanica*, facing neither. Second instar larvae of *Volucella* were used in the experiments because in this stage they actively feed and search for prey (Rupp 1989). The *Vespula* and *Volucella* larvae used in a given trial were never sourced from the same nest. Trails began with the release of the *Volucella* larva and lasted for 5 min. All trials were filmed using a webcam (Trust Webcam) for later, blind assessment. Petri dishes were washed with water and detergent after each trial and dried with paper. At the start of trialling, we recorded the body length of each *Volucella* larva at full extension as a measure of larval size. Overall, 64 *Volucella* larvae were

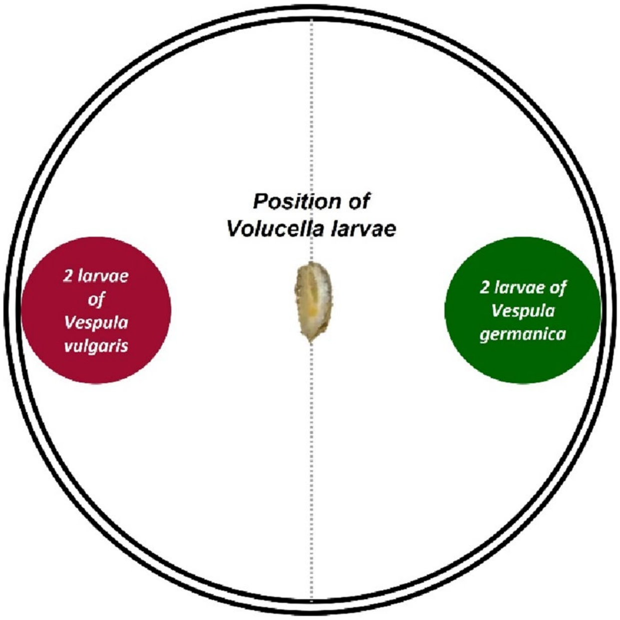

Fig. 1 Diagram of the test arenas used to investigate prey preference of *Volucella inanis* and *Volucella zonaria* between *Vespula vulgaris* and *Vespula germanica* larvae. Arenas were split into 'choice areas' - '*V. vulgaris*' in red, '*V. germanica*' in green. These choice areas were defined by circles of 1 cm radius around each pair of respective wasp larvae

tested (*V. inanis* n = 32 individuals, *V. zonaria* n = 32 individuals), and each larva was tested four consecutive times, providing 256 trials in total. Of the 32 V. *inanis* larvae used, 16 were extracted from nests of *Vespula vulgaris*, and 16 from nests of *V. germanica*. We did not discriminate the nests of origin for *V. zonaria* due to constraints in the availability of *V. zonaria* from nests of *V. germanica*. Any trials in which the *Volucella* larva did not move from the start position were removed from the dataset before analysis (6 trials, all involving *V. inanis*), leaving 250 trials for analysis.

To discern preference during the choice experiments, the arenas were split into three 'choice areas' – '*V. vulgaris*', '*V. germanica*', and 'No choice'. The choice areas for '*V. vulgaris*' and '*V. germanica*' were defined by circles of 1 cm radius around each pair of respective wasp larvae, and the 'No choice' area comprised of the remainder of the arena (i.e. any of the arena that was more than 1 cm away from any wasp larvae; Fig. 1). An observer blind to the identity of the *Vespula* species then measured the number of seconds that each parasitic larva spent within each choice area in each trial.

We then used a preference ratio commonly used in dichotomous choice preference tests (Houde 1997) to control for the total time during each trial that the parasitic larvae (*V. inanis* or *V. zonaria*) spent in either *Vespula* choice area. This index was defined as the difference in time spent in each *Vespula* choice area, standardised by the total amount of time in either of the *Vespula* choice areas [(time with Vv – time with Vg)/(time with Vv + time with Vg)], in which Vv represents *Vespula vulgaris* and Vg represents *V. germanica*. The ratio provides an index of preference between + 1, where all time was spent with *V. vulgaris*, and -1, where all time was spent with *V. germanica*, where a 0 value indicates equal time spent with each. The index was then used to decide binomial response results from each trial. Larvae were recognised as preferring *V. vulgaris* in trials with index values greater than 0, and as preferring *V. germanica* in trials with index values less than 0.

Statistical analyses

We tested for potential differences in prey preference between the two *Volucella* species using a generalised linear mixed-effect model (GLMM). The model included *Volucella* species and larval size as fixed effects, with binomial choice (*V. vulgaris* or *V. germanica*) as the response variable. Also, we included individual ID, repeat number (1st, 2nd, 3rd or 4th time each individual was trialled) and the side that *V. vulgaris* was presented on (left or right) as random factors. We checked the models for overdispersion.

