Fresh meat baits are currently the only available effective option to detect low-density *Vespula germanica* (Hymenoptera: Vespidae) populations in South Africa

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**Abstract**  
The eusocial wasp *Vespula germanica* is a problematic invasive species in the Southern Hemisphere regions. Especially in New Zealand, Tasmania and Argentina, population densities can be very high and result in large negative impacts. In these regions, the development of baits is used not only to monitor population sizes but also to poison wasps when they return with treated baits to their nests. In contrast, this wasp has been present in South Africa since 1974 but is still confined to a small geographical area. Therefore, detection of the presence of *V. germanica* with a low level of false negatives is important. The foundation of such a monitoring strategy is a reliable bait or lure that can be placed, in a standard way, in different environments to detect wasp presence. In this study, we tested two baits and two lures at eight localities in 2013 and two baits and four lures at nine localities in 2014. Trap catches confirm low population densities of the target species even in the core of its distribution in South Africa with an average between 3 and 11 wasps (median of 0) caught per trap. Confirming classical bait preference studies, meat baits, specifically lean smoked ham and lean beef mince, trapped significantly more foragers in both sampling years than the unbaited control treatments. However, all catches using synthetic lures with various compounds known to be attractive to *Vespula* species were almost always indistinguishable from control treatments. Consequently, more research is required in optimising baiting of *V. germanica* in South Africa, where it occurs at relatively low densities and worker activity peaks when seasonal conditions are unfavourable (hot and dry). Low population densities could explain why synthetic lures that are effective in other invaded continents were not effective in South Africa.

**Key words**  
Cape Floristic Region, invasive species monitoring, Mediterranean climate, synthetic lure.

**INTRODUCTION**

The German wasp or yellowjacket, *Vespula germanica* Fabricius, 1793 (Hymenoptera: Vespidae), is a prominent and intrusive invader worldwide (Clapperton et al. 1994; Landolt et al. 2000; Sackmann and Corley 2007; Beggs et al. 2011; De Villiers et al. 2017). Throughout its invasive range, the wasp has become a key pest, affecting tourism and outdoor activities due to their foraging behaviour and generalist, scavenger feeding (Clapperton et al. 1989a; Sackmann et al. 2001, Sackmann and Corley 2007; Landolt et al. 2007), thereby increasing their negative interactions with humans (Edwards 1980; Richter 2000; Austin and Hopkins 2002; MacIntyre and Hellstrom 2015). The wasps can also cause extensive damage as an agricultural pest by negatively impacting on viticulture, apiculture, horticulture and cattle farming (Clapperton et al. 1989; Braverman et al. 1998; Sackmann et al. 2001; Wood et al. 2006). In South Africa, nests are founded after overwintering queens emerge in September, and colonies are usually detected in February when there are a large number of workers foraging from the colony (Whitehead 1975). Typically, drones are found in nests in March and new queens from May onwards. Nests are usually no longer active (i.e. foraging workers) by June (Veldman, unpublished data).

Additional challenges are faced in New Zealand and Australia (Tasmania), as wasp colonies consisting of many individuals, occasionally overwinter in these regions (Whitehead and Prins 1975; Harris 1996). This contributes to high wasp densities, which increase the likelihood of negative interactions with humans (Moller 1996; Landolt et al. 2007; Rust et al. 2017). Wasp activity has also been shown to be affected by both previous season’s abundance and climatic variables during nest founding early in the wasp season (Masciocchi et al. 2016). Colonies are aggressively protected, and wasps will readily attack and sting any human or animal intruder. Consequently, detection and effective control of wasp nests, before large population sizes are reached, is vital. Such control actions include physical hand removal of nests, biological and chemical control and chemical repellents (Field and Darby 1991; Sackmann et al. 2001; Wood et al. 2006; Zhang et al. 2013; van Zyl et al. 2018). To date, no single method exists to effectively control this wasp species across its invasive range, in part due to local adaptations and between country differences that complicate standardised control actions. Thus, an evaluation of different control strategies is needed to find the best solution under localised settings (Landolt et al. 2000; Sackmann et al. 2001; Sackmann and Corley 2007; van Zyl et al. 2018).

