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Solenopsis ant magnetic material: statistical and seasonal studies

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Abstract

In this paper, we quantify the magnetic material amount in *Solenopsis* ants using ferromagnetic resonance (FMR) at room temperature. We sampled *S. interrupta* workers from several morphologically indistinguishable castes. Twenty-five oriented samples of each body part of *S. interrupta* (20 units each) showed that FMR line shapes are reproducible. The relative magnetic material amount was 31 ± 12% (mean ± SD) in the antennae, 27 ± 13% in the head, 21 ± 12% in the thorax and 20 ± 10% in the abdomen. In order to measure variation in the magnetic material from late summer to early winter, ants were collected each month between March and July. The amount of magnetic material was greatest in all four body parts in March and least in all four body parts in June. In addition, *S. richteri* majors presented more magnetic material than minor workers. Extending these findings to the genera *Solenopsis*, the reduction in magnetic material found in winter could be explained by our sampling fewer foraging major ants.

S This article has associated online supplementary data files

1. Introduction

Ants are a good model system to study social insect magnetism due to the high diversity, numerical majority, taxonomy knowledge, facility in collecting and ambient changes sensitivity [1]. Ants, as other animals, can adapt to environmental changes, such as temperature and humidity which may influence food availability. Ant colonies evolve mechanisms that adjust their physiology, role division of labor and behavior to warrant their survival [2–4]. Some recent studies have documented changes in colony population and organization modifying abiotic conditions in different ant species [4, 5]. In particular, fire ants [6] are capable of making complex choices concerning thermoregulation. For instance, their thermal preferences make them choose temperatures to maximize their growth at low metabolic costs.

Several ant species colonies have foraging exit holes through which scout workers reach the surface. A scout ant in search of food leaves the nest in a random search pattern until food is found; then it heads back to the nest [7], laying a pheromone trail. Other worker ants, the foragers, are then recruited to follow the trail directly to the food source [8]. In *Solenopsis invicta* ants, large workers tended to be recruited easily to a food source and to store food in their crops, but played little role in larval care. Medium workers had crops ranging from empty to full because they alternated between ingesting from and donating food to other colony members. Medium workers were the most versatile, engaging competently in food recruitment, larval grooming and feeding [9]. More recently, the foraging population was shown to be composed by two distinct groups, scouts (∼25%), and recruits (∼75%) that become scouts, as they age. Most of these recruits (2/3 of the recruits, i.e. 50% of foragers) wait in the nest, probably in foraging tunnels while the other 1/3 (25% of the foragers) wait in the field, near the tunnel entrance/exits [10].

The characterization of major and minor ants relies in few comprehensive studies of the size/shape relationships of all ant body parts [3, 11–13]. One of the first studies on the revisionary taxonomy of the imported fire ants presents the

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schemes of major and minor ant body parts of *saevissima* complex [14]. A more complete and complex allometric analysis in *S. invicta,* a much-studied fire ant, showed large workers with a somewhat different shape than small ones and the size-shape relationships were colony independent [15].

Foraging activity in *S. invicta* was monitored to determine how weather and season affect their activity rates. Soil temperature (at 2 cm) was the best predictor, with maximal foraging rate between 22° and 36 °C but occurring from 15° to 43 °C [16]. The ability to home under a variety of conditions is essential for an effective means of exploiting a temporary food resource. Ant orientation is based on a variety of cues such as sun compass, polarized light and landmark cues in initial homing [17–19]. The magnetic orientation mechanism has also been demonstrated in a few species of ants [17, 20–23]. One of the well-accepted hypotheses to explain the magnetic orientation is based on the presence of magnetic iron oxides in ant body parts that has been magnetically detected in *P. marginata* [24, 25], *Solenopsis substituta* [26], *S. interrupta* [27] and other ant species [28].

The low concentration of magnetic material in ants requires the use of several specimens in a sample, providing an average result, which needs to be confirmed as statistically significant. To investigate this significance, the variation in the total and relative amounts of magnetic material in different body parts and the repeatability of the results that were presented in an earlier study [27], we sampled workers from *Solenopsis* mounds and kept them in the laboratory for short-term FMR measurements (10 days). We also sampled workers from another mound across three seasons to verify the long-term behavior of those parameters.

2. Material and methods

S. interrupta (Santschi, 1916) and *S. richteri* (Forel, 1909) worker ants were collected in Citrolândia, Rio de Janeiro, Brazil. The ants were carefully washed with distilled water to clean them of nest soil. Body parts of *S. interrupta* ants were separated while they were still alive. All *S. richteri* were kept in water until they died. Samples were then dried for FMR measurements. Each *S. interrupta* sample was composed of body parts of 20 ants and each *S. richteri* sample was composed of 5 whole ants.