Secondly, we investigated the host preferences of *Volucella inanis* sourced from nests of different *Vespula* species (either *V. vulgaris* or *V. germanica*), using a similar GLMM approach. Here, the model included the *Vespula* species from which the *V. inanis* was sourced as a fixed effect, with binomial choice as the response variable, *V. vulgaris* larvae or *V. germanica* larvae. Again, individual ID, repeat number and the side that *V. vulgaris* was presented on were included as random factors. We did not test *Volucella zonaria* origin, as the larvae of *V. zonaria* were kept in the same container without discrimination of nest origin. All statistical analyses and data visualisation were performed in R version 4.0.3. (Team 2012), using the package *lme4* (Bates et al. 2015).

Results

Parasite prevalence

Parasitic species that were recorded from *Vespula* nests in 2018, 2019 and 2021 are displayed in Table 1. In each year, we were able to survey more *V. vulgaris* nests than of *V. germanica*. *Volucella inanis* were the most prevalent species found in 48 (88.9%) of the 54 nests surveyed. The next most prevalent species was *V. zonaria* which was found in 29 (53.7%) nests overall. *Metoecus paradoxus* and *Sphecophaga vesparum* were only collected from *Vespula vulgaris* colonies. From these nests, *M. paradoxus* were present in 17 nests or 31.5 % of the total surveyed. *Sphecophaga*

Table 1 Sampling information of collected wasp nests (n) and the prevalence of parasitic species (number of nests each species is present and in parentheses the percentage of infested nests/n)

Years	Wasp species	Nests (n)	*V. inanis*	*V. zonaria*	*M. paradoxus*	*S. vesparum*
2018	*V. vulgaris*	16	15 (94)	8 (50)	7 (44)	1 (6)
	V. germanica	4	3 (75)	3 (75)	0	0
2019	*V. vulgaris*	8	8 (100)	4 (50)	6 (75)	1 (13)
	V. germanica	2	2 (100)	2 (100)	0	0
2021	*V. vulgaris*	21	17 (81)	9 (43)	4 (19)	5 (24)
	V. germanica	3	3 (100)	3 (100)	0	0

Table 2 Prey preference of *Volucella inanis* and *Volucella zonaria* toward the larvae of *Vespula vulgaris* and *Vespula germanica*

(A)	Chisq	df	*P* value		
Species	3.99	1	0.045*		
size	3.77	1	0.052		
(B) contrast	odds ratio	SE	df	z ratio	*P* value
V inanis—V zonaria	3.17	1.83	1	1.99	0.045*
(C)	Chisq	df	*P* value		
Nest origin of *V. inanis*	1.64	1	0.2		

The generalised linear model (GLM) with trial, individual identification and side of the prey, were included as random factors. (A) Coefficients. (B) Contrast. Degrees of freedom (df), Standard error (SE), *z* ratio and *p* values. (C) Coefficients of nest of origin of *V. inanis.*

vesparum were the least prevalent, only being found in 7 nests (12.9%). The *Volucella* larvae for host preference choice test experiments were sourced from *Vespula* colonies collected in the 2021 nest survey. *Volucella inanis* and *V. zonaria* were both present in all three *Vespula germanica* nests used in the host preference trial. In the 21 *V. vulgaris* nests, *Volucella inanis* was present in 81% of nests, *V. zonaria* in 43%, *S. vesparum* in 24%, and *M. paradoxus* in 19% (Table 1).

Preference of *Volucella* species for *Vespula vulgaris* versus *V. germanica*

Across our experiment, *Volucella* larvae moved to within 1 cm of at least one of the *Vespula* larvae in all 250 of the trials, and made physical contact with a *Vespula* larva in 91.6% of trials. Additionally, *Volucella* larvae moved to within 1 cm of both *Vespula* species in 47.6% of trials. Firstly, we checked the initial choice, but the model was not significative, and it was left out the main results ($P=0.99$, Supplementary material). Using the preference ratio, we found an overall effect of species in the preference for *Vespula vulgaris* [proportion *V. vulgaris*, proportion *V. germanica*: in *Volucella inanis* ($n=121$ trials): 0.587, 0.413; in *Volucella zonaria* ($n=125$ trials): 0.512, 0.488; GLMM-preference: Species: $\chi2(1)=3.995$, $P=0.0456$]. *Volucella inanis* showed a significant preference for *Vespula vulgaris* compared to *Vespula germanica*, whilst *Volucella zonaria* displayed no significant preference (Table 2A, Fig. 2A).