*Vespula germanica* is attracted to both carbohydrates and proteins, depending on the colonies’ phenological state and nutrient requirements (Akre and Reed 1981; Archer 1985; Richter 2000;
Beggs 2001, as well as chemicals used in pheromone social communication (Buteler et al. 2018) or even the mating pheromones of other insects (Hendrichs et al. 1994). This complicates the search for and development of an effective lure for wasp sampling (Perrott 1975; Day and Jeanne 2001; Landolt et al. 2007; Sackmann and Corley 2007). Protein baits are often recommended in preference to carbohydrate baits as they are less attractive to non-target insects such as honey bees (Spurr 1995; Landolt 1998; D’Adamo and Lozada 2005; Sackmann and Corley 2007; Monceau et al. 2014). Furthermore, the attractiveness of baits may differ between locations due to the availability of alternative food sources, colony resource requirements, behavioural traits and local weather conditions (Spurr 1996; D’Adamo and Lozada 2005; Sackmann and Corley 2007). Baits should be equally or more attractive to the wasps compared to the alternative food sources available to them (Braverman et al. 1998; Stevens et al. 2002; Nelson and Daane 2007). It is often easier to prepare and use artificial lures specific to V. germanica, resulting in less non-target species being trapped (Wagner and Reierson 1969; Landolt 1998; Unelius et al. 2016). A large variety of baits and lures have been tested globally, but due to the extensive literature available on this topic, only selected references have been included (see Table 1). Nonetheless, given the geographical areas and the time frame covered, the literature listed is regarded as representative.

No work has thus far been conducted to determine the bait preferences of V. germanica in South Africa, despite the wasp being present since 1974 (Whitehead 1975; Whitehead and Prins 1975; Veldman et al. 2012). Consequently, the baiting of V. germanica across its perceived invasive geographical distribution is problematic (Veldman et al. 2012). In this study, the attractiveness of two fresh meat products and five artificial lures, known to be attractive and effective in other invaded countries, was tested during two consecutive years under South African field conditions. These findings contribute to the search for and development of a sampling method to monitor, under local and novel conditions, the presence and abundance of V. germanica in invaded areas of South Africa.

MATERIALS AND METHODS

Study sites

The attractiveness of Vespa germanica wasps to different baits and lures was determined by bait preference trials conducted in the Western Cape, Republic of South Africa. The region is characterised by a Mediterranean climate with dry, hot summers and cold, rainy winters (Cowing 1992). Study sites were mostly selected on deciduous fruit and wine farms and also included a few urban sites (Table 2). Trial sites were identified as a result of a wasp awareness campaign, encouraging the general public to report possible wasp presence. Potential sites were then visited to determine whether colonies were active, and wasp activity was determined by active search of V. germanica foragers at each site. The wasps’ nests are often difficult to locate, and at most sites, the location of nests was unknown. If no wasps were observed, traps covering the area where the wasps were previously seen were baited with ham and deployed. The traps were collected after 3 days, and if they contained wasps, the site was included in the study.

Trap and bait selection pre-trial

Following a comprehensive literature review, various commercially available traps, self-made traps and different meat products were evaluated from July 2012 to February 2013. The dome-shaped traps, funnel traps and malaise traps, often referred to in the literature, however, caught very few, if any, wasps (Barrows 1986; Landolt 1998; Landolt et al. 2000, 2007; Sackmann et al. 2001). In strong contrast, baited yellow delta traps with sticky pads (Chempac Pty Ltd., Paarl) proved to be the most effective trap type locally and subsequent screening of meat products commenced by using these traps in the field. Spurr (1995) found that V. germanica wasps are more attracted to raw fish and meat products than to their cooked counterparts, and therefore, only raw meat products were tested in the present study. Meat products provisionally tested included tinned tuna (in brine and in oil), pilchards, cat food, minced beef and extra lean beef, ‘polony’ – a locally made processed meat product made from different pork parts, different ham types, salami and a variety of meat spreads. Baited traps were placed at sites with known wasp activity, and traps were checked after 3 days for wasp presence. The highest numbers of foraging wasps were trapped with lean minced beef and lean smoked ham, and these two meat baits were subsequently selected for bait preference trials. Some specific chemical lures, as reported in the literature (Landolt 1998; Landolt et al. 1999, 2003, 2007; Day and Jeanne 2001), were also used in the trials (see Table 3) to represent non-meat baits.