FMR measurements were performed at room temperature, in an X-band electron paramagnetic resonance (EPR) spectrometer (Bruker ESP300E) operating at a microwave power of 4 mW with a 100 KHz modulation frequency and an ~2 Oe modulation field in amplitude, with the magnetic field applied perpendicular to the long body axis of the *S. interrupta* in the short- and long-term experiments and parallel to the long body axis of *S. ritcheri* in the caste experiments. The FMR absorption spectra areas, *S*, proportional to the magnetic material amount were calculated as the second integral of the derivative spectra starting at high field values, where the baseline is better defined, with software developed using the graphic language LabVIEW®. The spectra area, *S*, was log (decimal) transformed to allow the observation of the low-value range.

Statistical analyses were performed with INSTAT software that uses the Kolmogorov and Smirnov method for the normality test.

2.1. Short-term experiments

Part of an *S. interrupta* mound was collected on 21 April 2005 in field and kept alive in a plastic recipient in the laboratory with only a water supply. Twenty workers (without sub-cast identification), randomly collected in the laboratory recipient, were cut, just before measurement, into four body parts: a pair of antennae (ANTN), head (HEAD), thorax with feet (THOR) and abdomen with petiole (ABD). These four samples were labeled to keep their ant origin correlated. This procedure was performed during the following 10 days (time necessary for measurements), not every day, coming up to 25 samples of each body part so that a total of 500 (25 × 20) workers were used.

2.2. Long-term experiments

Each month about 50 workers were randomly collected outside a nest of *S. interrupta*, close to the exit of another mound (about 30 meters away from the short-term one), without nest destruction. Twenty ants were randomly selected and separated into four body parts, resulting in only one sample of each body part, each month. FMR measurements were performed on the sampling day (10 March, 10 April, 10 May, 10 June and 10 July of 2005).

Rain fall and the mean temperatures of the collecting days of 2005, measured in the Xerem meteorologic station, were obtained at the Instituto Nacional de Meteorologia (Nacional Instittue of Meteorology, Rio de Janeiro, Brazil).

2.3. Caste experiment

In order to quantify the magnetic material amount in major and minor workers, part of a third mound (about 10 m from the second mound and 20 m from the first one) was collected, in a field on 21 May 2009, identified as *S. richteri*. This was the *Solenopsis* species found in the same place where *S. interrupta* were collected 4 years before. Ants were kept alive in a plastic recipient in the laboratory with only a water supply. FMR measurements were performed on 23 May 2009 just after the washing procedure. Major and minor workers were selected by visual inspection for extreme body sizes. Two specimens of the sample ants measured are shown in figure 1, which were used to estimate minor and major body lengths of about 2.5 mm and 3.6 mm, respectively. The head lengths were estimated and a major/minor ratio of 1.5 was obtained in agreement with 1.4 obtained from the scheme shown in figure 1 of [14]. A total of 25 major and 25 minor ants were used.

Figure 1. Two major and two minor *S. richteri* ants. Distance between two rule divisions = 1 mm.

3. Results

3.1. Short-term experiments

Examples (4 of the 25 groups of ants) of the spectra of each body part of the same 20 *S interrupta* ants, are correspondingly shown in figures 2(*a*)–(*d*). The resulting spectra present a signal/noise ratio ~ 9. The high-field (HF) and low-field (LF) ferromagnetic broad lines, previously observed in the spectra of the body parts of other social insects [24, 26, 29, 31], in particular in those of *S. interrupta* [27], are also observed in this paper (arrows in figure 2). Except for the abdomen, the HF line, associated with isolated nanoparticles [24], of the spectra presents a normal distribution of the peak-to-peak line width ΔH_{pp}. The mean ΔH_{pp} (and standard deviation SD) of the body parts are 586 ± 205 Oe in the ANTN, 685 ± 229 Oe in the HEAD and 678 ± 254 Oe in the THOR. The log-transformed line width of the ABD spectra is normally distributed 2.77 ± 0.26 (original values in Oe, 633 ± 274 Oe). The resonant field, $H_{r,}$ of the HF line is normally distributed 3204 ± 89 Oe in the HEAD and 3203 ± 120 Oe in the THOR, whereas the log-transformed values in the ANTN and ABD present Gaussian distributions with 3.50 ± 0.015 and 3.51 ± 0.016 (original values in Oe, 3189 ± 111 and 3214 ± 125), respectively. The distributions of these FMR parameters are given in the supplementary data at stacks.iop.org/PhysBio/6/046012. The broad LF line, associated with aggregate or large nanoparticles [24], presents H_r value fields lower than 1000 Oe. Except for the ANTN spectra, a narrow line at $g = 2$, associated with free radicals [32], is clearly observed in the spectra of the body parts. Superimposing the normalized spectra of each body part, the spectral shapes of the ferromagnetic components (HF and LF) are reproducible, within the noise. The individual spectra raw data of the body parts and their average spectra and SD (of 25 spectra each) with the correspondent spectra (figure S1) are given in the supplementary data at stacks.iop.org/PhysBio/6/046012.

