doi:10.12741/ebrasilis.v9i1.526
e-ISSN 1983-0572
Publicação do Projeto Entomologistas do Brasil
www.ebras.bio.br

Fórum/Review

Magnetoreception in Social Wasps: An Update

Maria da Graça Cardoso Pereira-Bomfim[1]✉, William Fernando Antonialli-Junior[2] & Daniel Acosta-Avalos[3]

1. Universidade Federal da Grande Dourados, e-mail: airambio@yahoo.com.br (Autor para correspondência✉). 2. Universidade Estadual de Mato Grosso do Sul, e-mail: williamantonialli@yahoo.com.br. 3. Centro Brasileiro de Pesquisas Físicas, e-mail: dacosta00@gmail.com.

EntomoBrasilis 9 (1): 01-05 (2016)

Abstract. Magnetoreception is a mechanism of active orientation that occurs in animals with nervous systems. Social insects such as bees, ants, wasps and termites have been studied on the influence of the magnetic field exerts on its biology. The social wasps comprise species represented in Stenogastrinae, Vespinae and Polistinae, however studies on the influence of magnetic field on wasps Vespinae address only. The areas studied include the biomineralization of magnetic material and behavioral aspects related to changes in local intensity of the geomagnetic field. The objective of this review is to integrate knowledge of social wasps' magnetoreception in order to build an instructive overview of the current situation of studies, therefore, provide the conceptual framework for the development of future work on the topic.

Keywords: Hymenoptera; Magnetic Field; Magnetosensibility; Vespidae.

Magnetorrecepção em Vespas Sociais: Uma Atualização

Resumo. Magnetorrecepção é um mecanismo de orientação ativa que ocorre em animais com sistema nervoso. Insetos sociais tais como abelhas, formigas, vespas e cupins são estudados sobre a influência que o campo magnético exerce em sua biologia. As vespas sociais compreendem espécies representadas em Stenogastrinae, Vespinae e Polistinae, no entanto os estudos sobre a influência do campo magnético em vespas abordam somente Vespinae. As áreas de estudo incluem a biomineralização do material magnético e aspectos comportamentais relacionados a mudanças na intensidade do campo geomagnético local. O objetivo desta revisão é integrar o conhecimento sobre magnetorrecepção em vespas sociais, a fim de construir um panorama elucidativo da atual situação dos estudos, e assim fornecer uma estrutura conceitual para o desenvolvimento de trabalhos futuros sobre o tema.

Palavras-Chave: Campo Magnético; Hymenoptera; Magnetossensibilidade; Vespidae.

Wasps can be separated, according to the degree of sociability, into two groups: solitary species (Euparagiinae, Masarinae and Eumeninae) and social species (Stenogastrinae, Vespinae and Polistinae) (Carpenter 1982). Polistinae is the only subfamily of social wasps that occurs in Brazil, with a record of over 300 species, distributed in 22 genera in the tribes Epiponini, Mischocyttarini and Polistini (Carpenter & Marques 2001).

The geomagnetic field is an environmental abiotic factor that interacts constantly with living beings. It is as ancient as the origin of life on Earth (Jardine 2010). The perception of the environmental abiotic factors by microorganisms and animals led to the development of different mechanisms of orientation over time, which are responsible for the survival of the species, such as navigation, contributing to the process of natural selection (Skiles 1985; Gould 2008).

Magnetoreception is a mechanism of active orientation that occurs in animals with nervous systems, and involves detecting the geomagnetic field by a sensory mechanism coupled to cellular systems, such as mechanoreceptors that transduce this signal to the brain. To explain this mechanism there are basically three hypotheses or specific models (Schiff 1991; Shcherbakov & Winklhofer 1999; Lohmann & Johnsen 2000).

One hypothesis is based on Faraday's law of magnetic induction, which it is assumed that the organism detects a difference in electrical potential, generated in specialized organs such as the ampolla of Lorenzini in fishes, resulting from its motion through the geomagnetic field. Another hypothesis is the light dependent magnetoreception or radical pair mechanism, which is based on the fact that several chemical reactions can change their kinetics in the presence of magnetic fields. Currently it is assumed that cryptochrome molecules are involved in the radical pair mechanism, because after this molecule absorb light the chemical reactions that follows vary depending on the relative orientation of the molecular axis of symmetry with the direction of the geomagnetic field (Wiltschko & Wiltschko 2006).