Bait preference tests

Bait preference tests were conducted in field trials over two consecutive years. Most wasps forage on average about 200 m from their nest (Spradbery 1973; Edwards 1980). Consequently, sites chosen for bait preference tests were situated a minimum of 500 m (but preferably more than 1 km) apart from one another to ensure independent catches (see Reid et al. 1995). The study sites were sometimes clustered geographically and in other areas separated by more than 40 km as these were the only localities known to contain wasps in 2013. Following a wasp awareness campaign in 2014, additional sites were selected (see Table 2 for site specifics). However, as the public became more aware of the negative impacts of the wasps, they consequently wanted and/or initiated control actions as soon as nests were detected. As a consequence, the bait trials were started approximately a month earlier in 2014 to ensure wasp presence at sites throughout the specific trial period. Wasp densities sampled in 2013 would thus not be exactly comparable to those sampled in 2014 due to different stages of development, although this would only be a 4 week difference. This, however, allowed the attractiveness of baits to be tested slightly earlier in the wasp season but still when wasp forager densities were relatively high and likely to be detected and reported by the public.
Table 1  Summary of selected baits previously tested to attract *Vespula germanica* wasps worldwide

<table>
<thead>
<tr>
<th>Wasp species</th>
<th>Country</th>
<th>Protein tested</th>
<th>Carbohydrate tested</th>
<th>Other tested</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>V. germanica</em></td>
<td>New Zealand</td>
<td>NA</td>
<td>NA</td>
<td>Synthetic chemicals, synthetic soft drink flavours and solvent extracts</td>
<td>Perrott (1975)</td>
</tr>
<tr>
<td><em>V. germanica</em> and others</td>
<td>USA</td>
<td>Several brands of meat-based pet food</td>
<td>NA</td>
<td>Meat extracts</td>
<td>Ross et al. (1984)</td>
</tr>
<tr>
<td><em>V. germanica</em> and <em>V. vulgaris</em></td>
<td>New Zealand</td>
<td>Raw, cooked and canned meat varieties; raw and canned fish; fish meals, flavours and oils; and canned sardine cat food</td>
<td>NA</td>
<td>Preservatives; solvents; dyes; and fish and meat volatiles</td>
<td>Spurr (1995)</td>
</tr>
<tr>
<td><em>V. germanica</em></td>
<td>New Zealand</td>
<td>Canned sardine cat food (control)</td>
<td>Fondant sugar; dry icing sugar; dry raw sugar; raspberry and apple jam; apple-flavoured gel; molasses; honey; golden syrup; sweetened condensed milk; and 30% sucrose/water solution</td>
<td>25% sucrose solution + different bee repellents</td>
<td>Spurr (1996)</td>
</tr>
<tr>
<td><em>V. germanica</em> and <em>V. pensylvanica</em></td>
<td>USA</td>
<td>NA</td>
<td>NA</td>
<td>Isobutanol, heptyl butyrate, butyl butyrate and each + acetic acid</td>
<td>Landolt (1998); Landolt et al. (2005)</td>
</tr>
<tr>
<td><em>V. germanica</em> and others</td>
<td>USA</td>
<td>NA</td>
<td>NA</td>
<td>Acetic acid + several compounds structurally similar to isobutanol; isobutanol + acetic acid (control)</td>
<td>Landolt et al. (2000)</td>
</tr>
<tr>
<td><em>V. germanica</em></td>
<td>USA</td>
<td>NA</td>
<td>NA</td>
<td>Ripe pear volatiles; compounds structurally similar to isobutanol; chemicals typical of fruits and sugar; and isobutanol + acetic acid (control)</td>
<td>Day and Jeanne (2001)</td>
</tr>
<tr>
<td><em>V. germanica</em></td>
<td>Argentina</td>
<td>Raw minced beef; canned cat food (salmon flavour)</td>
<td>NA</td>
<td>NA</td>
<td>Sackmann et al. (2001)</td>
</tr>
<tr>
<td><em>V. germanica</em></td>
<td>South Australia</td>
<td>Fresh minced beef; fresh and freeze-dried kangaroo mince</td>
<td>NA</td>
<td>NA</td>
<td>Austin and Hopkins (2002)</td>
</tr>
<tr>
<td><em>V. germanica</em> and others</td>
<td>USA</td>
<td>NA</td>
<td>NA</td>
<td>Heptyl butyrate + drowning solution</td>
<td>Landolt et al. (2003)</td>
</tr>
<tr>
<td><em>V. germanica</em> and others</td>
<td>USA</td>
<td>NA</td>
<td>NA</td>
<td>Isobutanol + acetic acid; two citrus-based carbonated beverages</td>
<td>Wegner and Jordan (2005)</td>
</tr>
<tr>
<td><em>V. germanica</em></td>
<td>South Australia</td>
<td>Canned chicken and fish; freeze-dried chicken, fish and kangaroo</td>
<td>NA</td>
<td>NA</td>
<td>Wood et al. (2006)</td>
</tr>
<tr>
<td><em>V. germanica</em> and others</td>
<td>UK; Ireland; and Northern, Central and Southern Europe</td>
<td>NA</td>
<td>Beer</td>
<td>NA</td>
<td>Dvorak (2007)</td>
</tr>
<tr>
<td><em>V. germanica</em> and others</td>
<td>Hungary</td>
<td>NA</td>
<td>NA</td>
<td>Acetic acid, isobutanol, heptyl</td>
<td>Landolt et al. (2007)</td>
</tr>
</tbody>
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(Continues)
Argentina Fresh and freeze-dried V. germanica

