

Dorsal visual cues in German wasp navigation

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Abstract

The German wasp *Vespula germanica* is found in the Palaearctic region of the globe. Outside this area, it is highly invasive species. It has an omnivorous diet and is able to hunt other insects and scavenge for food from both natural and anthropogenic sources. It has been previously shown that this species has efficient and specialized foraging strategies depending on the resource. It is capable of navigating successfully through closed habitats, has a large landmark learning capacity as well as flexible responses to changing environmental variables. They are also able to recognize a shape irrespective of color and contrast with the background. Our study shows that this species is able to detect patterns and their orientation in the dorsal field, ability that is lacking in honeybees. Furthermore, our data suggests that each forager is able to remember landmarks associated with not only the current, but also the previous resource location, something that has already been proved in previous studies.

Introduction

Many insect species show an incredible ability to return to a precise location such as the nest or a recently discovered food source. How such complex tasks are performed by brains as small as 0.041 mm³ (O'Donnell et al., 2013), has been the subject of intense research. Such “central place foragers” have so far only been described within the Hymenoptera (Aculeata), the bees, wasps and ants. Many species of these insects are capable of repeatedly returning with a food load to the nest from a productive foraging site (Polidori et al., 2013). In order to do this, each individual must be able to memorize the route between two locations and retrieve this information as necessary.

In order to minimize the load on the nervous system, the endpoints of each journey are memorized in detail.

Nevertheless, a small amount of information is also stored concerning the route in between, with the exception of detailed memories for a few important landmarks (Cronin et al., 2014). These landmarks have the role of dividing the length of the route into segments, or “snap shots”, and upon return, these snap shots are recalled in sequence to allow the insect to find its way back to the nest (Collett et al., 2002).

In order to navigate from one landmark to another, central place foragers use a system called path integration, in which the distances traveled and angles turned are used to continuously update an estimation of their goal's direction (Chitkka et al., 1995). The reference angle, and thus the direction, is obtained by using celestial compass cues such as the sun, stars, moon or polarized- light pattern of the sky (Chitkka et al., 1995; Collett et al., 2013; Cronin et al., 2014). The

distance to a specific goal is obtained by measuring the optic flow for flying insects (Collett et al., 2002; Cronin et al., 2014) or by step counting, (which functions as an “odometer”) in ants (Wittlinger et al., 2006; Wittlinger et al., 2007).

Visual landmarks around the nest or foraging site are learned by performing an “orientation flight” or by “learning walks” (Jeanne and Taylor, 2009; Moreyra et al., 2012), in which the individual, facing the goal, backs away in a series of increasing arcs (Zeil et al., 1996).

During these maneuvers, “snapshots” of the predominant landmarks are memorized, together with the broader visual panorama (Collett et al., 2013). These memorized contextual cues ensure that the appropriate memories are retrieved at the appropriate time (Collet and Zeil, 1997).

Upon return through positional image-matching, the insect is able to pinpoint the exact location of the goal (Collett et al., 2013). Thus, insects will search for their goal at the location in which the retinal image and compass bearing of the landmark match those stored in the memorized snapshot (Cartwright and Collett, 1983).

German wasp or German yellowjacket (*Vespula germanica*) is a social wasp species of Palaearctic origin (Spradbery and Dvorak, 2010). This species is also a successful invader in many parts of the world (D'Adamo et al., 2000) such as New Zealand, Australia, South Africa, the United States, Canada (D'Adamo and Lozada, 2009), Argentina (D'Adamo et al., 2002) and Chile (Spradbery and Dvorak, 2010). Having a wide distribution range that consists of habitats with high heterogeneity (D'Adamo and Lozada, 2014), this species has an eclectic diet that includes both natural and anthropogenic food sources such as live invertebrates, fruits, honey-dew from aphids and processed human food (Greene, 1991). These resources are obtained

through hunting, scavenging or collection of sugar rich liquids (Richter, 2000).