The third hypothesis is the ferromagnetic hypothesis which is based on the presence of magnetic nanoparticles as magnetic field sensors. It is supported by the discovery of magnetite nanoparticles in various species of animals from insects (Gould *et al.* 1980; Esquivel *et al.* 1999, Wajnberg *et al.* 2010) to humans (Kirschvink *et al.* 1992) and this hypothesis is one of the most accepted due to evidence accumulated.

The studies of Blakemore (1975) and Bellini (2009) with aquatic bacteria demonstrated that the geomagnetic field is capable of producing effects in biological systems, verifying that magnetotactic bacteria directly respond to magnetic stimuli, swimming in the direction of the force lines of the geomagnetic field constituting the first unequivocal evidence that the magnetic field may directly influence the behavior of a living being.

The objective of this review is to describe the state of the art in the knowledge of social wasps' magnetoreception in order to get insights about the current situation of this topic and provide the conceptual structure for the development of future studies.

Funding Agencies: CAPES; CNPq

SOCIAL HYMENOPTERA

Among the social insects the bee *Apis mellifera* L. has been the most studied considering the sensitivity to the geomagnetic field. Despite innumerous evidences that they orient in this field, no one knows for sure what the reception mechanisms able to detect it and how the information is transmitted to the bee nervous system (Acosta-Avalos *et al.* 2000; Wajnberg *et al.* 2010; Válková & Vachá 2012).

One of the earliest evidence of the influence of the geomagnetic field on the behavior of bees was obtained by Lindauer & Martin (1968). They found that errors in the information transmitted during the execution of the waggle dance varied according to the direction and intensity of the Earth's magnetic field; and also found that when a swarm leaves the original hive worker bees build new combs in the same previous magnetic direction, and that apparently the circadian rhythms of bees could be given by the variations in the intensity and direction of the geomagnetic field (Towne & Gould 1985). Magnetic fields are known to have influence on the temporal and spatial orientation of these bees (Martin & Lindauer 1977; Korall *et al.* 1988; Martin *et al.* 1989).

The motility of the bees is not affected by a uniform magnetic field but when the same field is intermittently imposed (periods of 10 or 15 min) the mean activity oscillates in phase with the magnetic field oscillations (Hepworth *et al.* 1980).

Martin *et al.* (1989) found that artificial magnetic fields can influence physiological processes in bees. They reported that in non-homogeneous static magnetic field there is a reduction in the activity of flight and an increase of more than 60% in the life span of individuals, although higher chronological age, the content of lipofuscin of brain cells was slightly reduced in these bees, in relation to bees in geomagnetic field conditions.

Induced magnetization was measured in *A. mellifera* and this signal was associated to magnetic nanoparticles with diameters in the range 30-35 nm, which were assumed to be involved in the detection of magnetic fields by bees (Gould *et al.* 1980).

Schiff (1991) found, in the second abdominal ganglia of these bees, electrondense material identified as magnetite particles in the range of sizes characteristic of single-domain and superparamagnetic particles. The stability of the magnetic moment in magnetic nanoparticles depends on the type of mineral, the crystalline structure and the size. Particles with magnetic moment stable in the grain structure against thermal disorientation are known as single-domain particles, and particles with magnetic moment continuously disoriented by the thermal energy are known as superparamagnetic because they react easily to external magnetic fields (Bean & Livingston 1959). Superparamagnetic and single domain particles of magnetite can be used to detect the geomagnetic field parameters and their small variations and this information can be transmitted to the nervous system through secondary mechanoreceptors (Johnsen & Lohmann 2005).

Schiff & Canal (1993) found in the abdominal hairs of these bees, particles of magnetite that might be involved in the detection and amplification of the external magnetic field gradients. Other studies have also indicated the presence of iron oxides by biomineralization (Gould *et al.* 1978; Kuterbach & Walcott 1986; Hsu & Li 1994).

Bees can also be trained to do associations between food source and the presence and direction of local magnetic fields (Walker & Bitterman 1985; Frier *et al.* 1996).

In ants have been detected the influence of the magnetic field by Anderson & Vander der Meer (1993) who observed differences in the time to trail formation by fire ant workers (*Solenopsis invicta* Buren) in conditions of normal and inverted geomagnetic field. Recently it has been shown that this type of ant shows magnetic orientation in low light ambient, changing its orientation direction when the geomagnetic field direction changes (Sandoval *et al.* 2012).

