Introduction

Several experiments have shown that animals can use the geomagnetic field (GMF) for orientation and homing using a magnetoreception process (Wiltschko & Wiltschko, 2005). Social insects, such as bees, ants and wasps, can use magnetoreception for magnetic orientation in guidance and navigation tasks (Wajnberg et al., 2010; Pereira-Bomfim et al., 2015). Unlike magnetic orientation, there are some reports of sensibility to magnetic fields (MF) by insects, where variations in MFs can change common behaviors. Vowles (1954) presented a pioneer study with the ant Myrmica laevinodis (Nylander, 1846). He studied the orientation of ants to gravity and used tiny particles of soft iron cemented to different parts of the ant body to generate a magnetic couple, in the presence of a magnetic field of about 300 μT, to be added to the gravitational couple. He aimed to identify where the gravitation sensor is located in the ant body. During the experiments, Vowles observed that the magnetic couple does not alter the orientation to the gravitational force. Still, he observed that ants changed their behavior when the magnetic field was on: they stopped their movement or often cleaning their antennae when the iron particles were located in the funiculi or the scape of both antennae (Vowles, 1954).

The study of Kermarrec (1981) showed that Acromyrmex octospinosus (Reich, 1793) ants are sensitive to strong static MFs provided by magnets (of about 19100 μT and 27300 μT), by avoidance reactions including the repeatable movement.
of brood by workers. In the same study, no reaction was observed for magnetic fields of about 200 μT, and 500 μT. Anderson and VanderMeer (1993) showed that *Solenopsis invicta* (Buren, 1972) ants are sensitive to changes in the GMF direction analyzing the time of trail formation in an experimental arena. In those studies, with *M. laevinodis*, *A. octospinosus*, and *S. invicta*, the observed responses to MFs are examples of magnetosensibility, not necessarily related to orientation and homing. A magnetoreception mechanism essentially assumed in ants is the ferromagnetic hypothesis (Johnsen & Lohmann, 2005). It claims that the magnetic field transduction occurs through magnetic nanoparticles located inside some specialized cells associated with the nervous system. In *Pachycondyla marginata* (Roger, 1861) ants, the search for magnetic nanoparticles involved studies on their isolation (Acosta-Avalos et al., 1999), SQUID magnetometry (Wajnberg et al., 2004), ferromagnetic resonance (Wajnberg et al., 2000), and electron microscopy (Oliveira et al., 2010). Such studies allowed the identification of the antennae as the location of the magnetoreceptor. For other insects, such as *Atta colombica* (Guérin-Méneville, 1844) and *Schwarziana quadripunctata* (Lepeletier, 1836) (Lucano et al., 2006; Alves et al., 2014), similar studies identify the antennae as the body part with a higher magnetic signal.

Like other social insects, Ants show a high degree of cooperation among the individuals that interact in the colony (Zinck et al., 2008). For instance, workers play an active role in nest construction, colony protection against predators, foraging, and brood care (Ratnieks et al., 2006). The colony’s integrity depends on social interactions and communication among nestmates (Crozier & Pamilo, 1996). Those abilities are well developed in ants, and individuals from a foreign nest are usually attacked and rejected from foreign colonies (Crozier & Pamilo, 1996; Sturgis & Gordon, 2012). However, the level of aggression towards conspecifics non-nestmates, i.e., during nestmate recognition, can vary among species (d’Ettorre & Lenoir, 2010). Ants, in general, control and defend their territory, where they extract resources (Newey et al., 2010). Encounters among foragers from different colonies can generate conflicts that can turn into clashes, resulting even in individuals’ death (Matthews & Matthews, 2010). In some cases, ants can be tolerable to neighbors, implying that nestmate recognition and aggression can be associated with colony-recognition odors from environmentally derived cues, not only to the genetically derived ones (Chen & Nonacs, 2000; Frizzi et al., 2015). As far as we know, magnetosensibility has not been applied to analyzing the aggressive behavior during nestmate recognition in the presence of different magnetic fields.

The present study aimed to investigate magnetosensibility in *Ectatomma brunneum* (Smith). We hypothesized that the usual pattern of interaction among conspecifics could be affected by applied magnetic fields. We also looked for the presence of magnetic material in the ant’s body using SQUID magnetometry techniques.

