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ORIGINAL ARTICLE

How behavioral plasticity enables foraging under changing environmental conditions in the social wasp *Vespula germanica* (Hymenoptera: Vespidae)

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ABSTRACT. The foraging strategy at abundant resources of the social wasp *Vespula germanica* includes scanning in the direction of the nest while memorizing resource-specific landmarks and contextual cues. In the present study, we sought to explore wasps' behavioral

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plasticity on foraging trips to resources whose location and composition changed after a single visit. We evaluated how contextual modifications of food displacement and replacements 60 cm apart from the original site, affect re-orientation for re-finding previously memorized food resources. The results showed that wasps detected and collected the resource faster when more changes were introduced on the following visit. If returning foragers discovered several modifications on both the location and the kind of resource, they collected food more rapidly from the displaced dish, than if only a single parameter in the environment had been changed. These findings illustrate the grade of behavioral plasticity in *V. germanica* while foraging on abundant resources, which may contribute to the understanding of the prodigious invasive success of this species in anthropized environments.

Key words behavioral plasticity; environmental conditions; foraging; invasive insects; learning; social wasps

Introduction

Living beings are constantly facing impermanent milieus; experience is always changing and depends on particular contextual situations (Varela, 2000). The invasive social wasp *Vespula germanica* displays complex behavioral processes while collecting food in ever-changing anthropized environments (D'Adamo & Lozada, 2011; Lozada & D'Adamo, 2011, 2014; Moreyra *et al.*, 2012, 2016; Moreyra & Lozada, 2018; Pietrantuono *et al.*, 2018). As a social insect, when a forager wasp finds an abundant food source, it makes numerous trips between the resource and the nest where larvae are fed (Beugnon *et al.*, 2001; Toh & Okamura, 2003; Lozada & D'Adamo, 2014). During this re-orientation behavior, individual wasps learn to find objects of interest again, such as food itself, landmarks or other contextual cues, in order to identify the exact place where the resource is located (e.g., Zeil *et al.*, 1996; Collett & Zeil, 1998, 2018; Raveret Richter, 2000).

Previous research demonstrated that *V. germanica* exhibits great behavioral plasticity in relation to this relocating behavior (D'Adamo & Lozada, 2003, 2008, 2011; Lozada & D'Adamo, 2011; Moreyra *et al.*, 2006, 2012, 2014, 2017; Moreyra & Lozada, 2018). Such learning flexibility allows them to face new foraging challenges while collecting resources (Lozada & D'Adamo 2011; D'Adamo & Lozada 2014; Lozada & D'Adamo 2014). *Vespula germanica* wasps have an opportunistic and wide omnivorous diet, which includes garbage, carrion, insects, nectar, fruit and honeydew (e.g., Richter, 2000; Moreyra *et al*., 2016). Changes in food position may be a recurrent situation when they forage on un-depleted food sources in human settings. In anthropic environments, such as barbecues, picnics or campsites, food and contextual cues (e.g., plates, cutlery, bottles, etc.) suffer continuous modifications in their location as well as variations in food type (e.g., Lozada & D'Adamo, 2014). Moreover, it is frequently observed that the position of carrion can change, given that large animals such as dogs, cats or birds of prey displace or completely remove their resources, thereby altering the contextual scenarios on the wasps' successive foraging visits (e.g., Moreyra & Lozada, 2018). Thus, these different scenarios bring about diverse opportunities for novel learning abilities which require the need to release previous appetitive associations.