The success of this species may be explained by the fact that it exhibits efficient foraging strategies (D'Adamo and Lozada, 2009), depending on the food source. Thus, when the food source is composed of proteins, the learned location of the food source elicits more landing responses than the actual location of a newly displaced food source. The opposite is true for carbohydrate sources. This enables the scavenging individual to return to the exact location of the carrion. However, carbohydrate sources such as flowers are conspicuous, and often occur in patches, making the location of a specific source less important (D'Adamo and Lozada, 2003).

The habitat also has an impact on the foraging habits of German wasps. Compared with an open habitat, in a closed habitat foragers revisited the learned feeding location more often than the new location of a displaced feeder. When more landmarks were placed in the open habitat, the visits to the learned location increased. A larger number of landmarks in a closed habitat thus enable individual wasps to orient themselves more easily and thus return to the feeding site. The extra landmarks added in the open habitat play a similar role (D'Adamo and Lozada, 2007) since protruding objects act as beacons, guiding the forager wasp back to the food source (Collett and Zeil, 1996).

Vespula germanica individuals will return to the location of a food source even after it is no longer there. The number of returns is proportional to the number of visits made when the food reward was present (Lozada and D'Adamo, 2006). The wasps also show a preference for the most recent rewarding cue (Lozada and D'Adamo, 2009). However, even when a second task with a

conflicting response is learned, the memories associated with the first learned task are not erased (D'Adamo and Lozada, 2009). These learning abilities together with a flexible response to changing contexts are invaluable tools for these species, enabling them to colonize new environments (Lozada and D'Adamo, 2009).

In bees, the minimum visual angle at which the bees detect a stimulus is largest in the dorsal part of the eye which is incapable of using color information and together with the ventral part cannot detect pattern orientation (Giger and Srinivasan, 1997; Giurfa et al., 1999). The dorsal part of the eye is most probably used for skylight-based navigation (Giurfa et al., 1999) as the dorsal optic flow is involved in the control of speed (Portelli et al., 2011). Bees are able to discriminate between various closed shapes by using local parameters situated at the outline of the shape such as the position and orientation of edges (Campan and Lehrer, 2002). Wasps are able to do this irrespective of visual factors such as the color of the shapes or the type of contrast between these and the background (Lehrer and Campan, 2004).

Despite recent research, the different parts of the visual field are still poorly researched in German wasps. Wasps are superb navigators which are able to fly through closed habitats such as forests. It has been shown that other insects living in similar habitats are able to use the canopy pattern as a system of landmarks (Warrant and Dacke, 2010). However it is still unknown if *Vespula germanica* is able to use the dorsal region of the eyes in similar fashion. In the present study we determined whether *Vespula germanica* eye is indeed able to use landmark information in the dorsal visual field to learn the location of a food source.

Material and methods

Experimental animals

The experiments were conducted during September 2014 on the campus of Lund University, outside the Ecology building.



Figure 1. Frontal view of the head of a German wasp individual (courtesy of Haris Prin).

Marked wild individuals of the German wasp (*Vespula germanica*) were used in the experiment (Figure 1).

Individual wasps were first attracted to a sugar water feeder covered along its vertical length with blue paper (Figure 2, left inset). When the wasps visited the feeder regularly, they were marked with colored sequentially numbered bee tags that were glued on the thorax, between the wings. A total of 107 individuals were marked over the course of several days.



Figure 2. The experimental apparatus, consisting of a Y-maze screwed to a wooden sheet. The two insets represent the two types of feeders used: left – feeder used during training, right – feeder used during the experiments.