Combined kairomone lure

Heptyl butyrate

Lean smoked ham

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consistency (Ross et al. 1984) as this can affect the meat’s aroma (Wood et al. 2006). Therefore, one specific meat brand was purchased at the same shop throughout the period of study. In case of the chemical baits, the artificial lures consisted of a circular carton disk, containing 1.4 g of the specific chemical, were fastened inside the trap with a piece of wire. No other food bait was presented with any of the chemical lures. If a combination of lures was used, e.g. heptyl butyrate plus acetic acid in 2014 (Table 3), two carton disks were hung next to each other in the same trap. The combined kairomone lure used in 2013 was obtained from The New Zealand Institute for Plant and Food Research. All other artificial lures (Table 3) were obtained from Insect Science (Pty) Ltd, a South African company who sourced the lures from suppliers in the USA.

Trap locations were randomly selected at each site, and baits were randomly assigned to traps. The traps were placed on fences or in vineyard rows at a height of approximately 1.5 m and separated by 10 m from each other (Spurr 1995; Landolt 1998; Landolt et al. 2000; Day and Jeanne 2001; Sackmann et al. 2001). This prevented the baits from interfering in attractiveness with each other. Sticky pads were removed twice weekly (when baits and lures were also replaced), and the total number of wasps caught in each trap was counted (Spurr 1995; Wood et al. 2006).

**Data analysis**

Due to the spatial and temporal non-independence of bait stations (the same sites were sampled over time, with traps from the same site by chance being more similar than ones from other sites), generalised linear mixed models were used to determine the best predictive model for the number of wasps caught in 2013 and 2014, respectively, with bait treatment as a fixed effect, while setting site nested in sampling round as a random effect.

To determine best predictive model for number of wasps caught over both sampling years (2013 and 2014 combined) using the same baits (see Table 3), the total number of wasps caught per site per bait was summed. A generalised linear model (GLM) specifying a Poisson distribution for count data listed all possible terms (the same sites were sampled over time, with traps from other sites), generalised linear mixed models were used to determine the best predictive model for number of wasps caught in 2013 and 2014, respectively, with bait treatment as a fixed effect, while setting site nested in sampling round as a random effect.

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RESULTS

A total of 2264 foragers were caught in 2013, while only 1475 were recorded in 2014. A higher trap catch was present in 2013 when an average of 11.46 wasps per trap per week (SD = 26.77, CV = 233%, n = 200) were caught, compared to an average of 3.44 (SD = 9.40, CV = 237%, n = 441) in 2014. Wasp densities thus differed markedly between years (Fig. 1a,b) as well as between sites in both years (Fig. 1c,d).

In 2013, the meat baits (smoked lean ham and lean minced beef) attracted significantly more foraging wasps, compared to the control and the artificial lures (CKL and HB, Table 4). Compared to the control, *Vespa germanica* wasps were significantly attracted to HB, although far fewer wasps were caught compared to the two meat baits (Fig. 1a). Wasp densities were not attracted to the combined kairomone bait. Similarly in 2014, fresh meat baits attracted significantly more foraging wasps, compared to the control or any of the four tested artificial lures (HB, HB + AA, IB and IB + AA) but with no artificial lure being significantly different from the unbaited control (Table 5).