For the migratory ant *Pachycondyla marginata* (Roger), Acosta-Avalos *et al.* (2001) showed that the migration routes preferentially are in the geomagnetic North direction, showing the possibility of using the information of the geomagnetic field in the choice of the migration direction.

A compass response was shown in *Formica rufa* L. orientation (Camlitepe & Stradling 1995) and *Oecophylla smaragdina* (Fabricius) (Jander & Jander 1998). And in the absence of sunlight cues, *Atta colombica* Guérin-Méneville ants respond to magnetic field reversals (Banks & Srygley 2003). Distortions of the local geomagnetic field have been proposed for handling the leafcutter ant (Paz *et al.* 2012). Wajnberg *et al.* (2010) presented a review of recent magnetic orientation experiments in ants. Interestingly, experiments done with ants do not show light-dependent magnetoreception up to our knowledge, perhaps because of their subterranean life that makes ant's life be the most of the time in darkness or perhaps because experiments have not been planned to test specifically light-dependent magnetoreception.

The main model used to understand magnetoreception in insects is the ferromagnetic hypothesis. It implies that there must be magnetic nanoparticles in the ant body. The usual ways to detect these nanoparticles are measurements by magnetometry techniques and extraction and observation by transmission electron microcopy. Among the magnetometry techniques two have been used in ants: ferromagnetic resonance (FMR) and SQUID magnetometry (Wajnberg *et al.* 2010).

The presence of magnetic material, probably magnetite, was demonstrated by applying the FMR technique in smashed whole bodies of ants *Solenopsis* sp. (Esquivel *et al.* 1999), in crushed abdomens of the migratory ant *P. marginata* (Wajnberg *et al.* 2000), in abdomens of honeybees *A. mellifera* (El-Jaick *et al.* 2001) and in body parts of the termite *Neocapritermes opacus* Hagen (Alves *et al.* 2004). SQUID magnetometry done in samples of *A. mellifera* bees and *N. opacus* termites showed hysteresis curves with parameters similar to the observed in *P. marginata* ants (Ferreira *et al.* 2005)

Magnetic materials were found in different parts of the body of social insects. Hysteresis curves at 300K, obtained with SQUID magnetometry, of ants *P. marginata* (Wajnberg *et al.* 2004) indicate that the major contribution to the saturation magnetization comes from the antenna, as well as in stingless bees, *Schwarziana quadripunctata* (Lepeletier) (Lucano *et al.* 2006). In FMR results was observed greater amount of magnetic material in the heads with antennae than in abdomens with petioles of the ant *Solenopsis substituta* Santschi (Abraçado *et al.* 2005). These results points to the antennae as the place where the magnetoreceptor must be localized in ants and stingless bees, but until now this magnetic sensor has not been found. A study done with antenna of *P. marginata* ants indicates that the Johnston's organ and other antennae joints might host a magnetoreceptor sensor based in magnetic nanoparticles (Oliveira *et al.* 2010).

SOCIAL WASPS

The social wasps comprise representatives in Stenogastrinae, Vespinae and Polistinae (Carpenter 1982), but studies on the influence of magnetic fields on vespids so far include only Vespinae.

One of the first studies on social wasps was done by Kisliuk & Ishay (1977). In that study wasps of *Vespa orientalis* L. in different life stages were exposed to artificial magnetic fields, and the nest architecture construction and behavior were analyzed. Nests with 15 to 20 wasps were put inside and outside a square cross-section coil, and three experimental situations were studied: one with artificial uniform horizontal magnetic field of 23.3 Oe, other with artificial uniform horizontal magnetic field of 1.3 Oe and other with an artificial nonuniform horizontal magnetic field among 0.3 and 0.6 Oe. The local geomagnetic horizontal component was 0.33 Oe. After 16 days, several observations were done. The most interesting were: adult hornets died in the incidence of an uniform magnetic field in a period of 1 to 2 days and did not construct any nest; juvenile lasted more to died and showed a period of adaptation of 4 to 5 days in places were the intensity of the magnetic field was stronger (near to the coil), constructed nest and died with 5 to 7 days; in nonuniform fields juvenile did not die and constructed nests; the architecture of the nest was similar to the normal one, but with a higher distribution of orientations in the cylindrical cells, and the pedicles inverted its normal orientation (from downward to upward).