### Materials and Methods

#### Behavior experiments

We used a pair of coils connected to a digital power supply (Skill Tech, model SKFA-05D) to test the effect of magnetic fields on ants’ intraspecific interactions, as described by Pereira-Bomfim et al. (2015). The coils had a 30 cm diameter with a space of 15 cm between them. They were built with 58 spirals of Cu wire 14 AWG (Figs 1A and 1C), generating a non-uniform static magnetic field (Fig 1B) applied to a plastic container called “arena of encounters” (Fig 1C). The coils’ axis was kept in the South/North direction, oriented with a compass. When the power supply was switched on (15 V, 1.16 A), the horizontal component of the magnetic field (open circles in Fig 1B) inside the coils presented its polarity inverted in the region from 4 cm to 12 cm (Figs 1A and 1B). The intensity of the GMF in the lab was -16 μT horizontal, 21 μT vertical, and 16 μT perpendicular, meaning a total intensity of 31 μT. To measure the intensity of the MF, we used a sheet of graph paper. In this paper, we measured the intensity value in the vertical, horizontal and perpendicular directions at every centimeter. We took all measurements using a gaussmeter (GlobalMag, Model TLMP-HALL 050). The total magnetic field generated is shown in Fig. 1B. The essential characteristics in the generated magnetic field, relative to the standard geomagnetic field, are the inversion in the vertical component (open squares in Fig 1B), changing the sign of the inclination, the increasing of the magnetic field intensity from the center to the periphery, and the U-form of the field intensity. From 5 cm to 9 cm, the magnetic field gets its lower value of about 100 μT (about three times the local value in the lab, see the open triangles in Fig 1B). The magnetic field generated by the pair of coils corresponds with a quadrupolar field generated by an anti-Helmholtz configuration. The electrical current circulates in the opposite direction in each coil (Youk 2005). In contrast, in a Helmholtz configuration, the current circulates in the same direction in each coil generating a dipolar field. This magnetic field configuration is interesting because it changes non-uniformly all the parameters of the local GMF (intensity, inclination and declination) and the increase in MF intensity is very low compared with that generated by magnets, as was done by Vowles (1954) and Kermarrec (1981).

We collected a total of 56 foragers from six colonies of *E. brunneum* from their nests’ entrance. The colonies were in the campus of Universidade Estadual de Mato Grosso do Sul, Dourados, MS, Brazil. After transfer to the laboratory, we kept the individuals in a 250 ml plastic container with holes in the sides and lid to allow air to circulate, with water and molasses *ad libitum*, wrapped in red cellophane to minimize the stress caused by collection and luminosity. For acclimatization to laboratory conditions (24°C and 70% of humidity), a period of 24 hours was considered. Then, we performed induced encounters among intraspecific workers. To this end, the
ants were transferred to the “arena of encounters” (Fig 1C), a container of 16cm x 10cm x 10cm, inside which there was a smaller container (6cm x 4cm x 3cm) in the central inner part, where we placed one ant. Then, after one minute, a second worker from another colony was placed in the arena, outside the smaller container. This smaller container was only removed after 1 minute, thus enabling the encounter among the two workers.

We induced 24 encounters, peer to peer, among 48 workers of six colonies of the species *E. brunneum* whose nests were at varying distances from each other (Fig 2). As control of experimental conditions, we induced four nestmate encounters. We used each ant only once in the experiment to avoid pseudoreplication, and at each encounter, we used a new arena.

We observed each pair interacting for 45 minutes in sessions of 15 minutes. In the first 15 minutes, the interactions occurred with the coils switched off, i.e., before the change in MF; for the next 15 minutes, the coils were switched on to generate a different MF in them; and in the last 15 minutes, the coils were switched off again. We kept the coils always in the same position to avoid their influence on the behavioral responses.

To assess the level of aggression during the encounters, we scored behaviors from 0 to 2 as follows: 0 for ignoring (Thomas et al., 2004), touching and avoiding (Suarez et al., 1999); 1 for attempted seizure, seizure, antennal boxing, body lifting, gaster curling or aggression from one worker (Monnin & Peeters, 1999); and 2 for a fight, identified when both workers execute the aggressive behaviors (modified from Suarez et al., 1999). We observed the evolution in the aggressive behavior during each encounter and recorded scores when the behavior changed. For each encounter, we calculated the arithmetic mean of the score regarding the observed levels of aggression.

