Sociobiology 62(1): 99-104 (March, 2015) DOI: 10.13102/sociobiology.v62i1.99-104

Sociobiology

An international journal on social insects

RESEARCH ARTICLE - WASPS

Effect of Magnetic Field on the Foraging Rhythm and Behavior of the Swarm-founding Paper Wasp *Polybia paulista* Ihering (Hymenoptera: Vespidae)

MGC Pereira-Bomfim[1]; WF Antonialli-Junior[1,2] & D Acosta-Avalos[3]

1 - Universidade Federal da Grande Dourados, Dourados, MS, Brazil

2 - Universidade Estadual de Mato Grosso do Sul, Dourados, MS, Brazil

3 - Centro Brasileiro de Pesquisas Físicas - CBPF, Rio de Janeiro, RJ, Brazil

Article History

Edited by
Gilberto M. M. Santos, UEFS, Brazil
Received 10 July 2014
Initial acceptance 25 October 2014
Final acceptance 30 November 2014

Keywords
Social wasp; foraging; homing; Polistinae; Epiponini

Corresponding author
Maria da Graça C. Pereira-Bomfim
Programa de Pós-graduação em Entomologia e Conservação da Biodiversidade
Universidade Federal da Grande Dourados
Faculdade de Ciências Biológicas e Ambientais
241, 79804-970, Dourados,
Mato Grosso do Sul, Brazil
E-Mail: airambio@yahoo.com.br

Abstract

The geomagnetic field can be used by insects for navigation and orientation, through different magnetoreception mechanisms. Magnetic sensitivity is very well documented in honeybees, ants and termites, but few studies have examined this capability in social wasps. The present study analyzed the magnetic sensitivity of the paper wasp *Polybia paulista*. The wasps' behavior was analyzed in the normal geomagnetic field and in the presence of external magnetic fields generated by permanent magnets or by Helmholtz coils. The frequency of foraging flights was measured in both conditions, and the behavior of the individuals on the nest surface was also analyzed. The magnetic field from the permanent magnet produced an increase in the frequency of departing foraging flights, and also the wasps grouped together on the nest surface in front of the magnet. The electromagnetic field created by the Helmholtz coils also increased foraging flights, but individuals did not show grouping behavior. This Helmholtz electromagnetic field induced wasp workers to perform "learning flights". These results show for the first time that *Polybia paulista* wasps are sensitive to magnetic fields, including it in the list of animal models to study magnetoreception and magnetic sensitivity.

Introduction

Homing and foraging abilities are of fundamental importance in social insects, because these activities are related to the search for food and/or material to construct their nest (Spradbery, 1973). For successful foraging and homing, social insects must have good perception of environmental signals. This environmental perception allows animals to navigate and orient in space (Mouritsen, 2001). Multiple modalities are used in spatial orientation: vision, smell, and hearing, and detection of electric, gravitational and magnetic fields (Mouritsen, 2001; Wickelgren, 1996).

The magnetic field of the Earth provides animals with directional and positional information, even in darkness (Wiltschko & Wiltschko, 2006). Many animals detect and use the geomagnetic field for orientation and navigation (Wiltschko & Wiltschko, 2006). In the case of insects, the social insects are the best studied in this respect. Honeybees *Apis mellifera* are highly sensitive to magnetic fields (Kirschvink et al., 1997; Walker & Bitterman, 1989).

There are two accepted models to explain magnetoreception in animals: the ferromagnetic hypothesis and the radical pair mechanism. The ferromagnetic hypothesis assumes that intracellular magnetic nanoparticles are responsible for transducing magnetic fields to biological signals through detection of magnetic torques at cellular mechanoreceptors (Walker, 2008). The radical pair mechanism or light-dependent magnetoreception assumes that chemical reactions associated with the absorption of light can be modified by the presence of magnetic fields (Ritz et al., 2010). In the case of social insects, only the ferromagnetic hypothesis has been explored, but the radical pair mechanism cannot be discarded. Biomineralized magnetic material has been found in bees

Open access journal: http://periodicos.uefs.br/ojs/index.php/sociobiology
ISSN: 0361-6525

(Desoil et al., 2005) and ants (Acosta-Avalos et al., 1999; Esquivel et al., 1999; Slowick & Thorvilson, 1996; Slowick et al., 1997), supporting the ferromagnetic hypothesis. Magnetic material is deposited in hornet combs (Stokroos et al., 2001).