Experimental apparatus

The experimental apparatus consisted of a Y-maze (Figure 2), size 75 cm x 89 cm x 30 cm (length, width, height), built of UV-transmissive transparent Plexiglas sheets, 4 mm thick. The maze consisted of four main chambers comprising the entrance and the arms, each of which in turn were further divided in two smaller chambers (Figure 3). The entrance chamber (Figure 4A) and the first decision chambers were created by walls each containing a central circular hole with a diameter of 10 and 7 cm, respectively (Figure 3). The division of each arm in two subchambers was achieved by transparent Plexiglas walls that each contained a central hole of diameter of 1.5 cm (Figure 4B). All access holes were marked by a hollow circle, of thickness 5 cm, made of Q Connect A4 80gsm Bright Blue Ream Colored Copier Paper. This had the role of making the access hole visible to the experimental animals. During the experiment, the dividing walls inside the arms of the maze (but not the access holes) were covered with the same type of blue paper used previously. These had the role of obstructing the view of the feeders, thus not providing any visual cue about which arm contained the food reward. An additional removable Plexiglas wall was used to block the access to one of the maze's arms during the training phase of the experiment.

The roof of the maze consisted of separate Plexiglas sheets that could easily be removed, thus facilitating access to the maze (Figure 4). The dorsal visual stimuli were affixed to the Plexiglas sheets above each arm of the maze (Figure 2). The stimuli were comprised of a clear Lee UV-transmissive filter (LF 130) onto which stripes of black electrical tape (width 2 cm) were placed parallel to each other, and spaced at a distance of 2 cm. Thus, a pattern of even light and-dark stripes was created

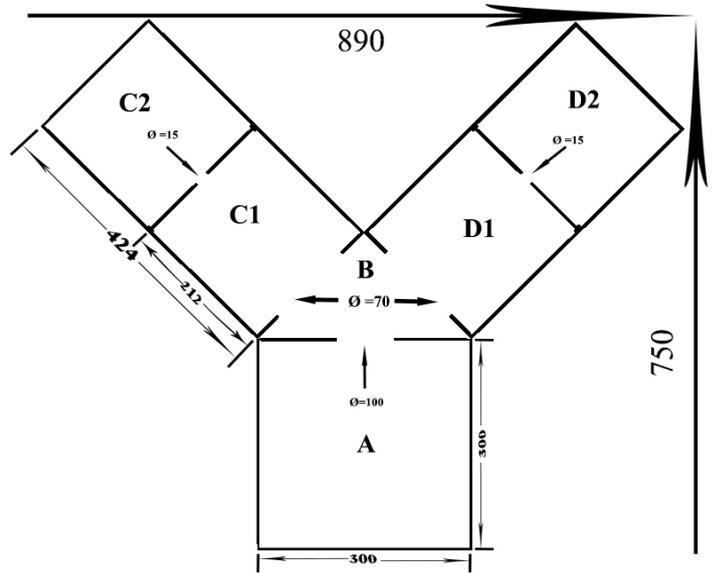


Figure 3. Top view of the Y-maze used in the experiment. A and B represent the entrance and the first decision chamber, respectively. C1 and D1 represent the second decision chambers. C2 and D2 represent the chambers where the feeder was placed during the experiment. The unit of measurement for the length of the maze and the diameter of the access holes is mm.

that could be placed parallel with, or perpendicular to, the main axis of the maze arm.

The maze was placed and fixed on a large wooden sheet (Figure 2). In order to eliminate external visual information visible through the clear walls of the maze, but nonetheless preserve optic flow information available to the wasps, the sides of the maze were masked on the outside with self-adhesive patterned vinyl window film. Thus, the same visual information was provided along the whole length of the maze on both sides (Figure 2).