However, it is notable that in 41% of trials the *V. inanis* larvae chose *V. germanica* (Fig. 2A), revealing that whilst displaying significant preference for *V. vulgaris* over *V. germanica*, *V. inanis* larvae are not averse to also predating upon *V. germanica*. *Volucella* size was also investigated as a fixed effect. Size was found to have no overall effect in host preference [GLMMpreference: Size: $\chi2(1)=3.776$, $P=0.0520$] (Table 2A).

Preference considering nest of origin in *Volucella inanis*

We found no overall effect of the species of origin in host preference [proportion *V. vulgaris*, proportion *V. germanica*: *V. vulgaris* origin ($N=62$ trials): 0.645, 0.355; *V. germanica* origin ($N=59$ trials): 0.525, 0.475; GLMMpreference: Nest of origin: $\chi2(1)=1.642$, $P=0.200$] (Table 2C, Fig. 2B). *Volucella inanis* showed no significant preference for the *Vespula* species from which they were collected (and therefore had had prior exposure to), nor any significant preference for a novel *Vespula* species (Fig. 2B).

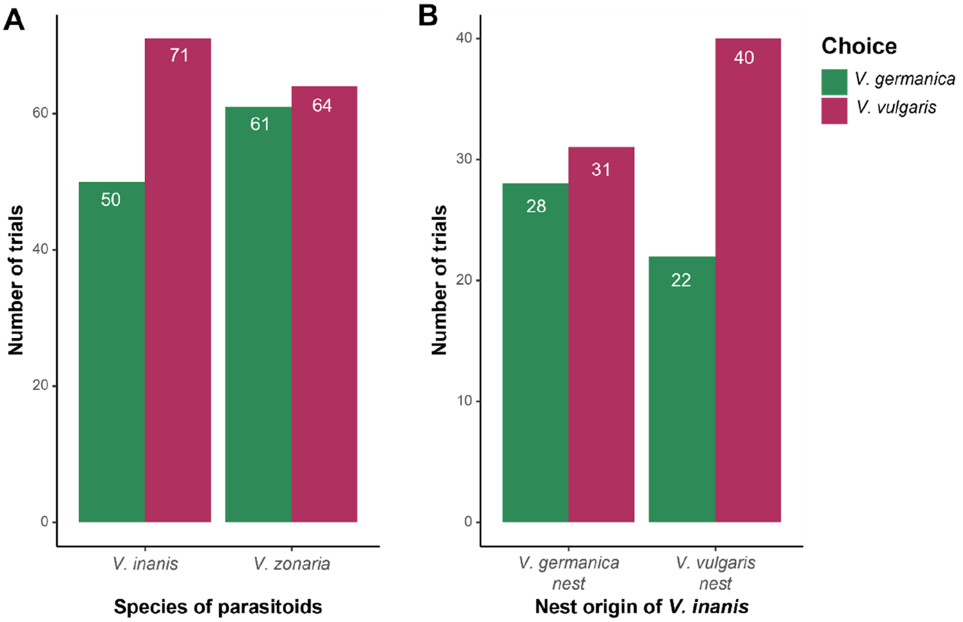

Fig. 2 Trials in which *Volucella* larvae made a prey choice. **A** Left bars represent the number of trials in which *Volucella inanis* chose either*Vespula vulgaris* (50) or *V. germanica* (71) as prey. One *V. inanis* did not make a choice and was excluded. Right bars represent the number of trials in which *Volucella zonaria* chose *Vespula vulgaris* (61) and *V. germanica* (64) as prey. Three *V. zonaria* larvae did not make a choice and were excluded from analysis. **B**. Breaks down the 121 prey choices made by *V. inanis,* presented in Fig 2A, by comparing their choice in the assay with the host species they were collected from. The left bars indicate the choices made by *V. inanis* larvae that originated from *V. germanica* colonies and the right bars show choices made *V. inanis* larvae originally from *V. vulgaris* nests