The absorption curve area (*S*) values of the 25 samples of each body part were used to quantify the amount of magnetic material. Except for the HEAD, the *S* value distributions of the body parts are not normally distributed; therefore, the log-transformed values are shown in histograms of figure 3(*a*). These log-transformed distributions are Gaussian and only the ANTN one is peaked at the lowest values. The mean log(*S*) (±SD) of the body parts is (7.3 ± 0.5) in the ANTN, (7.2 ± 0.5) in the HEAD, (7.2 ± 0.5) in the THOR and (7.2 ± 0.6) in the ABD and are also indicated in 3(*a*) (solid symbol and bar).

The magnetic material fractions were then calculated resulting in normalized distributions (figure 4(*a*)). The magnetic material mean fractions were calculated as (mean ± SD) (31 ± 12)%, (27 ± 12)%, (21 ± 12)% and (20 ± 10)% in ANTN, HEAD, THOR and ABD, respectively, shown as a solid symbol and bar in figure 4(*a*). The magnetic fraction in the head plus antennae is (58 ± 24)%.

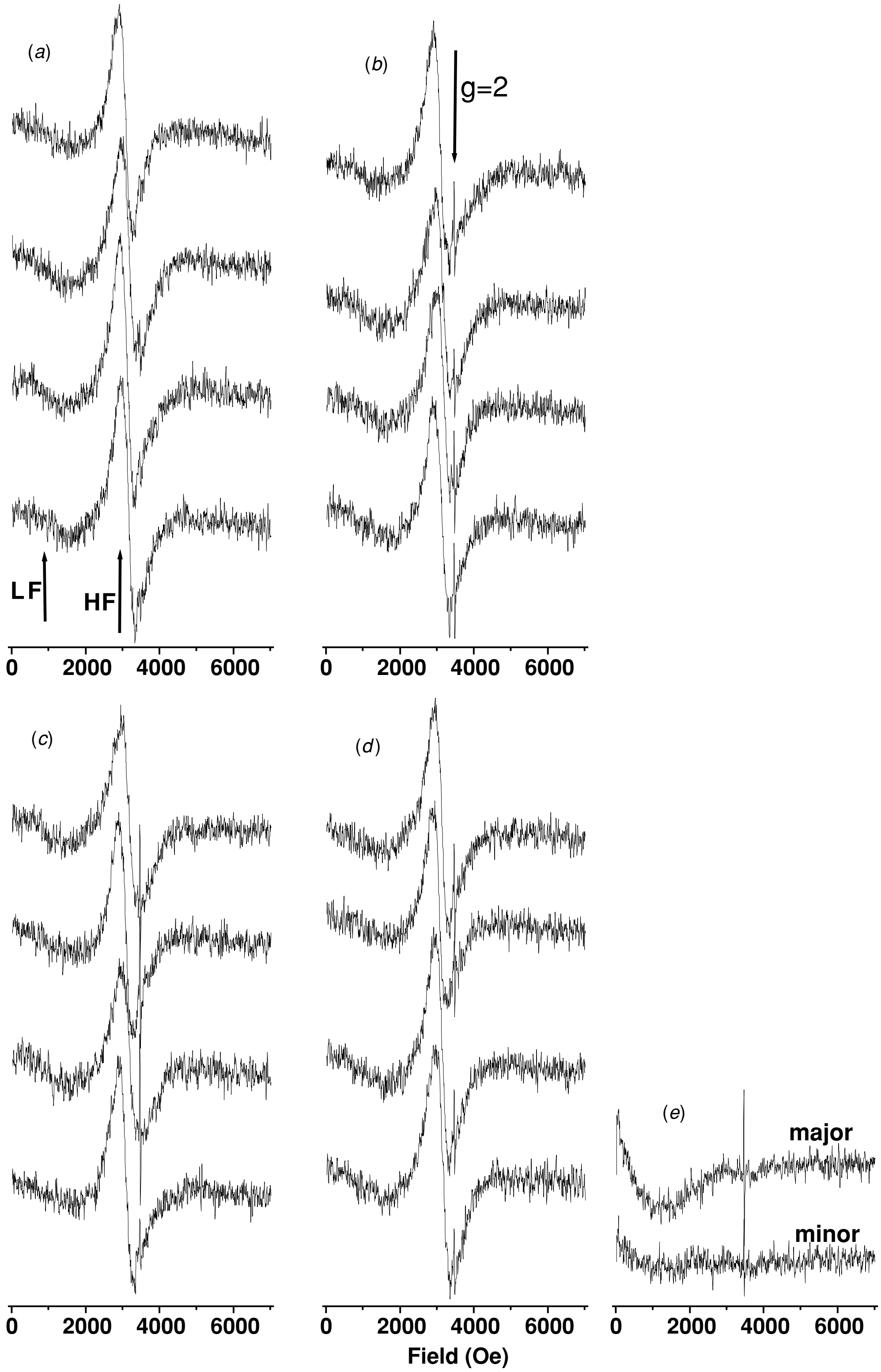

Figure 2. FMR spectra of four representative groups of the same 20 *S. interrupta* ants (*a*) ANTN; (*b*) HEAD; (*c*) THOR; (*d*) ABD. Ants were collected on 21 April 2005 in a field and kept in a laboratory for 10 days for measurements. The LF and HF broad components and the narrow line at $g = 2$ are indicated by arrows. (*e*) Mean of five FMR spectra of major and minor *S. richteri* ants.

3.2. Long-term experiments

Five monthly measurements of another mound sampling were performed, which involved three seasons: summer, fall and winter. The spectra shapes are very similar to the short-term ones with the characteristics HF and LF ferromagnetic broad lines, but with different absorption areas.

The experimental log(S) and magnetic material fraction values with the experimental error obtained for the five samples