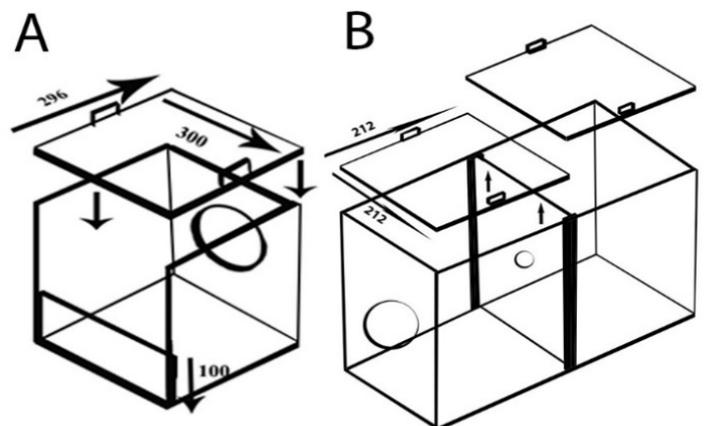


Figure 4. The Y-maze **A.** Chamber A, representing the entrance into the maze. **B.** Schematic representation of an arm of the maze with its two subchambers.

There were two types of feeders used in this experiment (Figure 2, insets). The first type (Figure 2, left inset) was a bee feeder composed of a white plastic bottle to which was attached a round plastic plate containing narrow grooves in which sugar water flowed. The plastic bottle was covered with blue paper in order to increase the attractiveness for the wasps.

The second feeder (Figure 2, right inset) used during the experiments was also composed of a white plastic water bottle. However, the bottle was placed with the mouth upwards, instead of downwards as in the first feeder, and a plastic funnel attached to a long transparent plastic tube was inserted. The funnel and tube were filled with dish washing sponges which had the role of containing the sugar water reward. The funnel and its sponge were blue, thus acting as an attractive visual cue that guided the individual wasps to the reward. In order to maximize the attractiveness of the funnel, the water bottle was not covered with blue paper. The amount of sugar solution contained in the sponge was regularly checked, and if needed, more sugar solution was manually added.

Experimental procedure

Training phase

In the initial phase of the training, the feeder was placed in front of the maze, until the marked wasps were regularly visiting it. Gradually the feeder was moved into the first and then the second chamber of the maze.

Again, sufficient time was provided for the wasps to find the food source and to get accustomed to the inside of the maze. When this was achieved, the feeder was once again moved from the second chamber of the maze to the first subchamber of the appropriate arm of the maze. The second chamber of the maze together with the first subchamber in each arm represent the first and second

decision chambers, respectively. Once this initial phase was achieved, the actual training commenced.

The training was divided into 10 minute sessions in which the feeder was in one arm of the maze, whereas the other was blocked with a transparent Plexiglas sheet. The wasps were trained using the dorsal pattern turned such that the stripes were perpendicular to the long axis of the maze arm. Following each training session, the arms were interchanged in order to avoid the wasps acquiring any side preference. When the wasps were accustomed to the procedure, the feeder was placed in the second subchamber of the appropriate arm. In order to make the access to this new position of the feeder more obvious, a small piece of paper towel was soaked in sugar solution and placed into the hole – this created a transition between the subchambers. When the wasps found this, they simply walked on it and thus into the second chamber. The sugar solution acted as an incentive to further explore the paper. Once the wasps passed through this hole regularly, the paper was removed.

The training was concluded when, with both arms accessible and the same dorsal stimulus pattern was present in each, the frequency of visits was approximately 50% for each side. By having the trained pattern on both arms, a 50:50 ratio ensured that the wasps chose randomly, thus indicating that no side preference developed during the training.

Experimental phase

Over the course of four days, the testing phase of the experiment took place. The training feeder was replaced with two test feeders (Figure 2, right inset), one for each arm of the maze. Both feeders contained sugar solution and each arm of the maze had one of two dorsal visual patterns: the trained pattern or a novel pattern in which

the stripes were parallel (rather than perpendicular) to the long axis of the maze arm. In order to prevent wasps from accessing sugar solution from the “wrong choice” feeder, a net was placed on top and fixed with a rubber band. This made it impossible for the wasps to reach the food reward. When the rewarding arm of the maze was interchanged, the net was moved to the other feeder. By always having two feeders in place, but only one net that changed places, the confounding effects of olfactory cues were kept to a minimum.