Discussion

The prevalence of sphecophiles in *Vespula* nests showed that the four species, *Volucella inanis, Vollucela zonaria, Sphecophaga vesparum* and *Metoecus paradoxus,* were all found in *Vespula* nests examined in southeast England. *Volucella inanis* was the most ubiquitous of four parasitoids, with its larvae present in the majority of nests searched. The closely related *V. zonaria* was found to be less prevalent, inhabiting half of the nests, whilst *Sphecophaga vesparum* and *Metoecus paradoxus* were both observed in no more than a quarter of nests. The two *Volucella* species were found in nests of both *Vespula vulgaris* and *Vespula germanica*, but *S. vesparum* and *M. paradoxus* were found only in the nests of *V. vulgaris.* The results of prey preference experiments using *Volucella* revealed that (1) *Volucella inanis* larvae have a prey preference for *Vespula vulgaris* over *Vespula germanica*, but are nonetheless not averse to predate *Vespula germanica*, and (2) *Volucella zonaria* larvae exhibit no preference for either Vespidae species. These results contradict our initial hypothesis that there would be no prey preference in both *Volucella* sp. We also found that (3) the natal nest of *V. inanis* larvae (either *V. vulgaris* or *V. germanica*) has no effect on the preference of prey species. This corroborates our hypothesis that nest of origin would have no effect on prey preference in *V. inanis*.

The release of *V. inanis* has recently been approved to control *Vespula* populations in New Zealand (Brown 2021a, b), and our results corroborate the choice of *Volucella inanis* as a promising biocontrol agent. Firstly, the relative high prevalence of *V. inanis* suggests that it is capable of infiltrating large proportions of nests in inhabited regions, supportive of the notion that the parasitoid could impact *Vespula* populations at regional scales. Then, although displaying a preference towards *V. vulgaris, V. inanis* also still predates upon *V. germanica*—a result that is further supported by the observed presence of *V. inanis* in nests of both *Vespula* species. This is reassuring that *V. inanis* will likely parasitise both *Vespula* species in areas where invasive populations have established in sympatry (e.g. in New Zealand) and also parasitise *V. germanica* populations where it is the only invasive Vespidae wasp (e.g. in Argentina, Masciocchi and Corley 2013). Furthermore, our results are indicative that *V. inanis* larvae reared in nests of either *V. vulgaris* or *V. germanica* will predate upon both *Vespula* species—hence it can be expected that *V. inanis* extracted from nests of *V. vulgaris* would predate upon *V. germanica* brood, and vice versa.

The association between adult and larval host preference is variable among parasitoid species (Giunti et al. 2015). Although there is evidence that pre-imaginal experience can have little bearing on preferences in adulthood (Jaenike

1983; Corbet 1985; Giunti et al. 2015). In some species, the Hopkins host selection principle (Hopkins 1909) supports the conservancy of behaviour of larval holometabolous insects and behaviour observed in adults. Pre-imaginal experience has been found to influence the preferences of several adult holometabolous insects (Hopkins 1909; Tully et al. 1994; Ray 1999; Rietdorf and Steidle 2002; Moreau et al. 2008; Ning et al. 2018). The methodologies of implementing *V. inanis* as biocontrol agents involve either introducing larvae directly to nests, or releasing cocoons or adults to then naturally increase the density of the parasite's populations. Requiring less manipulation, the latter approach is likely more attractive in the long term. In the case of conserved larval-adult preference, our results therefore have key implications for the predicted behaviour of released adults of both *Volucella* species regarding their choice of host species. Further investigation into the behaviour and preference of female adults is crucial for understanding the extent to which the preferences (and lack there-of) observed in *V. inanis* larvae are conserved into adulthood.

It is of note that the exploration of the four parasite prevalence reported here was a preliminary investigation and that studies over a wider area are needed to confirm our findings. Further investigation would benefit from collecting and searching nests from across the home range of the *Vespula* species, and across the nest development, as for example *V. zonaria* is likely to be more frequent in nest decline. Other species are known to inhabit *Vespula* nests (e.g. *Pneumolaelaps* mites Felden et al. 2020), which was not included in our survey.

Whilst our findings provide early optimism for the success of *V. inanis*'s future as an agent of biocontrol, *Volucella* species and their ecology remain understudied. Given the potential for *Vespula* biocontrol to deliver strong ecological and economical benefits, we call for further research into *Volucella spp.* to improve our understanding of *Volucella* biology, and likely enhance the efficacy of biocontrol efforts. Understanding the prevalence and preferences of proposed bioagents, alongside host-parasitoid compatibility, is evidently valuable to the long-term success of biocontrol programs.

Author contributions

JS and CAO contributed to the study conception and design. Material preparation, data collection and analysis were performed by JS, RLB and CAO. FS analysed the videos. The first draft of the manuscript was written by JS and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials The datasets and R scripts are available on Supplemental Material.

Declarations

Conflict of interest The authors declare have no competing interest.

Ethical approval The research described here aligns with the code of conduct for collecting insects and other invertebrates—Invertebrate Link (JCCBI). No licences or permits were required for these experiments. The higher arthropods specimens used in this research are not at Cities list (Convention on International Trade in Endangered Species of Wild Fauna and Flora). All authors consent to publish the final manuscript.

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