For the comparison between baits that were tested in both years (HB, lean smoked ham and lean minced beef), only ham and mince were significantly different from the control (Table 6). These baits thus showed consistent results in proportion catch over the 2 years, after accounting for the higher wasp abundance in 2013 (Fig. 2a,b). The artificial lure, HB, however, did not differ significantly in attractiveness compared to the control in 2014. Neither ham nor HB differed in the percentage catch between the 2 years, but mince caught a higher proportion of the wasps in 2014 compared to 2013 (Fig. 2b).

Bycatch of other non-target insects was low, e.g., in 2014, only 14 honey bees, 4 *Polistes marginalis* and 170 *Polistes dominula* (another invasive Vespidae in South Africa) were caught. In comparison, if only looking at controls, one honey bee and one paper wasp were caught. Bycatch is thus not a potential problem with monitoring *V. germanica* using yellow delta traps in South Africa.

DISCUSSION

Globally, the determination of local bait preferences of *Vespa germanica* has been onerous due to often contradicting results reported between different study sites, areas and countries (e.g. Spurr 1995, 1996; Sackmann et al. 2001; Wegner and Jordan 2005; Unelius et al. 2016). Furthermore, the attractiveness of baits for a given wasp population may also differ over time, because as colony development takes place, changes in the wasps’ energetic requirements occur (Sackmann and Corley 2007). *V. germanica* colonies reach peak sizes by late summer to early autumn (Reid and MacDonald 1986; Beggs and Wilson 1991; Dvorak and Landolt 2006). In South Africa, peak densities are reached at the start of April with a low percentage of colonies becoming perennial and remaining active after June (unpublished data). This coincides with the driest part of the season before appreciable rainfall is received. Without water supplementation, *V. germanica* struggles to persist at the range edge of its invaded
distribution as shown by recent CLIMEX modelling (De Villiers et al. 2017). With the present invaded range in South Africa, V. germanica experiences conditions that are marginal compared to the optimal conditions found, e.g. in Argentina or New Zealand (Masciocchi et al. 2016; Rust et al. 2017).

**Table 4** Generalised linear mixed model (Poisson) for explaining number of wasps caught in 2013 per baited trap with sampling locality (eight) nested in sampling occasion (five) set as a random effect

<table>
<thead>
<tr>
<th>Explanatory factor</th>
<th>d.f.</th>
<th>Significant category level</th>
<th>Estimate ± SE</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1</td>
<td></td>
<td>-1.681 ± 0.324</td>
<td>-5.181***</td>
</tr>
<tr>
<td>Bait treatment</td>
<td>5</td>
<td>HB</td>
<td>2.972 ± 0.234</td>
<td>12.685***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ham</td>
<td>3.912 ± 0.231</td>
<td>16.952***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mince</td>
<td>3.884 ± 0.231</td>
<td>16.827***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CKL</td>
<td>0.423 ± 0.294</td>
<td>1.438</td>
</tr>
</tbody>
</table>

Random effects: site:round, 40 groups with intercept variance of 2.045 ± 1.430; round, five groups with intercept variance < 0.001 ± 0.001. % deviance explained = 56.1%; AIC = 1768.6, deviance = 1754.6, remaining d. f. = 193.

***P < 0.001.

CKL, combined kairomone lure (see Unelius et al. 2016); HB, heptyl butyrate.

**Table 5** Linear mixed model (Gaussian) for explaining number of wasps (log(n + 1)) caught in 2014 per baited trap with sampling locality (nine) nested in sampling occasion (seven) set as a random effect

<table>
<thead>
<tr>
<th>Explanatory factor</th>
<th>d.f.</th>
<th>Significant category level</th>
<th>Estimate ± SE</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1</td>
<td></td>
<td>0.000 ± 0.036</td>
<td>0.000</td>
</tr>
<tr>
<td>Bait treatment</td>
<td>7</td>
<td>HB</td>
<td>0.030 ± 0.049</td>
<td>0.606</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HB + AA</td>
<td>0.058 ± 0.049</td>
<td>1.186</td>
</tr>
<tr>
<td></td>
<td></td>
<td>IB</td>
<td>0.049 ± 0.049</td>
<td>0.999</td>
</tr>
<tr>
<td></td>
<td></td>
<td>IB + AA</td>
<td>0.063 ± 0.049</td>
<td>1.294</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ham</td>
<td>0.751 ± 0.049</td>
<td>15.430***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mince</td>
<td>0.903 ± 0.049</td>
<td>18.569***</td>
</tr>
</tbody>
</table>

Random effects: site nested in round, 63 groups with intercept variance of 0.009 ± 0.093; round, seven groups with intercept variance of 0.000 ± 0.000 and residual of 0.075 ± 0.273. % deviance explained = 75.7%; REML criterion at convergence: 170.9; remaining d. f. = 431; difference with null model (no fixed effects): ΔAIC = 415.05, d.f. = 10, χ² = 427.05.