Visits from both marked and unmarked individuals were recorded. When the number of unmarked individuals reached a level that made the observation of marked individuals more difficult, a second training feeder (Figure 2, left inset) was placed in front of the maze. This second feeder contained a sugar solution of lower concentration than the one used in the maze. It thus had the role of attracting new and untrained wasps, thereby decreasing the number of individuals in the maze. The effect on the marked and trained individuals was low as these already knew the location of the feeders, and knew that these provided a more abundant food source.

Data analysis

Graphs were created using IBM SPSS Statistics version 22. The statistical analysis was performed using XLSTAT version 2014.06.01. Only one choice per individual per experimental session was recorded. If an incorrect choice was made during this period together with several correct choices, an incorrect choice was recorded. This was chosen, as an individual could learn where the reward feeder was placed in that specific session. The total number of choices made by all individuals each day, as well as these values pooled together were analyzed for differences using a McNemar test. This test assess the significance of the difference

between two correlated proportions such as those obtained from the marked individuals. The effects of time, temperature, wind and precipitation were tested against the performance of individuals 11, 75 and 97 with Pearson correlation tests. These are the individuals present in all experimental days and the correlation tests had the role to discover any relationship between their success rate and any of the factors mentioned above.

The environmental data was downloaded from the archive of Sweden’s meteorological and hydrological institute (SMHI). The air temperature (mean value at 06:00 and 18:00) and precipitation (daily mean values) were registered at the SMHI’s meteorological station in Lund. However, the wind speed data (mean value between 09:00-17:00) was obtained from the Malmö Aut meteorological station, this being the closest station to Lund that records this weather parameter.

Results

The percentage of correct choices made by each individual on each day of the experiment is presented in Figure 5. The horizontal reference line was considered to be the level at which an individual makes choices randomly.

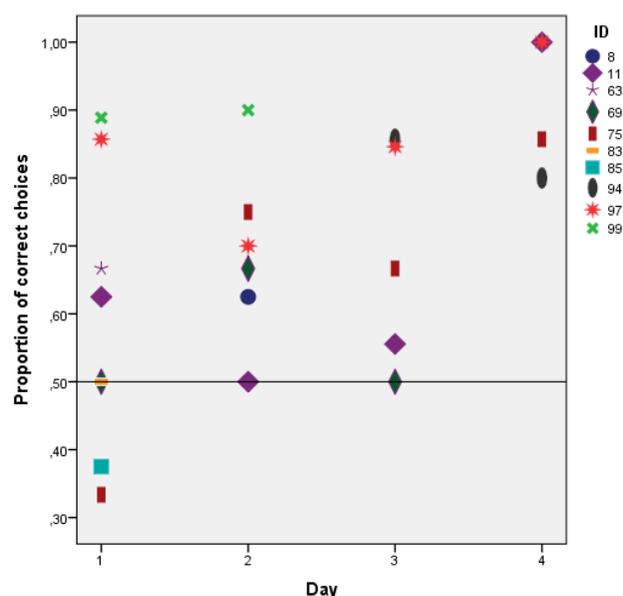


Figure 5. Individual proportions of correct choices on each day of the experiment from each wasp. Horizontal reference line marks the limit between random and non-random choices.

Thus, all values above 50% are an indication that the individual is able to distinguish between the dorsally presented visual cues and use this information to find the food source. Values above 90% strongly indicate that German wasps can use visual patterns perceived within the dorsal visual fields of the eyes.