Several social insects such as ants, bees, wasps and hornets, can also deal with contextual modifications when gathering resources during several trips to the nest. Although numerous investigations have studied social insects' responses when contextual cues are modified (e.g., Graham & Cheng, 2009; Wilson-Rankin, 2015; Freas & Cheng, 2017, 2018; Collett & Zeil, 2018; Freas & Spetch, 2019), to our knowledge, little research has evaluated how these species respond to modifications of food location (e.g., Toh & Okamura, 2003; Graham *et al.*, 2007; Cheng *et al.*, 2012; Czaczkes & Heinze, 2015). It has been shown that even a first collecting visit can impact on subsequent foraging performance by hindering the perception of food in a novel site (e.g., Toh & Okamura, 2003; Durier *et al.*, 2004; Graham *et al.*, 2007; Lozada & D'Adamo, 2014; Moreyra & Lozada, 2018). For example, in *Vespa mandarinia*, it has been found that when the resource is displaced or removed from the learned location, hornets spend some time searching for food in the previously collected site (Toh & Okamura, 2003). Moreover, after a single collecting visit, the ant *Lasius niger* deposits pheromones on the new food site which was different from the original location (Czaczkes & Heinze, 2015). Diverse studies in *V. germanica* have shown that foragers always return to the exact place where food was previously located; that is, wasps fly directly to the resource, without displaying any searching behavior over the array (e.g., D'Adamo & Lozada, 2011, 2014; Lozada & D'Adamo, 2014; Moreyra *et al.*, 2012, 2016; Moreyra & Lozada, 2018). The fact that wasps are able to memorize food locations having visited the site only once was also observed when food was completely removed (Lozada & D'Adamo, 2006, 2011) and even when it was displaced 30 cm away from the learned site (Moreyra & Lozada, 2018). Interestingly, a recent study revealed that when two dishes with different amounts of meat were simultaneously offered, wasps preferred to collect food from the dish with more quantity. However, when the position of the dishes was switched after the first collecting visit, wasps chose the dish placed in the previously learned location even though it had less amount of carrion (Moreyra & Lozada, 2018). Another research demonstrated that after several random changes of resource location, wasps spent more time searching for food in the previously learned site than in the subsequent displaced ones. This suggests that foragers learn about changes in food location (Moreyra *et al.*, 2016). Furthermore, D'Adamo and Lozada (2014) found that contextual changes on a second visit facilitated the detection of the new food position. That is, when food displacement is accompanied by changes in visual cues (color) wasps found the resource at the novel site faster than if those cues had remained unaltered. This mismatch favored the release of their previous past experience related to food location (D'Adamo & Lozada, 2014). In line with this, we hypothesize that these memory processes will be involved in *V. germanica* relocating behavior when other changes, such as food type, will be encountered in subsequent visits. Since these wasps coexist with humans who are constantly changing food location in outdoor scenarios, it seems plausible that a certain resource could be replaced by another one. Therefore, these variations might be a frequent experience in foraging wasps.

In the present work we analyzed whether different changes in food type and location contributed to finding the new food site more rapidly than if no modifications were conducted. We sought to explore how foragers respond to food displacement along with the replacement of the kind of resource collected on their first visit. We assessed wasps' behavior under four different conditions by varying the number of contextual changes introduced on the second visit. That is, we evaluated wasps' response when food was displaced 60 cm away from the original site and replaced by a novel resource in the previously learned location; when only food was displaced; when only food was replaced and when food remained in the same location on both visits. We expect to find that wasps returning from the nest to the food site will release past experience more rapidly when more environmental changes are encountered.

Materials and methods

The experiments were carried out in San Carlos de Bariloche (41 º S, 71 º W), Río Negro, Argentina, conducted under similar weather conditions (sunny, calm and a temperature range of 22 to 27ºC), during February through April 2017. Each treatment was performed at a different site, separated from each other by 200 m. We worked with a single re-identifiable *V. germanica* wasp per experiment and site. That is, each individual wasp was only allowed to visit its original treatment place twice. Upon a further return, this target wasp was removed. When another novel wasp randomly arrived at the treatment site, it was tagged with a colored dot, and its behavior was analyzed as it returned to this place again. In all treatments we set 4 yellow cylinders (2 cm in diameter and a height of 60 cm) on the ground, forming a square (i.e., 30 cm between cylinders). On the right and left sides of this square (i.e., opposite each other) we placed a white plastic dish of 7 cm in diameter; one of which contained 20 g of fresh minced meat (M) as it is an appropriate way to offer food, since wasps can handle it, collect a tiny piece and take it back to the nest (e.g., Lozada & D'Adamo, 2014) (Fig. 1A). On the first visit, when a forager wasp landed on the dish placed at site 1 (S1) it was marked with a washable ink dot on the abdomen, for individual identification. This marking procedure did not disturb the wasps. We worked with a single individual wasp per treatment; any other forager landing on the resource was removed; i.e. only one forager was allowed to collect food from the dish. Foragers were randomly assigned to each treatment and food position was also changed at random throughout the experiments. Wasp behavior was recorded by one researcher always sitting at a distance of 0.5 m from the experimental setting, as conducted in previous studies (e.g., D'Adamo & Lozada, 2014; Moreyra & Lozada, 2018). In all Treatments, we recorded the time taken to land and collect food either from the previously learned site (S1) or from the novel resource (S2). This time started when wasps hovered over the array and ended when wasps landed and collected food from the dish. If wasps took more than 3 minutes upon their return (i.e., cut-off period), this behavior was considered as a non-collecting episode.