***P < 0.001.

AA, acetic acid; HB, heptyl butyrate; IB, isobutanol.

differences between localities were not statistically analysed but instead only shows variation in number of wasps caught. AA, acetic acid; CKL, combined kairomone lure; HB, heptyl butyrate; IB, isobutanol.

**Fig. 1**. Number of Vespula germanica caught per tap per sampling occasion in 2013 and 2014 (note the difference in y-axis range between years), expressed as using different baits (a, b) and between different localities (c, d). Different letters indicate significant differences at \( P < 0.0001 \) between baits (see also Tables 4,5); differences between localities were not statistically analysed but instead only shows variation in number of wasps caught. AA, acetic acid; CKL, combined kairomone lure; HB, heptyl butyrate; IB, isobutanol.
Table 6  Generalised linear model (Gaussian) for explaining percentage of catch of wasps caught in 2013 and 2014 in total per baited trap by sampling year and bait treatment

<table>
<thead>
<tr>
<th>Explanatory factor</th>
<th>d.f.</th>
<th>Significant category level</th>
<th>Estimate ± SE</th>
<th>z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td></td>
<td></td>
<td>0.276 ± 3.665</td>
<td>0.075</td>
</tr>
<tr>
<td>Bait treatment</td>
<td>3</td>
<td>Ham</td>
<td>45.491 ± 5.183</td>
<td>8.776***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Heptyl butyrate</td>
<td>9.851 ± 5.183</td>
<td>1.901</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mince</td>
<td>43.065 ± 5.183</td>
<td>8.308***</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>2014</td>
<td>−0.276 ± 5.037</td>
<td>−0.055</td>
</tr>
<tr>
<td>Bait × Year</td>
<td>3</td>
<td>Ham:2014</td>
<td>−8.036 ± 7.124</td>
<td>−1.190</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Heptyl butyrate:2014</td>
<td>−8.866 ± 7.124</td>
<td>−1.245</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mince:2014</td>
<td>16.019 ± 7.124</td>
<td>2.249*</td>
</tr>
</tbody>
</table>

% deviance explained = 84.6%; deviance per d.f. = 1.00, remaining d. f. = 60.

*P < 0.05.

**P < 0.001.

Fig. 2. Total number of Vespula germanica caught per bait per site in 2013 and 2014 expressed as percentage catch in a given year. Different letters indicate significant differences at P < 0.0001, and different capitals indicate significant year–bait interactions at P < 0.05 (see Table 6 for more details). HB, heptyl butyrate.

Large annual variations in V. germanica populations are a well-documented worldwide phenomenon (Akre and Reed 1981; Dvorak 2007). Possible reasons for this include yearly fluctuations in weather conditions, diseases and the availability of suitable nesting sites and food sources (e.g. Akre and Reed 1981; Sackmann et al. 2001; Masciocchi et al. 2016). Compared to 2014, a significantly higher wasp abundance was noted in 2013 in our study, even though the sampling effort was greater in 2014, ranging over a longer time period and including more bait treatments and sites. This indicates that the earlier stage of nest development in 2014 could markedly have affected trap catches compared to 2013, but what is important is that the baits tested preformed consistently.

Our results suggest that fresh meat baits (lean smoked ham and lean minced beef) were consistently attractive to V. germanica and could therefore potentially be part of future developmental options for wasp monitoring. The attractiveness of meat baits is, however, not unexpected. Wood et al. (2006) found that V. germanica was attracted to five types of processed meat products in South Australia; Reid and MacDonald (1986) reported V. germanica to be significantly attracted to lean ham in the USA, and Sackmann and Corley (2007) showed fresh minced beef to be the most preferred bait in Argentina. Furthermore, Spurr (1995) determined that V. germanica is less attracted to meat products with a high fat content. This was also true in the present study. During pre-trials, low wasp numbers were trapped with polony and minced beef containing a higher fat content, compared to the subsequent high wasp numbers trapped with lean smoked ham and lean minced beef.