Several studies have demonstrated the existence of magnetic sensitivity in bees (Frier *et al*. 1996; Lindauer & Martin, 1972; Wiltschko & Wiltschko, 1995), ants (Acosta-Avalos et al., 2001; Anderson & Vander Meer, 1993; Banks & Srygley, 2003; Çamlitepe & Stradling, 1995; Çamlitepe et al., 2005; Jander & Jander, 1998; Kermarrec, 1981; Klotz et al., 1997; Riveros & Srygley, 2008; Rosengren & Fortelius, 1986; Sandoval et al., 2012). As far as we know, the only studies of magnetic sensitivity in wasps (Vespidae) are in the subfamily Vespinae (hornets; Kisliuk & Ishay, 1977; 1979). Comb building in *Vespa orientalis* is modified when the local magnetic field is increased by more than 60 times the corresponding local intensity; treated hornets built the nest comb with irregular cells, starting in the region of high intensity and continuing to construct in the direction of decreasing field intensity. This field intensity was lethal to both adults and larvae (Kisliuk & Ishay, 1977). In a different experiment, the same authors showed that the vertical component of the local geomagnetic field influences the wasps' building orientation (Kisliuk & Ishay, 1979). These studies provided evidence that social wasps are sensitive to changes in the magnetic field. The present study investigated, for the first time, the magnetic sensitivity of social paper wasps (subfamily Polistinae).

We tested magnetic sensitivity in the swarm-founding paper wasp *Polybia paulista,* through analysis of the effect of external magnetic fields on foraging and clustering behavior.

Material and Methods

Eighteen colonies of *Polybia paulista* (Ihering, 1896) were used in the experiment; nine colonies were used as controls, and nine colonies were subjected to experimental external magnetic fields. The colonies were located in Batayporã, Mato Grosso do Sul, Brazil (22º 17' 96''S, 53º 15' 77''W) and were analyzed during the period from March 2012 to January 2014. The geomagnetic field parameters in this region are: inclination -29.3°, declination -17.4°, horizontal intensity H = 0.19 Oe, vertical component Z = -0.11 Oe and total intensity F = 0.22 Oe (1 Oe = 100 uT. Oe is the acronym of Oersted).

To evaluate the change in foraging rhythm and colony behavior, the frequency of departing and homeward flights was measured, as well as the behavioral response of worker wasps located on the outer surface of the nest.

To guarantee homogeneous experimental conditions in all the colonies, they were observed in the post-emergence stage (Jeanne, 1972), because this stage has the largest number of individuals involved in foraging activities. Each experimental session was conducted in daytime during the period of peak wasp activity, between 09:00 and 15:00 hs (Andrade & Prezoto, 2001; Elisei et al., 2005; Elpino-Campos et al., 2007; Lima & Prezoto, 2003).

The foraging rhythm was evaluated by observing the frequency of departing flights and homeward flights by individual wasps from the nest. The behavior of the individuals was observed *in situ*, in a sample for each colony, divided into two sessions of 15 minutes each. The first session (Period A) corresponds to the colony in the presence of the normal geomagnetic field, without any altered magnetic field (AMF). The second session (Period B) corresponds to the colony in the presence of the normal geomagnetic field plus an AMF. We sampled the behavior of wasps present on the outer surface of the nest during the trials, and observed if they executed grouping and "learning flights" (*"ad libitum" sensu* Altmann, 1974). Short time intervals in each session were used, to minimize the effects of changes in other abiotic factors that might have influenced the results.

The local geomagnetic field was altered in two different ways. In four colonies used for the magnetic experiments, the magnetic field was altered using permanent magnets, fixed in the west side and suspended with a stick placed 10 cm away from the comb, generating a magnetic field with dipolar characteristics. The total intensity was 5.2 (± 3.1) Oe being the higher value 13.9 Oe and the lower 1.5 Oe. The component with higher values were in the East-West direction being higher near to the magnet and with average value of 5.1 (± 2.9) Oe, the component in the North-South direction showed a dipolar character being negative in the North side and positive in the South side (higher value of ±4.6 Oe and lower value of ±0.3 Oe, average value 0.07 (±1.5) Oe). The vertical component had their values among -2.0 Oe and +0.1 Oe (average value 0.34 (± 0.56) Oe). The average inclination was -1.6°±4.4°. The magnet generates a strong static magnetic field in the region of the comb and also a gradient in the East-West direction (about 0.9 Oe/cm).