Four treatments were conducted by recording wasps' behavior on the second visit, i.e., the testing phase, as explained below.

Treatment 1- Resource displacement and replacement (D & R)

On the first visit, the target wasp collected meat from a dish located in a certain position (S1). After the first collecting experience, food was displaced 60 cm in the opposite direction (S2), and a novel dish with a different resource was located in the previously learned site (the original one). For example, in the first collecting experience the dish with meat (M) was located on the left side of the yellow cylinders. When the target wasp collected food and flew back to the nest, the dish with meat was displaced to the right and a new dish with 7 : 3 honey and water (H) was placed at the original location (Fig. 1B). Therefore, after their first collecting visit, wasps encountered a greater number of environmental changes (resource displacement and replacement). $N = 25$.

Treatment 2- Resource displacement (D)

In this treatment, food was displaced from the original learned site (S1). For example, on its first foraging visit, the target wasp collected meat located on the left side of the experimental setting; on its second visit, the dish with meat was displaced 60 cm to the right of the previously learned site (S2), and an empty dish was placed in S1 (Fig 1B). N=23.

Treatment 3- Resource replacement (R)

In their first experience, wasps collected food from a dish that contained meat (M) (S1). After that, it was replaced by another one containing a different resource. That is, on the first collecting visit, the dish with meat was located on the left side of the cylinders; after a single collecting experience, the dish with meat was replaced by a dish containing 7 : 3 honey and water (H) (S1), and the dish located on the right always remained empty (S2) (Fig. 1B). In this experiment, target wasps found a novel resource in the previously learned location. N = 25.

Treatment 4- Resource remained in the same location (Re)

In this treatment, the meat dish remained unchanged throughout the two consecutive visits (S1). That is, on their second visit, the forager wasp encountered the same scenario (Fig 1B). N = 25.

Data analysis

Given that data followed a non-normal distribution, non-parametric Kruskal-Wallis Tests were performed to compare searching time, and Mann-Whitney tests to analyze pair comparisons.

Results

The majority of returning wasps (88%) encountered the displaced resource when the meat dish was moved to the opposite site and the original food type in site one was replaced by honey (Treatment 1, D & R) as observed in Figure 2. Interestingly, only 12% chose to collect honey from the previously learned site (i.e., S1). In this Treatment, wasps spent 18.24 sec

(SE: ±3.65, n = 25) to collect the resource (see Fig. 3). In Treatment 2 (D), when the meat was moved 60 cm away from the original site (S2), all the wasps landed on it after 25.6 sec (SE: ±5.33, n = 23). In Treatment 3 (R), when the dish with meat was replaced by honey (S1), only 60% of wasps collected it and 40% flew away without gathering any resources at all throughout the cut-off period of 3 minutes. Wasps took 102.9 sec (SE: ±20.6, n = 25) to land and collect honey from the dish. In Treatment 4 (Re), when the dish with meat remained in the same location (S1), all foragers flew directly towards the food and landed on it immediately, i.e., they detected it either visually and/or olfactorally within an odor gradient (Fig. 2).