There are, however, problems associated with the use of fresh meat baits under field conditions, which include (1) guaranteeing meat of a constant quality (Ross et al. 1984; Reid and MacDonald 1986); (2) drying up of fresh meat products when exposed to the sun (although meat with higher moisture content decreases the likelihood of crust ing, it is also more likely to deteriorate quicker), leaving it less palatable to the wasps (Reid and MacDonald 1986; Spurr 1995); (3) unsavoury smell and spoiling of bait due to fresh meat deteriorating more rapidly during warm summer days (Ross et al. 1984); and finally, (4) the use of fresh meat is labour intensive and expensive as it needs to be replaced more often than synthetic lures (Reid and MacDonald 1986; Landolt 1998). Both Ross et al. (1984) and Spurr (1995) have postulated that the use of synthetic volatile meat extracts as an alternative to fresh meat baits to attract V. germanica might overcome the problems associated with fresh meat baits. Volatile meat extracts could be as attractive as raw meat while being easier to use in the field. For example, Rust et al. (2017) have suggested the combining of meat flavours in hydrogels to ensure effective bait acceptance. There is thus a need to investigate the use of synthetic volatile meat extracts, in more invaded countries.

Contrary results were found with all the synthetic lures that we tested, as was also found elsewhere in the world, notably with HB and AA (Landolt et al. 2003, 2007; Spurr et al. 1996; Reed and Landolt 2002). The reason for V. germanica finding HB more attractive than the control in 2013 but not in 2014 in the current study remains unknown, and this could still be investigated further. However, trapping consistency is a key factor for developing a baiting program to monitor the occurrence of V. germanica. The development and HB is thus likely to not be cost effective in future testing given the observed initial variability and low catch percentage. In Hungary and in the USA, V. germanica is attracted to IB and AA when the latter is presented singly in a trap, but it is strongly attracted to these chemicals when used in combination (Landolt 1998; Landolt et al. 1999, 2007). This increase in attractiveness can be ascribed to synergy (Day and Jeanne 2001). Many food materials naturally attractive to V. germanica contain IB and AA – e.g. different fruits, sugars and molasses. It is thus thought that V. germanica is attracted to these chemicals while searching for other carbohydrate-based food (Day and Jeanne 2001; Landolt 2003, 2007; Spurr et al. 1996; Reed and Landolt 2002).
REFERENCES

It was therefore unexpected to find that V. germanica showed hardly any attraction to IB or the combination of IB and AA in the present study.

Another possible reason for the poor performance of synthetic lures is competition with more attractive olfactory cues, such as natural carbohydrate-rich resources, which do in fact then also provide a reward. This was also noted by Landolt (1998), who suggested that different food sources in the environment might be competing with one another, confusing the wasps’ reaction to AA. In our study, however, V. germanica also showed no attraction to the combined kairomone lure developed in New Zealand. This is despite this lure specifically being formulated to replicate multiple food sources and tested as highly effective under field conditions (Unelius et al. 2016). There thus appears to be a general problem with using known V. germanica lures in South Africa, which requires further investigation. For example, the use of synthetic meat volatiles should be included in future bait preference trials (see also Rust et al. 2017). As an alternative, Vespx® is a protein-based bait matrix with 0.1% fipronil that is very attractive to Vespula species and successfully used in New Zealand to reduce wasp numbers (Edwards et al. 2017). This could be a useful bait for future monitoring in South Africa and should thus be tested under local conditions. At this stage, the main requirement is still simply to robustly monitor V. germanica’s occupancy and range limit in South Africa so as to guide appropriate management strategies and control actions. Further research to find an optimal attractive artificial bait/lure that can locally detect populations at low densities remains a priority.

ACKNOWLEDGEMENTS

Farm owners and managers are thanked for allowing access onto their properties. Gerhard Booyzen from Insect Science (Pty) Ltd is acknowledged for providing the artificial lures free of charge and Andrew Twiddle (The New Zealand Institute for Plant and Food Research) for providing their wasp lures. Max Suckling, Francois Roets and Phil Lester are thanked for their valuable comments on previous versions of the manuscript. The South African National Biodiversity Institute (SANBI) funded this project through the South African Department of Environmental Affairs.

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