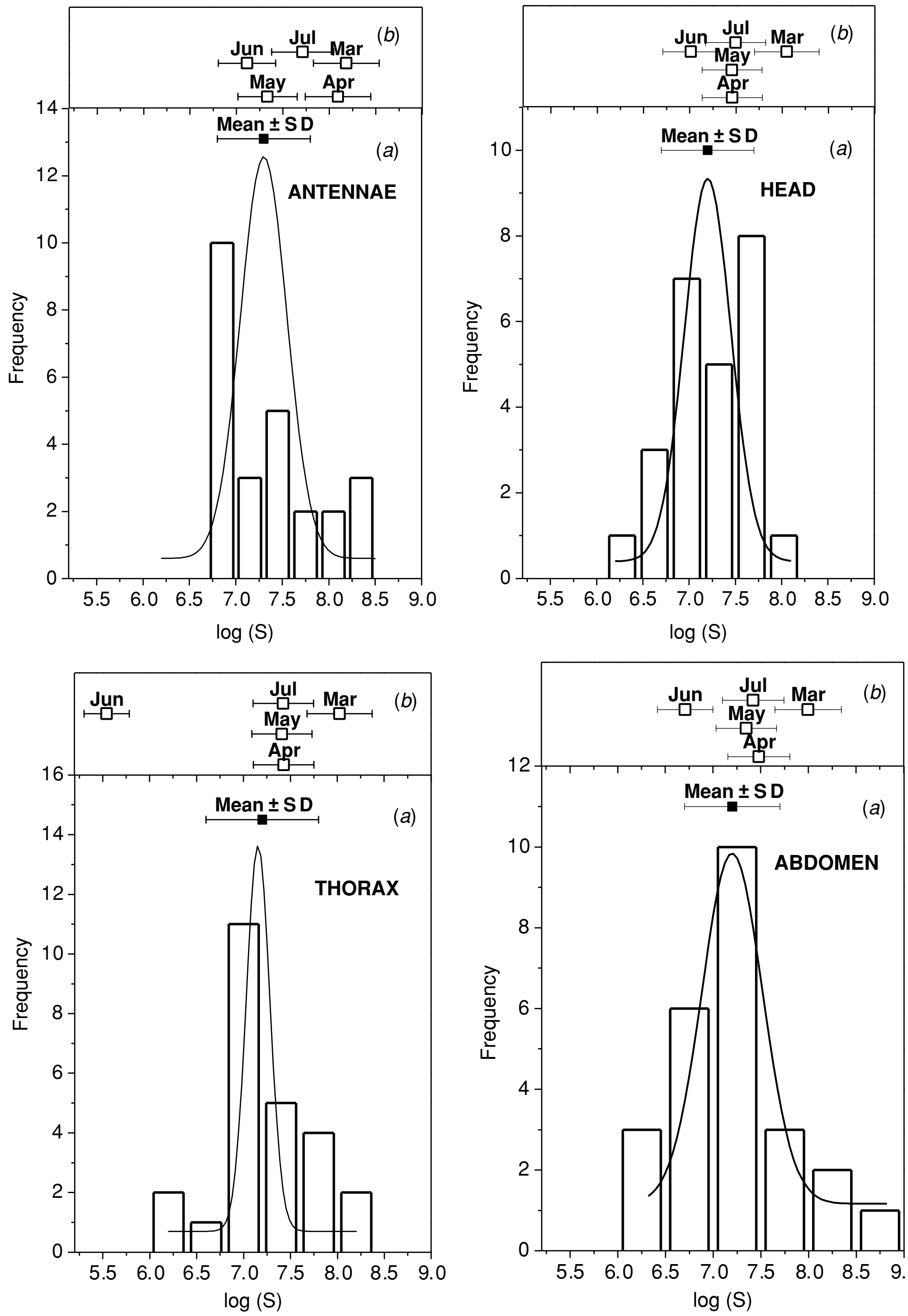

Figure 3. Magnetic material amount of *Solenopsis interrupta* ant body parts ANTN, HEAD, THOR and ABD. *x*-axis: *S*, magnetic material amount, log transformed. (*a*) Distribution of the material of ants collected on 21 April 2005 for the short-term experiment, full symbol and bar (mean ± SD) of the distribution. The line is the Gaussian curve. (*b*) *S* values of samples collected every 10th day for the long-term experiments, open symbol and bar (value ± experimental error).

are shown in figures 3(*b*) and 4(*b*), respectively (open symbol and bar). Comparing these monthly long-term values to the respective short term we observe that only the THOR value in June is out of the reference interval (mean ± 2 SD) of the short-term ones (figure 3). A similar comparison of long to short values of the magnetic material fraction (figure 4) shows that only in April the ANTN value is out of the short-term ones.

Climatic parameters reflect the seasonal changes. Then the local temperature of each collecting day is compared to the long-term magnetic parameters in figure 5. The four body parts spectra present a minimum *S* value about June, with a reduction of the March magnetic material amount value (*S*) of at least 80% (log transformed in figure 5(*a*), easily observed in the inset). These values qualitatively correlate to the mean temperature (figure 5(*a*)). On the other hand, no qualitative