Significant differences were found in all treatments when we compared the time taken by wasps to land and collect food on the second visit ($\chi^2_{(98, 3)} = 40.4$, $P < 0.05$) (Fig. 3). Paired comparisons between Treatment 1 (D & R) and Treatment 2 (D) demonstrated that wasps spent less time to collect the resource when the meat dish was displaced and replaced by honey than when the dish with meat was only displaced (S2) ($Z = -2.16$, $n_{1,2} = 25, 23$; $P < 0.05$). Thus, at feeding site (S1) when the meat dish was replaced by honey, it favored the discovery of the dish with meat at the new site (S2) faster than when the original dish remained empty (S1), since wasps hovered over the previously learned location for a longer period of time. The paired comparison between Treatment 1 (D & R) and Treatment 3 (R), revealed that the time taken for wasps to collect the resource was less when the dish with food was displaced and replaced than when only one modification was performed, i.e., when the resource remained at the original site but was replaced by honey ($Z = -4.19$, $n_{1,2} = 25, 25$; $P < 0.05$). The paired comparison between Treatment 1 (D & R) and Treatment 4 (Re), showed that the time taken was greater when the dish with meat was displaced (at S2) and replaced by honey (at S1) than when the meat remained at the same location (S1) throughout both consecutive visits (Z = 6.48, $n_{1,2}$ = 25, 25; P < 0.05). Interestingly, a comparison between Treatment 2 (D) and Treatment 3 (R) revealed that wasps spent less time before landing on a resource when the dish with meat was displaced to a novel location (S2) (D) than when the dish with meat was replaced by honey at S1 (R) (Z = −3.51, $n_{1,2}$ = 23, 25; P < 0.05). Moreover, a further comparison between Treatment 2 (D) and Treatment 4 (Re) showed that wasps took longer to collect meat when the dish was displaced at S2 (D) than when the dish with meat remained at the original site (S1) (Re) (Z = 6.40, $n_{1,2}$ = 23, 25; P< 0.05). Furthermore, when comparing Treatment 3 (R) and 4 (Re), we found that wasps spent more time searching the resource when the dish with meat was replaced by honey at S1 (R), than when the meat was left unchanged at the same location throughout the two consecutive visits (Re) (Z = 6.50, $n_{1,2}$ = 25, 25; P < 0.05) (Fig. 3).

Discussion

The current study demonstrates that wasps can release a previously learned experience faster when non-matching conditions are presented on a second foraging visit, i.e., when additional environmental changes are introduced. We observed that when *V. germanica* wasps returned to the foraging site after the first collecting experience and found modifications with respect to location and type of resource (D & R), they detected the new food site more rapidly than when only one environmental change was performed. That is, on their second visit, when the food was displaced and the kind of resource was replaced, the time taken to collect food was less than when fewer changes were carried out. These findings suggest that foragers' relocating behavior is conditioned by a previous experience (i.e. food location on the first collecting trip). Wasps can let go of this recent past memory more easily, when additional contextual cues do not match those encountered on their second visit. New learning processes seem to be facilitated when a different scenario is met, thus enabling a greater behavioral plasticity when relocating resources.

The present findings are in line with a previous study which revealed that wasps can find a novel food location more quickly when the color of the array (i.e., cylinders) is modified on their second visit. That is, these environmental changes favored the discovery of the displaced food, allowing for the detection of an unexpected modification of the previously learned position (D'Adamo & Lozada, 2014). In that experiment, returning foragers found that visual and spatial cues did not coincide with those experienced on their first collecting visit. This mismatch could have prompted the release of any previous associations related to food location. In contrast, in the current research, instead of changing the color of the cylinders, we changed the location of the meat dish and we replaced the type of resource (honey) at the original site. The replacement of meat by honey on the second visit, introduced a novel situation, since new odor and visual cues were encountered by returning wasps. Therefore, these additional changes could have prompted the search for food at a different site from the previously learned one as in D'Adamo and Lozada (2014), a result that ties in well with the fact that *V. germanica* wasps forage in recreational outdoor settings in which food items go through constant modifications, either in their position or in their resource type.

Earlier studies have shown that *V. germanica* tends to learn several behavioral paradigms after only one foraging experience (e.g., D'Adamo & Lozada, 2011; Lozada & D'Adamo, 2014; Moreyra *et al.*, 2016). For instance, after food was removed, returning wasps remembered the exact site where food was originally placed on their first visit (Lozada & D'Adamo, 2006, 2011). A similar pattern is observed even when food is displaced at a short distance (such as 30 cm) away from the previously learned site (Moreyra & Lozada, 2018). Since wasps take, on average, about 8.4 min (SE: ±0.78, n = 90) to return to the previously rewarded site (Moreyra *et al.*, 2014), it is highly improbable that any trails of mince meat odor remained at the experimental area after this lapse of time; however, it is desirable that future studies confirm this hypothesis. Interestingly, it has also been found that wasps collect food from the previously learned location even when, on the second collecting visit, a dish with a greater amount of meat is placed nearby (Moreyra & Lozada, 2018). Previous investigations in other hymenopteran species indicate that foragers also learn the location of food after a single experience (e.g., Menzel, 1993, 1999; Graham *et al.*, 2007; Czaczkes & Heinze, 2015; Freas & Spetch, 2019). Moreover, it has been shown how a single past experience can condition food search causing delayed perception of a known resource at a novel site (Toh & Okamura, 2003; Durier *et al.*, 2004; Graham *et al.*, 2007; Cheng *et al.*, 2012). A previous work revealed that when wood ants (*Formica rufa*) collected food from a feeder presented in a certain location and was subsequently displaced ants gradually modified their trail to the novel site (Graham *et al.*, 2007). Interestingly, in other studies it has been observed that when changes are presented successively on several returns, wasps tend to reduce the time taken to discover a new food location (Moreyra *et al.*, 2016).