In the other five experimental colonies, the magnetic field was altered using Helmholtz coils, following an adaptation of Gonçalves et al. (2009). The apparatus consisted of a pair of Helmholtz coils 30 cm in diameter oriented in the East-West direction, each coil consisting of 46 spirals of Cu wire 15 AWG (cross section 1.5 mm^2, resistance 0.01 Ω), polished and wound in a 2cm-wide band. The pair of coils was connected to a digital electrical source, that provided a current of 1.16 A and a constant voltage of 15 V, generating a magnetic field almost uniform among the coils (total intensity 5.4 ± 0.8 Oe). As can be seen, the variability in the intensity is lower compared with the magnet field. The same uniformity is observed in the West-East direction (average value of 5.2 ± 0.8 Oe), the North-South direction (average value of 1.0 ± 0.9 Oe) and the vertical component (average value 0.7 ± 0.9 Oe). The average inclination was -6.9°±4.4°. We positioned each coil 2 cm from the comb edge (Fig 1), and the comb edges were about 5.5 cm from the middle of the comb. In the middle of the comb the average magnetic field from the coils and the magnet was similar but in the case of the coils there was not a magnetic gradient. In this configuration the

Helmholtz coil generated electric and magnetic fields at the surface of the comb. Each coil is an equipotential with difference of electric potential of 15 V meaning that between both coils there was an electric field of about 100 V/m, that is similar to the atmospheric electric field (Clarke et al., 2013). The magnetic field was monitored using a single axis magnetometer (GlobalMag, model TLMP-Hall-050).

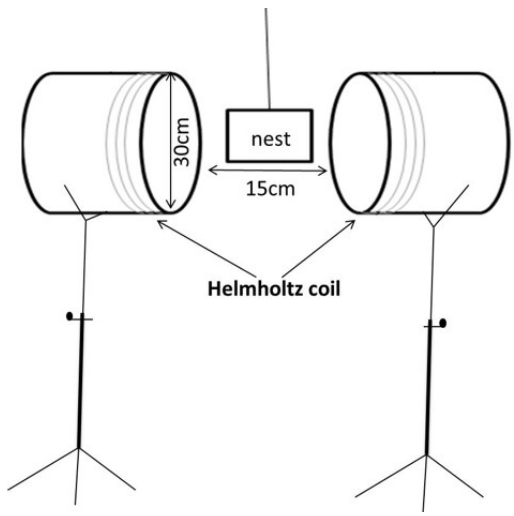

Fig 1. Representation of the Helmholtz coil apparatus with the variable-length pole, permitting the generation of altered magnetic field, in the region of the wasp nest.

To check only the effect of the AMF and to exclude the effect of physical objects approaching the colonies, control observations were made for nine other colonies. Four of them were studied using a sham magnet, consisting of a plastic object similar in color, shape and size to the permanent magnet. The sham magnet was positioned similarly to the permanent magnet, and the wasps' behavioral response was observed during two 15-minute sessions, session 1 before the sham magnet was positioned in front of the colony, and session 2 with the sham magnet in front of the colony. The control experiments in the other five colonies were done with the pair of coils positioned as above, but in this case the digital electrical power source was turned off, and two 15-minute sessions were conducted as described above.

To detect possible differences between the categories, the samples were grouped and compared using the Mann-Whitney test, with a 5% significance level. We compared the frequencies of departing and homeward flights measured in the experiments.

Results and Discussion

The total frequency of departing flights from the four colonies with the permanent magnet was 193 during session A and 235 during session B. In the control experiment, the frequency of departing flights was 84 in session 1 and 105 in session 2. The comparison between the experimental results permits the conclusion that the increase in the intensity of the local magnetic field may have stimulated the foraging activity in the colony (Fig 2).