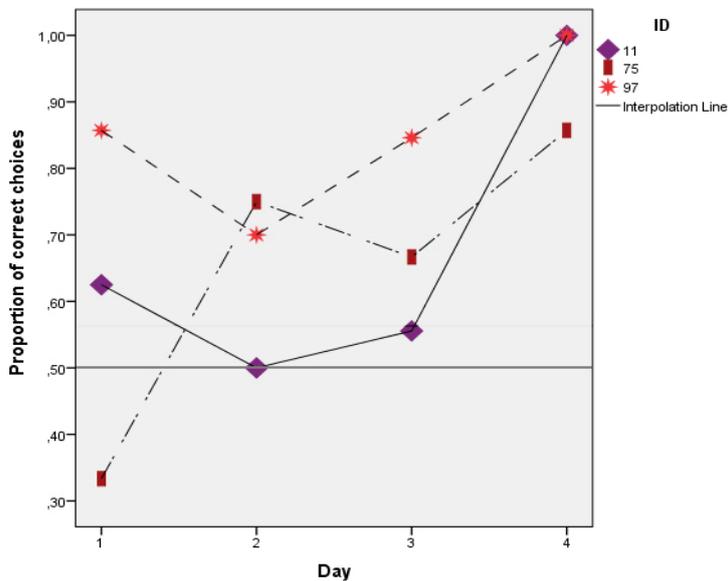


Figure 6. Individual proportions of correct choices on each day of the experiment obtained from individuals 11, 75 and 97. The dashed and continuous lines represent the interpolation lines for each individual. Horizontal reference line marks the limit between random and non-random choices.

Several individuals (Figure 6), ID 11, 75, 97, show a decrease in the percentage of correct choices either on the second or the third day. On the fourth day this percentage increased with approximately half the values of the previous day. The experimental days were not consecutive: day 1 was September 24th, day 2 September 26th, day 3 September 29th and day 4 September 30th. Thus on the day between day 1 and day 2 no training occurred because of unfavorable weather conditions. Similarly, a weekend occurred between day 2 and day 3, during which no experiment took place.

The mean percentage of choices pooled from all individuals each day is shown in Figure 7. An increase in the correct choices on day 2 was followed by a slight decrease on day 3. On the last day of the experiment, the

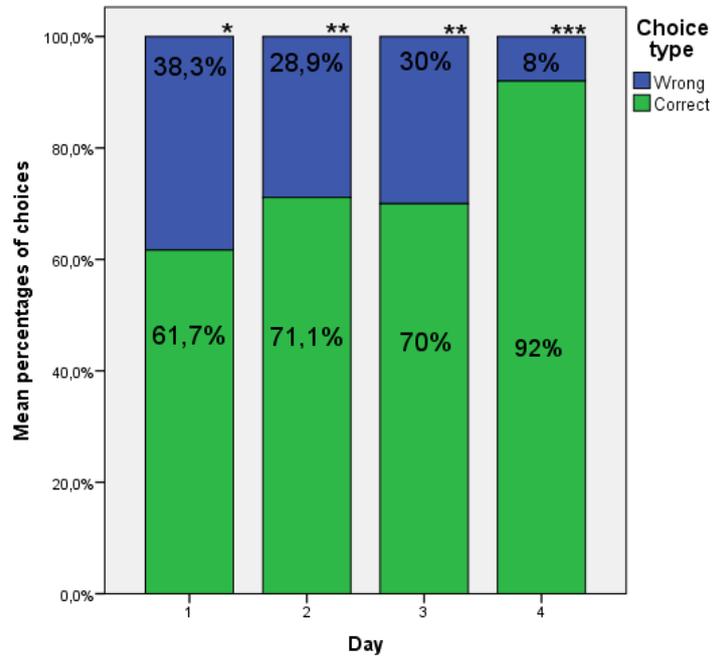


Figure 7. Mean percentages of choices pooled from all individuals on each day of the experiment. On all four days the proportion of correct choices was significantly larger than incorrect choices (day 1: $p=0,026^*$; day 2: $p=0,0012^{**}$, day 3: $p=0,0166$; day 4 $p<0,0001^{***}$; * represents the level of statistical significance).

proportion of correct choices increased dramatically, almost reaching 100%.