In sum, the current findings contribute to the demonstration of how wasps can learn about changes in both visual and spatial cues as well as in the type of resource throughout successive foraging visits. This highlights the great behavioral plasticity of *V. germanica* species, which might favor invasive processes in anthropized environments. The present work shows that returning foragers can cope with varying situations while letting go of past memories. It also illustrates how wasps' decision-making under outdoor disturbed scenarios is malleable. Thus, our investigation, conducted under open field conditions which corresponds to *V. germanica* invasive wasps' daily experience, provides additional evidence of their cognitive flexibility which, we hypothesize, could be related to its invasive success worldwide (Lester & Beggs, 2018). Nevertheless, further studies, carried out under this species' outdoor foraging environments, would be needed to reconfirm our prediction. Moreover, it would be interesting to evaluate whether the behavioral plasticity observed in the present research is also found when other types of resources are offered in the current experimental setting.

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Disclosure

Mariana Lozada and Sabrina Moreyra have no involvement in anything that could bias their work. Their research does not respond to any external interests other than looking for authentic answers to the questions they investigate.

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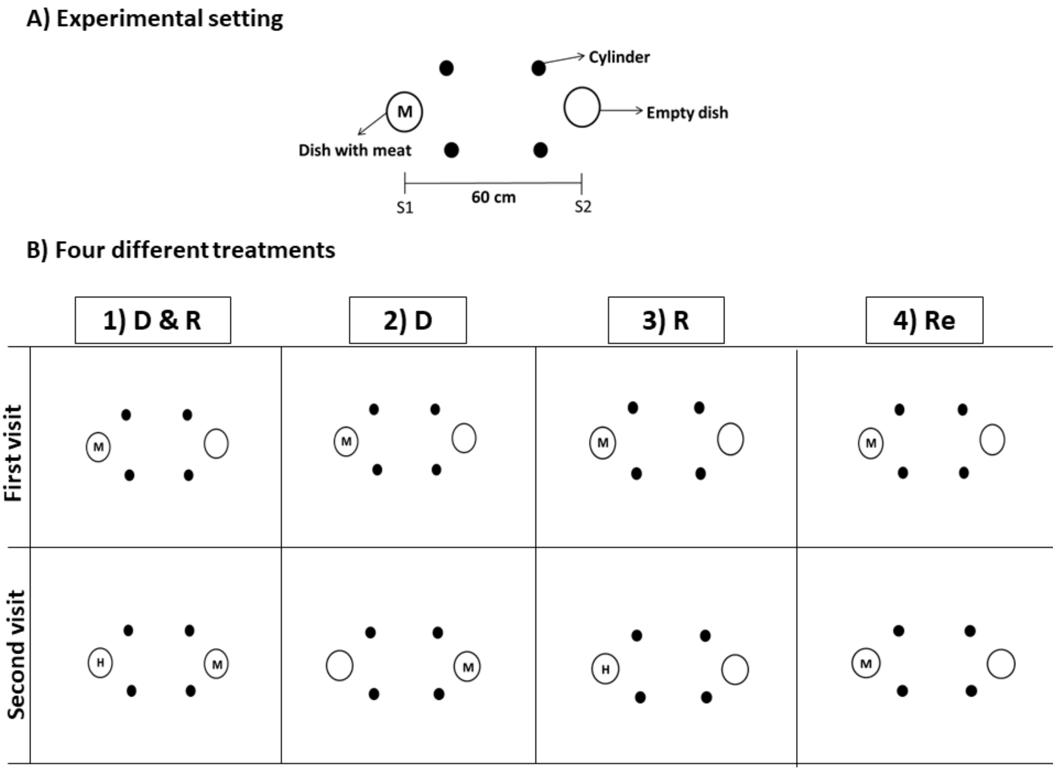