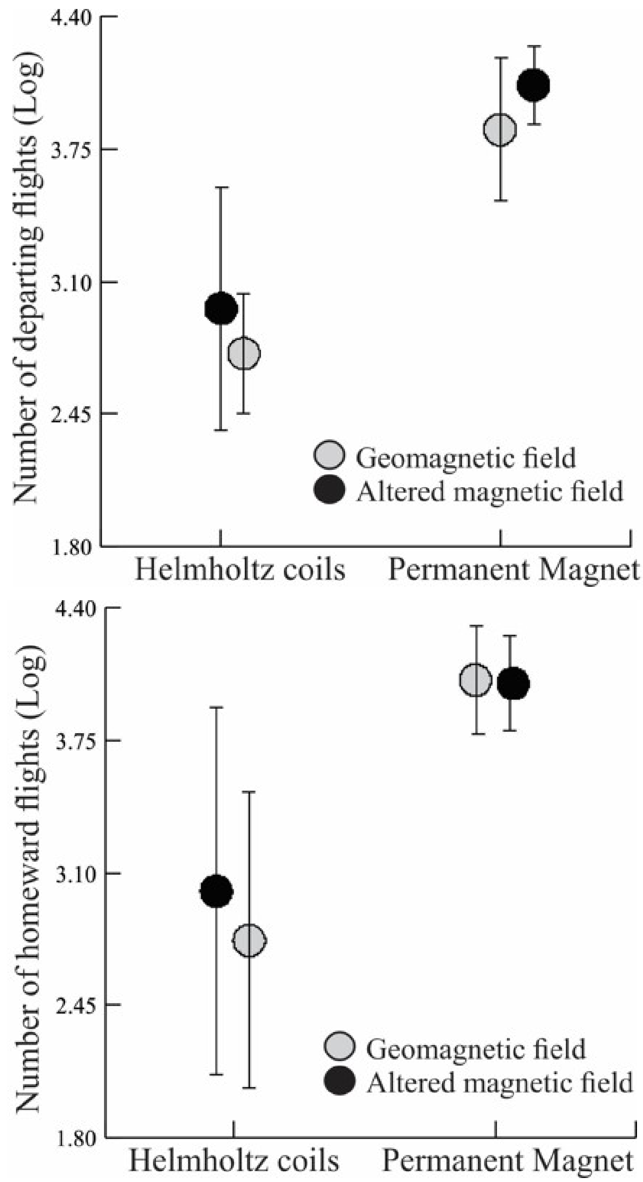

Fig 2. Mann-Whitney test of the number of departing flights and number of homeward flights performed by workers of the colonies of *Polybia paulista*, during the experiments with the Helmholtz coils (geomagnetic field H=6,00; p=0,014 and altered magnetic field H=6,06; p=0,014) and permanent magnet (geomagnetic field H=6,00; p=0,014 and altered magnetic field H=6,21; p=0,013).

In the same group of four experimental colonies, the frequency of homeward flights was 233 in session A and 228 in session B.

During session B, workers formed clusters on the outer surface of the nest (Fig 3). The workers oriented themselves with the head and antenna pointing toward the perturbation source. Kudô et al. (2003) observed that wasps respond to any potential source of threat by grouping outside the nest, orienting their heads and antenna toward the perturbation source. It is possible that this behavior is a defense strategy, perhaps indicating that the intensity of the magnetic field used in these experiments was interpreted as a source of threat. During session B the wasps remained still or moved only the antenna or the first pair of legs, and also walked randomly over the surface of the nest. This grouping behavior was not observed in the control experiments. Therefore, the behavior can be interpreted as a result of the increase in the local magnetic field.

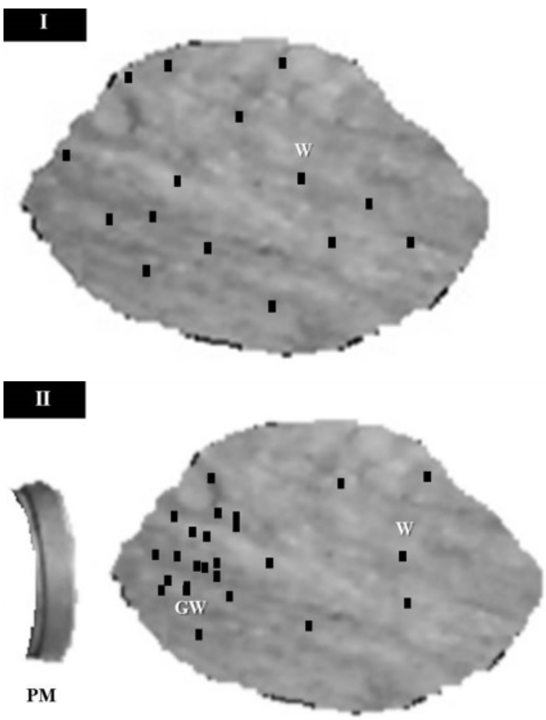

Fig 3. Representation of the grouping behavior of *Polybia paulista* workers (GW) on the nest surface during session A (I), before the application of the altered magnetic field with the permanent magnet (PM); and during session B (II), with the permanent magnet in place. GW – Grouping of Wasps; W- Wasp.

For the five colonies studied with the Helmholtz coils, the frequency of departing flights was 80 in session A and 108 in session B. The frequency of homeward flights was 93 in session A and 125 in session B. In the experiments with the five control colonies, the frequency of departing flights was 127 in session 1 and 111 in session 2, and the frequency of control homeward flights was 125 in session 1 and 134 in session 2. These results showed that the magnetic and electric field modified by the Helmholtz coil also altered the wasps' foraging behavior (Fig 2).

In these experiments, the grouping behavior described in the case of the permanent magnet was not observed, suggesting that the two sources of magnetic fields are perceived in different ways.