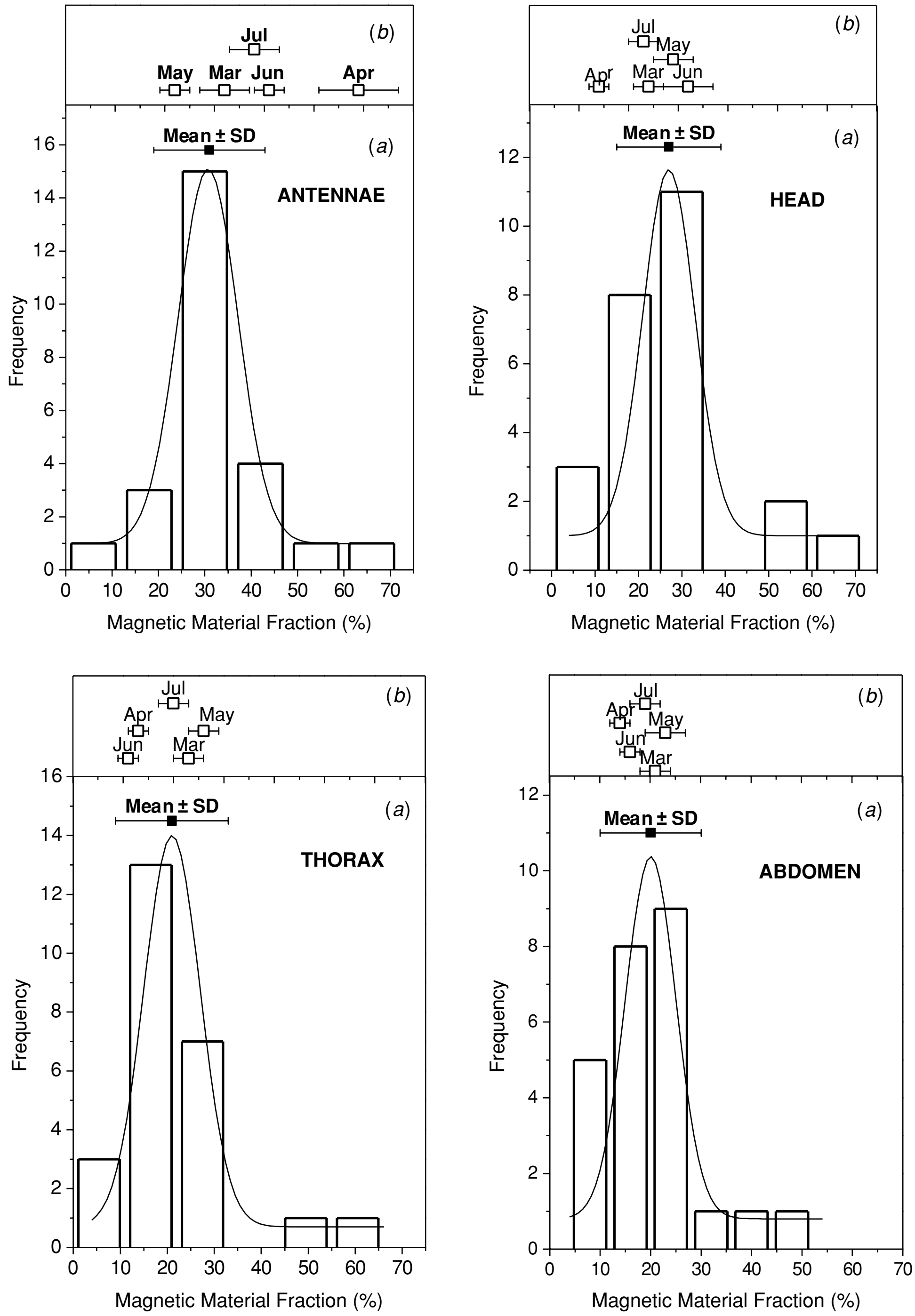

Figure 4. Magnetic material fractions of *Solenopsis interrupta* ant body parts ANTN, HEAD, THOR and ABD. (*a*) Distribution of fractions of ants collected on 21 April 2005 for the short-term experiment, full symbol and bar (mean ± SD) of the distribution. The line is the Gaussian curve. (*b*) Material fraction of samples collected every 10th for the long-term experiments, open symbols and bar (value ± experimental error).

correlations of the magnetic fraction to the mean temperature are observed for any of the four body parts (figure 5(*b*)). The rainfall values of these days were 0.2 mm on 10 May and 10 June and 0.0 mm on the other three collecting days. Also, the minimum *S* value occurred in rainy collecting days (May and June). These figures evidence the same behavior of