When the data were pooled from all individuals and all days, significant differences between the numbers of choices made for the correct (trained) and incorrect (novel) pattern were found ($P<0.0001$, $n=150$). A secondary McNemar test showed that the choices made for the trained pattern were statistically significantly greater than those for the untrained pattern ($P<0.0001$, $n=150$).

An analysis on the daily pooled data from all individuals was performed to see if any variation existed. This also found significant differences between the chosen types of pattern. The exception was day 1 in which the differences were non-significant (Table 1). However, a secondary McNemar test showed that the trained pattern (perpendicular) elicited more choices than the untrained (parallel) pattern on all the experimental days, including day 1 (Figure 7).

Table 1. Results of the statistical analyses on the daily pooled data from all individuals (t - perpendicular pattern = correct choice, l- parallel pattern = incorrect choice). t≠l represents the results of the analysis of between pattern choice differences and t>l the analysis on which pattern elicited more responses.

	Day 1		Day 2		Day 3		Day 4	
Pattern type	t ≠ l	t > l	t ≠ l	t > l	t ≠ l	t > l	t ≠ l	t > l
P-value	0,092	0,026	0,0066	0,0012	0,017	0,0032	< 0,0001	< 0,0001
n	60	60	45	45	40	40	25	25

When the performance of the three individuals present in all experimental days was tested against time, to see if any improvement occurred, no significant results were obtained (ID: 11 P=0,404, R²=0,356; 75 P=0,151, R²=0,722 and 97 P=0,395, R²=0,366). The statistical analysis of several environmental factors (air temperature, wind speed and precipitation) together with the pooled performance of individuals number 11, 75 and 97 showed no correlation either.

Discussion

Studies conducted on social wasps are rare when compared with similar studies performed on honeybees and bumblebees. Unlike these, wasp colonies cannot be bought and maintained in a laboratory. As a result, all experiments need to be conducted outdoors, making the vision in wasps a poorly researched field. Most of the existing studies are mostly concerned with color discrimination (Beier and Menzel, 1972; Beier, 1984; Shafir, 1996), memory (D'Adamo and Lozada, 2009; D'Adamo and Lozada, 2014; Moreyra et al., 2012) and landmark use when foraging (D'Adamo and Lozada, 2003; D'Adamo and Lozada, 2007; Lozada and D'Adamo, 2009; Lozada and D'Adamo, 2006). There are even fewer studies on the shape discrimination ability of wasps. Beier, (1984) found that German wasps could discriminate between different shapes on the base of their

degree of disruption, when presented on a horizontal plane near the feeder. Similar results were found by Jander et al. (1970) in a study conducted on *Dolichovespula saxonica* near the nest entrance. Lehrer and Campan, (2004) found that *Paravespula germanica* is able to discriminate between a variety of convex shapes irrespective of color and the contrast with the background. The present study is the first to test the ability of *Vespula germanica* to discriminate between two differently oriented patterns, when these are presented to the dorsal part of their eyes.

The results presented above show that the individuals of this species are able to distinguish between two dorsally presented patterns. By training the wasps to associate a transversal bar pattern with a food reward, we could show that, when confronted with a longitudinal bar pattern, they were still able to choose the trained pattern (transversally oriented). In a similar study on honeybees, Giger and Srinivasan showed in 1997 that the dorsal and ventral part of the eye is unable to detect pattern orientation. Furthermore, bees have also difficulty detecting colored targets, when using only the dorsal region of their eyes. Thus, when given the opportunity to use solely this region, the bees shift their body longitudinal axis from a horizontal position so that the stimulus impinges on the frontodorsal visual field.

From an ecological perspective, wasps and bees have different lifestyles. Honeybees feed solely on flower nectar and pollen which they collect mostly in open landscapes. However, this is not true for all bees. The nocturnal bee *Megalopta genalis* native to the rainforests of Central and South America is able to forage through dense vegetation at night. This species is able to use landmarks in low light conditions (10 times dimmer than starlight illumination). Furthermore it is also able to recognize and utilize landmarks placed directly above the nest entrance (Warrant et al., 2004). Thus, it is a strong possibility that this species may use its dorsal region of the eyes in pattern recognition.