All these results show that wasps are sensible to magnetic fields. It is known that wasps use as reference to nest architecture the gravitational field (Ishay & Sadeh 1975). The influence of the magnetic field on the architecture and orientation of wasp nests show that, in some way, there is a relation among the perception of the gravitational field and the magnetic field. Also the mentioned research is not related to magnetoreception in wasps but only to magnetic sensibility.

The hexagonal cells of immatures inside the comb in nests of *V. orientalis* are uniform in their architecture and orientation. Stokroos *et al.* (2001) found that each cell contains a small crystal stuck with saliva of the wasp, which projects down from the center of its domed roof having about 100 µm in diameter and composed of polydomains, and with a typical composition of the magnetic mineral ilmenite ($FeTiO_3$). These crystals form a network that can help the wasps to assess the symmetry, the balance of the cells and the direction of gravity, while building the comb. It is not known what the wasps perceive of ilmenite, because as well as being a magnetic material it also reflects infrared light. These two properties make this material an excellent source of information for spatial orientation (Ishay *et al.* 2008).

These wasps possibly collect the crystals of the local environment, but it is not ruled out biomineralization, because the titanium and the iron are present in their bodies (Stokroos *et al.* 2001).

As mentioned above, the construction of the combs in Vespinae is always in the vertical direction, and on the roof of each cell at least a small magnetic stone is incorporated and fixed by saliva. Thus Ishay *et al.* (2008) attempted to identify, and characterize these stones that exist in the roof and walls of the combs of *V. orientalis*, using bio-ferrography to isolate magnetic particles on slides. The slides, as well as the original cells were analyzed by a variety of analytical techniques in an environmental scanning electron microscope. These authors verified that both the roof and the walls of each comb cell contained minerals such as ferrites, as well as titanium and zirconium. The last two components were less abundant in the soil around the nest and are known to reflect infrared light. Infrared images showed a thermoregulatory center in the dorsal thorax of adults. However it is not known whether these insects can sense infrared light.

Magnetic remanence has been detected in abdomens of *Vespa affinis* L. (Hsu 2002). This suggests that magnetic materials are present in the body of these wasps. Subsequently, Hsu (2004) found the deposition of intracellular iron in *V. affinis* using transmission electron microscopy and atomic emission spectroscopy. He shows that the deposition would begin on the 2nd day after hatching. Also noted that vesicles containing granules of iron would be randomly distributed within the cytoplasm of trophocytes below the cuticle of hornets. The iron granules are formed by aggregation of dense tiny particles, and deposited in vesicles of iron, a double membrane, which appear to derive from the endoplasmic reticulum. These granules continuously expand by adding dense tiny particles until the 5th day after hatching. Then, granules and vesicles merge and expand. The existence of a blurred area under the inner membrane of the vesicle plays an important role in the formation of small dense particles. The elemental composition analysis indicated that the granules were composed mainly of iron, phosphorus and minor amounts of calcium.

Thus the deposition of intracellular iron was first demonstrated in cells of honeybees (Kuterbach *et al.* 1986; Hsu & Li 1994), then in bumblebees (Walcott 1985) and later in wasps by Hsu (2004).

Recently Pereira-Bomfim *et al.* (2015) showed that the social wasp *Polybia paulista* (Ihering) is sensible to modifications in the local geomagnetic field. The experiments were done with magnets and coils, and in both cases the foraging flight frequency increases when the geomagnetic field was modified.

CONCLUSIONS

There are few studies in social wasps considering magnetoreception and magnetosensibility, compared to similar studies in bees, ants and termites. More studies must be done to understand the influence of the geomagnetic field and artificial magnetic fields on the behavior of wasps.

Studies conducted in different animals have shown that magnetoreception can depend on the existence of intracellular magnetic nanoparticles or depend on light absorbing molecules sensible to magnetic fields (light-dependent magnetoreception) (Wiltschko & Wiltschko 2006). In social insects, the most studied has been the bee *A. mellifera* however some studies has been inconclusive (Válková & Vachá 2012) and there are still many studies to be done to show the type of magnetoreception (dependent or independent of light) in these insects. Ants are the second most studied group. However, in all cases is still unknown the location of the magnetorreceptor and their nature (Wajnberg *et al.* 2010).

It is expected that in bees and wasps the same will happen, not in the abdomen as has been discussed. A recommendation for future studies in wasps is the search for magnetic particles on the head and antennae and the analysis of the effects of monochromatic light combined with magnetic fields.