Figure 1 A) Diagram of the experimental setting, consisting of four yellow cylinders and two dishes, one of which contained food (M=meat). S1 (site 1) indicates food position on the first visit (original feeding location) and S2 (site 2) indicates food position on the second visit, i.e., a new location 60 cm diametrically opposite the original one. B) Diagram of the four treatments, after the first visit: 1) The food was displaced and replaced by a novel resource (H=honey) (D & R); 2) Displaced meat dish (D); 3) Meat dish replaced by honey (R); and 4) Meat dish remained at the same site (Re).

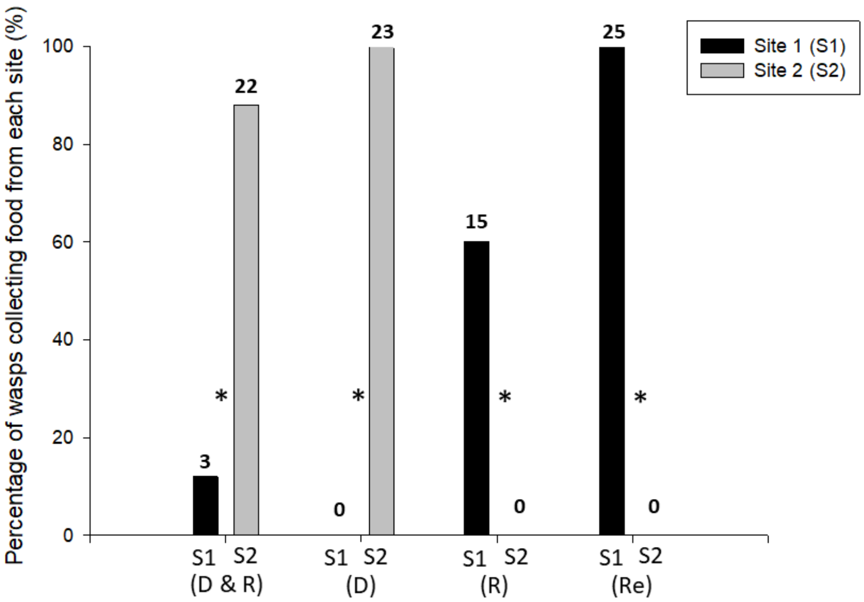

Figure 2 Percentage of wasps that started collecting food from either site (S1 or S2) on the second visit. Numbers above the bars indicate the absolute number of wasps at each site. Asterisks denote significant differences between both sites.

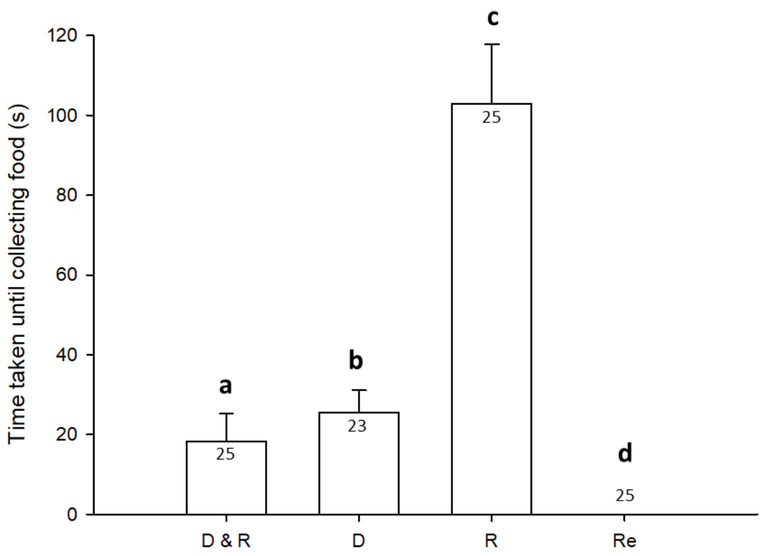

Figure 3 Time taken for wasps to start collecting food on their second visit, in each treatment. Letters on top of bars denote significant differences between treatments. Numbers inside each bar indicate the total number of wasps tested in each treatment.

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