Wasps also forage on carbohydrate sources. However, they also require animal protein for their larvae, which is obtained from carrion or from hunting smaller insects (Greene, 1991). As German wasps have a more complex lifestyle than honeybees, it would only be beneficial to be able to use the dorsal area of the eyes in pattern detection. This would not only help in the detection of potential prey, but it would also enable foragers to navigate in denser habitats, by using patterns in the canopy. As found in a previous study (D'Adamo and Lozada, 2007), the number of revisits was higher to a learned location when it was placed in a closed habitat. Their foraging strategy varies with the type of exploited resource. The learned location of a protein source, elicits more landing responses even when the food is displaced, while the opposite is true for carbohydrate resources (D'Adamo and Lozada, 2003). This strategy together with the ability to better remember a location when it is found in denser habitats, enables this species to not only hunt in habitats such as forests, but also scavenge for animal proteins which are often found here.

In our study we saw that the individuals which participated in all the days of the experiment had a decrease in performance on the second or third day of the experiment. These decreases were followed by an increase the following day. In order to find the cause for this, the effects of three environmental factors were analyzed: wind, precipitation and air temperature. Each of these factors could be responsible for this decrease, as it has been found that lower temperatures decrease the food load carried back by an individual on each trip (Jandt et al., 2010). Wind together with rain may also decrease the flying capabilities of the wasps. When a statistical analyses was performed on these factors, no correlation could be found. The differences in mean temperature were only 1°C and wind speed varied with approximately 1 m/s. Precipitation occurred only during the first and last day of the experiment.

Another possible explanation for this decrease exists. When no experiment occurred, the maze was covered with a black plastic bag to protect against rain and a feeder used during the training was left in front of it. Between day 1 and day 2 as well as day 2 and day 3, one and respectively two days with no experiment occurred. During these days, the foraging individuals could have learned to associate new landmarks with the new position of the feeder. It has been found that this species is able to learn the cues associated with a food source after only one visit (Moreyra et al., 2012). Although new cues are rapidly memorized, the landmarks associated with a previous food resource are not completely forgotten (D'Adamo and Lozada, 2009). The capacity to integrate new and old memory is the most likely explanation for the observed decrease in performance. Thus, during the days when no experiment occurred, the landmarks for the new location of the feeder were learned. However the

dorsal cues associated with the previous food reward position, inside the maze, were not completely forgotten. On the following experiment day, when the maze was uncovered and used, the foragers were able to find the feeder once more, even though with a slightly lower success rate. It should be noted that individual variations exist as individuals 11 and 97 presented a decrease in performance during day 2. For individual 75 two days with no experiment were needed, prior to day 3, for a decrease in performance to occur. Because of these days in which performance decreased, no statistical correlation could be found between time and performance. However, an increase in performance did occur with time. This shows that improvement of the memorized landmarks associated with food occurs with passing time.

In conclusion, our study proves the ability of *Vespa germanica* to detect and use dorsally presented cues, thus enabling it to navigate and forage through dense vegetation. It seems that the capability of the dorsal area of the eyes, is not family specific but rather habitat linked. Thus species which live in complex habitats, or have a complex lifestyle, may have developed eyes with more proficient dorsal areas. This together with advanced cognitive abilities and a flexible response to changing environmental cues, enables the German wasps to successfully colonize new habitats. This highly prolific species is unfortunately a successful invader in other parts of the world.

Further studies will be necessary to see how accurate the ability to detect pattern orientation is, when the patterns are oriented other than transversally and longitudinally. It is still unknown if more complex patterns similar to those produced by canopy gaps could be used by this species in locating a food source. Another interesting question is if dorsally presented patterns of polarized light are

sufficient to guide foragers to a food source, when other landmarks are absent.

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