The dissimilar effects of an oscillating and a static magnetic field was also observed by Martin et al. (1989), who examined their influence on the execution of the honeybee "waggle dance". They found that the rhythm of the dance was slower in the oscillating field and increased in the static magnetic field.

In our experiments, the magnetic and electric fields generated by the Helmholtz coils induced the workers to perform "learning flights" as a response to the presence of this altered field. During the learning flights the wasps acquire landmark information examining the location to which it will return (Zeil et al., 1996). These flights were observed only during session B, with a mean number of 7.8 ± 2.6 (Fig 4).

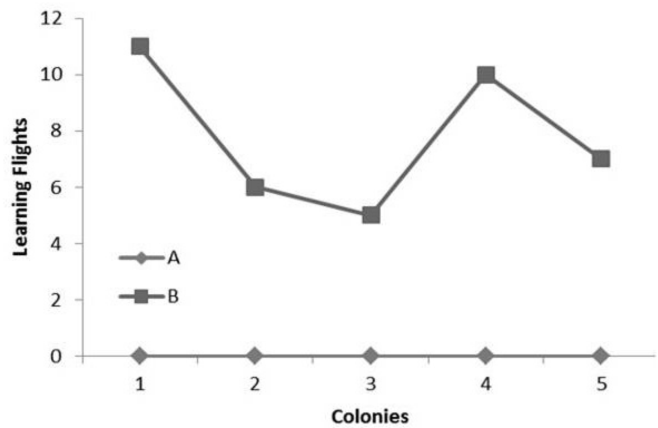

Fig 4. Number of "learning flights" performed by workers of the five colonies of *Polybia paulista*, during the experiments with the Helmholtz coils. A: normal geomagnetic field. B: altered magnetic field.

The "learning flights" were not observed in all the control experiments with the Helmholtz coils off. This kind of flight is typically performed by young workers as a way to acquire visual information to be used during foraging, and is less intense later in adult life (Wei & Dyer, 2009). According to Wei et al. (2002), the performance of these flights by older individuals indicates a response to environmental uncertainty or change. This worker behavior may be the result of the presence of an electric field in the field generated by the Helmholtz coil and that is not present in the permanent magnet, as it is known that bumblebees are able to detect electric field from flowers (Clarke et al., 2013) and perhaps this ability is shared by wasps, or perhaps the wasps did not identify the magnetic field as a threat and tried to understand the magnetic field configuration better in order to use this information when it was time to return to the nest, recalibrating their orientation to the new local magnetic configuration.

Another behavior observed was a kind of disorientation shown by some workers returning to the nest and that were not present when the electromagnetic field was applied. Apparently they were not able to land on the nest surface at the first attempt. However, the same behavior was observed in the control experiments, showing that the presence of the coils alters the landmarks around the nest, leading to a sudden disorientation in the wasps returning to the nest after foraging.

The present results showed that the wasp *Polybia paulista* is sensitive to modification of the local geomagnetic field by external sources, as has been described for other social insects including ants, bees and termites (Wiltschko & Wiltschko, 1995). The modified behaviors related to the presence of magnetic fields were the frequency of foraging flights, the presence of "learning flights" and the grouping on the surface of the nest. The next question to be addressed is what mechanisms are involved in detecting the magnetic field. Could it be magnetic nanoparticles, as predicted by the ferromagnetic hypothesis? Or could radical pair reactions be occurring in the eyes or in ocelli? Or perhaps another kind of magnetic field detection is combined with the gravitational field detection? Recently, Valkova and Vacha (2012) discussed the possibility that honeybees use both mechanisms to detect the geomagnetic field. The stimulation of foraging flights by modified magnetic fields, as was observed in our study, is also intriguing. Could the wasps correlate the intensity of the magnetic field with the appropriate time for foraging? The intensity of the geomagnetic field changes during the day (the daily variations), but the maximum increase is about 0.1 µT (Skiles, 1985). Kisliuk and Ishay (1977) showed that magnetic fields of about 60 times the normal geomagnetic field are lethal to hornet workers. Our study used magnetic fields of about 22 times the normal geomagnetic field, which were not lethal.

In conclusion, magnetic or electric sensitivity has been demonstrated for the first time in *Polybia paulista* wasps, adding this species to the list of animal models for studies of magnetoreception and electroreception.

Acknowledgments

The authors thank Janet W. Reid (JWR Associates) for the revision of the English text and Yzel Rondon Súarez for their assistance with the statistical analysis. We are grateful to CAPES for a doctoral fellowship awarded to the first author. WFAJ acknowledges his research grant from CNPq. DAA acknowledges CNPq financial support.

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