THOR and ABD magnetic fractions and a higher magnetic material fraction in HEAD plus ANTN, in good agreement with the short-term analysis.

3.3. Caste experiments

The spectra of the five samples of whole major and five of whole minor *S. richteri* ants were averaged and the result is shown in figure 2(*e*). These spectra show that the magnetic material amount (*S*) in major workers is 3.1 ± 0.9 times higher

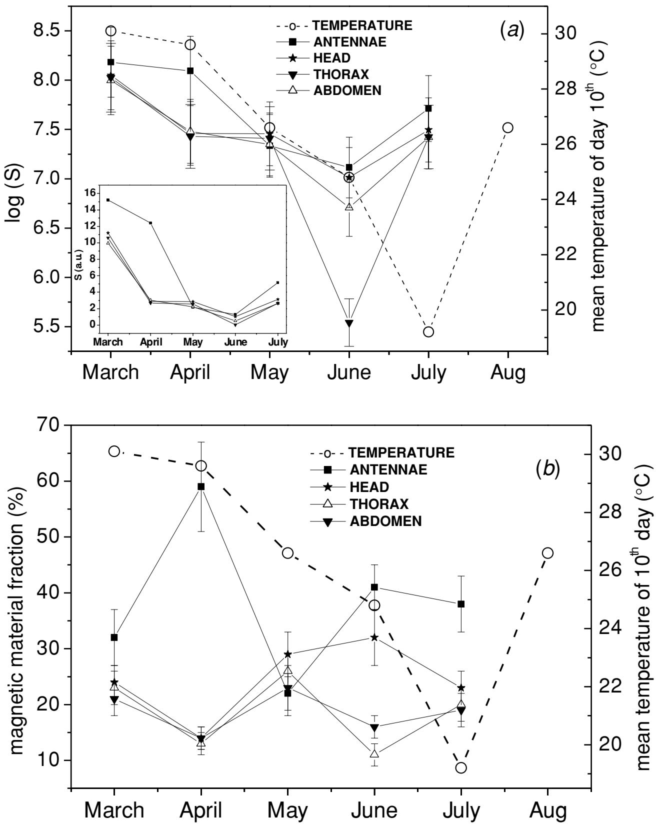

Figure 5. Left axis—(*a*) magnetic material amount (log transformed) in *Solenopsis interrupta* ant body parts; inset: magnetic material amount in arbitrary units (au). (*b*) Magnetic material fraction in *Solenopsis interrupta* ant body parts. Right axis—mean temperature of the collecting days in 2005.

than in the minor ones and that the LF component is the dominant one.