![Fig 1](image1.png)

**Fig 1.** Pair of coils configuration and the magnetic field generated. A. Representation of the orientation of the MF components measured among the coils. A* represents the arena of encounters. B. Intensity of the magnetic field components as a function of the distance among the coils. The first coil is positioned at x = 1cm and the second coil is at x = 15cm. Also is represented the total intensity of the magnetic field, whose variation corresponds with a quadrupolar field. C. Photography showing the pair of coils, made of 58 spirals of Cu wire 14 AWG. In the middle is shown a plastic box that corresponds to the “arena of encounters”.

While functioning, the coils can increase the temperature. To assess whether the increase in temperature could lead to behavioral response changes, we photographed all encounters with a thermal camera (Testo® 870). We took thirty pictures at each step of the experiment from random encounters. With the aid of the software Testo IRSOFT, we selected ten random points of thermal photos from both the arena and ants’ bodies to establish the mean temperature of the ants’ body during the encounters and assess whether the ant temperature varies when coils are switched on/off.

**SQUID magnetometry**

To assess whether there are magnetic nanoparticles on the ant’s bodies, we collected individuals of *E. brunneum* (Eb).
Afterward, we separated the heads + antennae (denominated only as head) and abdomens, kept these body parts in the fridge, and preserved them in a solution of 70% alcohol. We used a SQUID magnetometer (MPMS Quantum Design) to search for magnetic material in these body parts. Five abdomens and five heads of Eb were dried and placed inside a gelatine capsule, which we placed in a plastic straw fixed on the magnetometer’s sample holder for magnetization measurements. We took two magnetization measurements as a function of temperature: Zero Field Cooling (ZFC), where the sample is cooled from room temperature in the presence of a null magnetic field; and Field Cooling (FC), where the sample is cooled in the presence of a magnetic field, which was 10000 µT (100 Oe) in our measurements. After cooling the sample, a magnetic field was applied to it, and the magnetization was measured as the temperature increased. The temperature range was between 10 K and 330 K, under a magnetic field of 10000 µT (100 Oe). We took hysteresis measurements at 300 K or 150 K, on a magnetic field range between -1T and +1T (1T = 10^6 μT). Based on the hysteresis curves, we determined the saturation magnetization ($M_s$), remanent magnetization ($M_r$) and coercive field ($H_c$). $M_s$ results from all contributions to magnetization, while $M_r$ is solely composed of the ferromagnetic component. As heads and abdomens have different sizes and masses, we calculated $M_s$ and $M_r$ dividing the original values by analyzing the parts’ total mass.

**Statistics**

We evaluated the difference in aggression levels among the three experimental conditions (coils off, on, and off again) using a Kruskall-Wallis test. To assess whether there were significant differences between the thermal photos’ mean temperature during the same encounters, we applied a Kruskall-Wallis test. We performed all statistical tests using the free software R 3.2.1 version.

**Results**

**Aggressive behavior**

We recorded a total of 1571 behaviors during the encounters between workers of E. brunneum. From this total, 43.7% occurred before the change in MF, 27.6% during the change in MF, and 28.7% after the change in MF. The main behaviors performed by workers of E. brunneum were seizure (10.6%), attempted seizure (9.73%) and antennal boxing (9.35%). During controls, we did not observe aggressive behavior (touch and antennation represented 100% of behaviors).

The mean level of aggression between workers from different colonies of E. brunneum was 1.5 ± 0.3 before the change in MF, 1.1 ± 0.1 during the change in MF, and 1.3 ± 0.2 after the change in MF (Fig 3). The Kruskal-Wallis test showed significant differences between the groups ($\chi^2 = 17.8 p < 0.05$).