4. Discussion

Magnetic material was found in the four body parts of *Solenopsis interrupta* worker ants. The magnetic material is not uniformly distributed through the body parts. The highest magnetic material fraction was found in the antennae plus head (58 ± 24)%, as previously observed in *P. marginata* ants [25] and *Schwarziana quadripunctata* bees [31]. It is in agreement with a slightly higher magnetic material amount observed in smashed heads with antennae than in abdomen with the petiole of the *S. substituta* ant [26]. The angular dependence of the resonant field was observed only in the heads and antennae of *S. interrupta,* which suggests the presence of an oriented and biogenic magnetic material in these body parts [27]. It cannot be discarded that the magnetic material can be ingested from the soil by ants, but this material would only be found in the thorax and abdomen.

It is very difficult to measure the magnetic material amount in living beings, mainly because of its relatively low concentration in a special region in the biological material. A relative analysis is available from the few papers [26–28, 30, 31, 33, 34] which have used the *S* parameter absorption area of FMR spectra. Only one [34] relates *S* to the saturation magnetization, *J*, although the absolute magnetic material amount was not estimated in termites. Magnetic measurements have indirectly shown the variability of the magnetic material amount in eusocial insects due to conservation solution, elapsed time between sample collecting and/or preparation and measurement, insect age [35], sample orientation relative to the magnetic field [27, 30] and the geomagnetic field at the nest [28]. Even controlling these parameters, dealing with a complex biological system, such as insect colonies and food source, seasonal effects can still be reflected in the magnetic measurements. In particular, different FMR spectral parameters, magnetic material amount and fractions were observed in ant samples collected in the same nest (unpublished data). Individual function differences in the colony have been associated with the difficulty in obtaining reproducible magnetic results [35], in agreement with the observed distribution of this material in *S. interrupta* in this paper.

It was shown that worker honeybees (*Apis mellifera*) pass through distinct behavioral phases during their life. Young bees perform various tasks inside the nest, while older bees forage [36, 37]. There is some plasticity in the age-based pattern enabling this colony to adapt the work force to the colony's need in response to environmental changes [37, 38]. Honeybees orient to the magnetic field. Their magnetic moment apparently develops in the old pupal state and it persists in the adult, which suggests that the magnetic material is constructed in an orderly way which might well make it suitable for use as a detector [39]. Iron-rich granules were observed in *A. mellifera* drones and the concentration appears to be age-correlated [40]. These results point to a correlation between the magnetic material amount and individual age-function in this bee.

In ants, a division of labor among workers is usually based on differences in the probabilities of performing the different tasks associated with colony life, as in most eusocial insects. Worker tasks are determined by several factors in a dynamic process. The division of labor is roughly regulated by age and size and a flexible response yields refinement of task selection [41–43]. In the polymorphic *S. invicta,* recruitable workers become scouts as they age [10] and major workers are more likely to be involved in foraging [9]. If homing of forager (major) ants is based on magnetic orientation, it would then be reasonable to consider that the magnetic material is correlated to this function, under the ferromagnetic hypothesis. This is confirmed by our observation of more magnetic material in major than in minor ants of *S. richteri.* As both *S. interrupta* and *S. richteri* species belong to the *saevissima* complex, it is then considered in this paper that the magnetic material amount is size-correlated and probably age-correlated in *Solenopsis*, as in the bee [39, 40].

The short- and long-term results were similar. The long-term values of magnetic material amount and fractions fall within the range of the variation of the short experiment, except for one single datum of each parameter. As ants found out of the nest are more likely to be majors and both minor and major ants are found inside the nest [10], the sampling of the long- and short-term experiments led to different worker size distribution in the two groups of samples. The samples used in the long-term experiment would be composed mainly of foraging majors and those of the short term would have a wider distribution of worker sizes and consequently a wider distribution of magnetic material amount than the long-term one. We then speculate that the magnetic material amount of the long-term experiment falls in a narrowed region shifted to high values of the short-term distribution. The maintenance of the mound in the laboratory, for 10 days, for the short-term experiment data with nothing but water, while in the long-term experiments data was acquired on the collecting day, could also introduce a wider variability to the short-term distribution. Under these conditions the usual 95% probability, used to test if the long-term data fall within two standard deviations of the short-term mean, is too restrictive.

Magnetoreception in social insects is still poorly known [44]. In the current stage, the quantification and the characterization of the magnetic material in these insects are fundamentals for understanding magnetoreception, under the ferromagnetic hypothesis. The main purpose of this study has been to determine a representative sample of workers from a *Solenopsis* nest, based on the analysis of the distribution of magnetic material amount and relative fractions in its body parts in a short-term experiment, by FMR. The determination of this representative sample size would allow the analysis of the effect of other parameters, in particular the seasonal effect in the long-term experiment. Despite the high sensitivity of modern FMR spectrometers, the low magnetic material amount present in the intact insect body part and the limited number of parts in the sample holders result in difficult magnetic measurements. Nevertheless, FMR has been proved as a useful technique to study the magnetic material in social insects. The sensibility of the spectra parameters to the magnetic material properties has been shown.

The resonant field of the HF component was reproducible within a colony over the short term, while the line width data is more spread out supporting the combination of 20 body parts to represent the colony workers. The relative amounts of magnetic material in the body parts of the colony workers over the short term were normally distributed, although derived from non-normal distribution of the absolute magnetic material amount. Differences among the magnetic material (amount and fractions) of the 25 samples can be due to small variations in the relative orientation of the parts within a sample and of the sample itself relative to the magnetic field, differences in ingested magnetic material present in the thorax and abdomen and individual worker differences, so that the magnetic material amount (log transformed) of 25 samples (of 20 body parts each) is representative of this *Solenopsis* population with 0.21 (0.26 for thorax) confidence interval and 95% confidence level. It also enabled obtaining average magnetic amount values that resulted in the fraction reproducibility, with relative standard errors of 12% (THOR), at most.

The long-term measurements of magnetic material in *S. interrupta* worker body parts involved three different seasons, from late summer to early winter. The magnetic material ratios of the body parts are within the short-term distributions, except for the April value of the ANTN (figure 4) which also presents a different monthly behavior from the other body parts (figure 5(*b*)). A minimum magnetic material amount of the four body parts was observed about June. The mean magnetic material amount in the ant body parts is statistically significant (figure 3), with relative standard errors lower than 10%. Then, under the short versus long-term sample composition and the related considerations given above, that the statistical analysis was too restrictive, the changes observed during the 5 months may be due to a seasonality effect, as observed on *S. invicta* foraging [16], and not due to sample variability. It was shown that the variability of workers and the percent major workers changed over the year in *S. invicta* ant colonies, in Florida. Moreover, a lower mean number of *S. invicta* ants out of the colony was related to a minimum daily energy cost observed in winter [45]. In the South hemisphere winter, which occurs from 21 June to 20 September, it would therefore be reasonable to expect a lower mean number of forager ants going out of the nest. The minimum magnetic material amount in *S. interrupta* in the midwinter period can thus be related to this lower mean number of forager ants out of the nest, as this material is supposed to be involved in their homing behavior.

The complexity of the sociometry and sociogenesis is not restricted to fire ant colonies [10, 16, 45]. Characteristics of the *Pogonomyrmex badius* worker varies strongly with colony size, location in the nest, and season. [46]. *Pheidole morrisi* colony demography responds to seasonal fluctuations in food availability through behavioral changes rather than physical alterations [4]. The foraging behavior of *Pheidole ceres* colonies, tested in the field and laboratory, was influenced by season and colony composition and was not affected by moisture levels. *Pheidole ceres* workers appear to adjust their foraging preferences according to the colony's needs [5]. The workload of *Temnothorax albipennis* workers was shown to depend on colony size [47]. Raiding and migratory activities of the *Pachycondyla marginata* ant appeared to be affected by seasonal factors [48]; hunting is more frequent in the dry/cold season than in the rainy/hot season and migration is significantly oriented 13° with the magnetic North–South axis in the dry season [49].

Magnetic material properties and relative amount in ants add to this complexity. The two ferromagnetic components (HF and LF) and the absorption spectra area of six different ant species suggested that the magnetic material amount in the ant bodies increases as the local magnetic field intensity increases [28], which points to an adaptation of these ants to the magnetic environment characteristics.

The results presented here guide further systematic magnetic studies based on the average magnetic material in ants to verify the adequate sample size, as a first step, based on a statistical analysis. The dependence of individual size of major and minor workers, age-function and the seasonality effect should also be considered. The present paper suggests that the average magnetic material amount in body parts of workers of one *Solenopsis* nest reflects the seasonality on the number of foragers out of the nest. Further statistical research on the magnetic material based on their individual function, age and size is needed. Future studies should have data taken throughout a whole year, in shorter intervals than this paper. A determination of local climatic parameters, when sampling, could also help to elucidate magnetic material seasonality. These results can also be useful in orienting studies of magnetic material in other social insects.

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