**Magnetometry**

Fig 5 shows the ZFC and FC curves for the head and abdomen. All the curves are compatible with the presence of magnetic nanoparticles. For the abdomen, the nanoparticles show a strong dipolar interaction and a smaller size than the head.
As for the head, in low temperatures, we observed a sudden increase in magnetization. This phenomenon is characteristic of paramagnetic contributions due to spins not compensated on the surface of the nanoparticles (Peck et al., 2011). From Fig 5 is observed that the blocking temperature for the abdomen is 282 K that can be associated with nanoparticles with an average diameter of about 24 nm (considering magnetite as the magnetic material). For heads, the blocking temperature must be higher than 340 K associated with the presence of magnetic nanoparticles whose sizes are bigger than 26 nm (considering magnetite as the magnetic material). Fig 6 shows an example of magnetization curves for abdomens and heads after removing the diamagnetic + paramagnetic contributions. Table 1 shows the results at 300 K for the coercive field $H_C$, the remanent magnetization $M_R$ and the saturation magnetization $M_S$. Fig 7 shows $M_S$ and $H_C$ as a temperature function. The results show that the abdomen has higher $M_S$ values and lower $H_C$ values compared to the head. The value of $M_R/M_S$ for the abdomen is compatible with the presence of superparamagnetic particles in the paramagnetic
state, producing higher MS values. On the other hand, those values for the head are compatible with single domain or blocked superparamagnetic nanoparticles, producing higher coercivities. The superparamagnetic fraction (fsp) was calculated as:

\[ \text{fsp} = \frac{\text{M}(150K) - \text{M}(300K)}{\text{M}(150K)} \]  

The values obtained for fsp are compatible with the values for \( \frac{M_s}{M_g} \); the abdomen shows a higher amount of superparamagnetic particles than-the head. The crude curves \( \text{M(B)} \) showed diamagnetic + paramagnetic contributions as a function of temperature. From these outcomes, it is possible to calculate the paramagnetic susceptibility \( \chi_{\text{PM}} \) showed in Table 1. The head shows a higher value of \( \chi_{\text{PM}} \) compared to the value for the abdomen. That correlates with the low temperature behavior observed for heads in the ZFC-FC curves (Fig 5). PM’s higher value could mean that the nanoparticles in the head are single domains with defects in the surface producing an extra paramagnetic contribution (Peck et al., 2011).

![Fig 7. Saturation magnetization (M_s) and Coercive field (H_c) as a function of the temperature, for heads and abdomens of Ectatomma brunnneum.](image)

**Discussion**

In normal conditions, under the influence of the geomagnetic field, we found higher levels of aggression among *E. brunneum* ants (scores for before in Fig 3A) whose nests were further apart in more than 100 m (Fig 2). This finding means that these ants are tolerant to individuals from nests in a radius of 100 m. Pereira et al. (2019) showed that *E. brunneum* colonies are more tolerant to ants from nearest nests. This recognition ability and consequent intolerance among themselves are related to competition for resources (Temtess, 1994; Sanada-Morimura et al., 2003). This type of dispute has been described in the ants *Pogonomyrmex barbatus* (Smith, 1858) (Gordon, 1989), *Pristomyrmex punctatus* (Smith, 1860) (Sanada-Morimura et al., 2003), *Linepithema humile* (Mayr, 1868) (Thomas et al., 2004), and the termite *Nasutitermes corniger* (Motschulsky, 1855) (Dunn & Messier, 1999).

We can explain the observed results through the change in the local temperature generated by the coils when they were turned on because of resistive losses. Some studies have reported that temperature changes can affect the behavior of various animal groups (Walther et al., 2002; Deutsch et al., 2008; Dell et al., 2011, 2014; Huey et al., 2012; Gilbert et al., 2014; Sunday et al., 2014; Vasseur et al., 2014; Woods et al., 2015). However, our results demonstrate that the temperature variation in the surface of the ants’ body is not statistically significant (Fig 4), so the temperature is not a stressing factor to explain the ant behavior observed.

The fact of ants being intolerant to foreign ants is probably due to the ability to recognize non-nestmates through chemical signals, especially cuticular hydrocarbons already investigated in several studies (Jutsum et al., 1979; Liang & Silverman, 2000; Sorvari et al., 2008; van Zweden et al., 2009; van Zweden & D’ettorre, 2010; Helanterä et al., 2011).

When the coils were turned on, the change in MF decreased the aggression score (see scores for During in Fig 3A). For *E. brunneum*, a significant decrease is observed only for further nests. When the coils were turned off, the aggression score increased, but it did not recover the same level as it had at the beginning of the encounter. Therefore, when the coils were turned on, the change in MF seems to have caused disorientation on the ants, consequently changing the pattern of interaction displayed when the coils were turned off. A piece of evidence that supports the previous comments is that during the encounters with the MF turned on, ants showed “immobility”, an atypical behavior of them, remaining still without even moving the antennae and, after a period, they started to clean their antennae more often than usual. Our results show for the first time that *E. brunneum* is magnetosensible, being perturbed by local changes in the MF. We cannot claim that MF changes affect the aggressive ant behavior but that changes in MF change the ant behavior.

The magnetometry measurements show the presence of magnetic nanoparticles in the head and the abdomen of *E. brunneum* ants. In each case, the nanoparticles show different magnetic properties at room temperature: in the abdomen, parameters obtained from the hysteresis curve at 300 K: coercive field (H_c), remanent magnetization (M_r) and saturation magnetization (M_s). The superparamagnetic fraction fsp was calculated as indicated by Eq. (1). \( \chi_{\text{PM}} \) is the paramagnetic susceptibility.

**Table 1.** Parameters obtained from the hysteresis curve at 300 K: coercive field (H_c), remanent magnetization (M_r) and saturation magnetization (M_s). The superparamagnetic fraction fsp was calculated as indicated by Eq. (1). \( \chi_{\text{PM}} \) is the paramagnetic susceptibility.

|          | H_c (Oe) | M_r (emu/g) | M_s (emu/g) | M_r/M_s | fsp   | \( \chi_{\text{PM}} \) |
|----------|----------|-------------|-------------|---------|-------|-------------------|
| Abdomen  | 11       | 3.9x10^4    | 1.4x10^4    | 0.03    | 0.9   | 3.1x10^-4         |
| Head     | 160      | 4.9x10^4    | 1.3x10^3    | 0.38    | 0.1   | 9.1x10^-4         |
the nanoparticles are mainly in the superparamagnetic state, and in the head, the nanoparticles are mainly single domains and superparamagnetic nanoparticles in the blocked state. Magnetometry studies done in other ants have shown that all parts of the ant body are magnetic (Wajnberg et al., 2010), but the abdomen and the head show different magnetic properties. Those studies led to the proposal that the magnetosensor must be in the antennae for Pachycondyla marginata, Atta colombica, and Schwarziana quadrupunctata (Wajnberg et al., 2004; Lucano et al., 2006; Alves et al., 2014). Our results show that the abdomen and the head have different magnetic properties, and both can host the magnetosensor responsible for the observed magnetosensitivity. In both cases, the type of magnetosensor must be different. On the one hand, the abdomen has an arrangement of superparamagnetic nanoparticles sensitive to the magnetic field intensity. On the other hand, the head has an arrangement of magnetic single domains sensitive to the magnetic field vector’s intensity and direction (Johnsen & Lohmann, 2005).

Our results and other studies (Wajnberg et al., 2010) show that ants can detect MF intensity changes. Oliveira et al. (2010) proposed that *P. marginata* ants can perceive the magnetic field through magnetic nanoparticles in the antennae. Since the orientation of those magnetic nanoparticles and their magnetic moment can be rapidly altered when ants walk inside the “arena of encounters”, because the MF is displaced from the center of the arena (Fig 1B), the increase in cleaning behavior suggests an attempt to adjust the magnetic sensor to the new MF configuration. Another evidence that the MF is perceived by ants and causes changes in behavior is that soon after the coils were turned off, the ants stopped performing the above-listed behaviors, and aggression levels increased again, but not to the same level of aggression shown before the coils were on.

**Conclusion**

Our results show that *E. brunneum* ants tolerate ants from other nests at distances lower than 100 m. For the first time, our results show that *E. brunneum* ants are magnetosensitive, changing their behavior under the effect of applied MF. Their body presents magnetic nanoparticles with different properties in the abdomen and the head. As the MF changes are about three times the local magnetic field, the change in behavior can be associated with disturbance and/or disorderation in some magnetosensor located in the ant’s body. Our results do not discard the presence of a magnetoreceptor based on the radical pair mechanism. Future experiments must address the impact of MF on several ants’ physiological and ethological traits, to establish the origin of the reported magnetosensitivity and understand its biophysical basis.

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**Authors’ contribution**

MC Pereira: conceptualization, methodology, investigation, formal analysis, writing, review & editing
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