Special emphasis should be given to the fact that flying insects should feel magnetic fields in the same way as birds, showing both types of magnetoreception.

ACKNOWLEDGMENTS

The authors gratefully the CAPES for a doctoral fellowship awarded to the first author. WFAJ acknowledges his research grant from CNPq. DAA acknowledges CNPq financial support.

REFERENCES

Abraçado, L.G., D.M.S. Esquivel, O.C. Alves & E. Wajnberg, 2005. Magnetic Material in Head, Thorax and Abdomen of *Solenopsis substituta* Ants: a Ferromagnetic Resonance (FMR) Study. Journal of Magnetic Resonance, 175: 306-316. DOI: http://dx.doi.org/10.1016/j.jmr.2005.05.006.

Acosta-Avalos, D., D.M.S. Esquivel, E. Wajnberg, H.G.P. Lins de Barros, P.S. Oliveira & I. Leal, 2001. Seasonal patterns in the orientation system of the migratory ant *Pachycondyla marginata*. Naturwissenschaften, 88: 343-346. DOI: http://dx.doi.org/10.1007/s001140100245.

Acosta-Avalos, D., E. Wajnberg, D.M.S. Esquivel & L.J. El-Jaick, 2000. Insetos sociais: um exemplo de magnetismo animal. Revista Brasileira de Ensino de Física, 22: 317-323.

Alves, O.C., E. Wajnberg, J.F. Oliveira & D.M.S. Esquivel, 2004. Magnetic material arrangement in oriented termites: a magnetic resonance study. Journal of Magnetic Resonance, 168: 246-251. DOI: http://dx.doi.org/10.1016/j.jmr.2004.03.010.

Anderson, J.B. & R.K. Vander der Meer, 1993. Magnetic orientation in fire ant, *Solenopsis invicta*. Naturwissenschaften, 80: 568-570. DOI: http://dx.doi.org/10.1007/BF01149274.

Banks, A.N. & R.B. Srygley, 2003. Orientation by magnetic field in leaf-cutter ants, *Atta colombica* (Hymenoptera: Formicidae). Ethology, 109: 835-846. DOI: http://.doi.org/10.1046/j.0179-1613.2003.00927.x.

Bean, C.P. & J.D. Livingston, 1959. Superparamagnetism. Journal of Applied Physics, 30: S120-S129.

Bellini, S., 2009. On a unique behavior of freshwater bacteria. Chinese Journal of Oceanology and Limnology, 27: 3-5.

Blackemore, R.P., 1975. Magnetotactic bacteria. Science, 19: 377-379. DOI: http://dx.doi.org/10.1126/science.170679.

Camlitepe, Y. & D.J. Stradling, 1995. Wood ants orient to magnetic fields. Proceedings of the Royal Society of London, 261: 37-41. DOI: http://dx.doi.org/10.1098/rspb.1995.0114.

Carpenter, J.M, 1982. The philogenetic relationships and natural classification of the Vespoidea (Hymenoptera). Systematic Entomology, 7: 11-38. DOI: http://dx.doi.org/10.1111/j.1365-3113.1982.tb00124.x.

Carpenter, J.M. & O.M. Marques, 2001. Contribuição ao estudo dos vespídeos do Brasil (Insecta, Hymenoptera, Vespoidea, Vespidae) [CD-ROM]. Cruz das Almas – BA, Brasil. Universidade Federal da Bahia, Escola de Agronomia, Departamento de Fitotecnia/ Mestrado em Ciências Agrárias. Série Publicações Digitais, 2.

El-Jaick, L.J., D. Acosta-Avalos, D.M.S. Esquivel, E. Wajnberg & M.P. Linhares, 2001. Electron paramagnetic resonance study of Honeybee *Apis mellifera* abdomens. European Biophysics Journal, 29: 579-586. DOI: http://dx.doi.org/10.1007/s002490000115.

Esquivel, D.M.S., D. Acosta-Avalos, L.J. El-Jaick, A.D.M. Cunha, M.G. Malheiros, E. Wajnberg & M.P. Linhares, 1999. Evidence for magnetic material in the fire ant *Solenopsis* sp. By Electron Paramagnetic Resonance measurements. Naturwissenschaften, 86: 30-32. DOI: http://dx.doi.org/10.1007/s001140050564.

Ferreira, J., G. Cernicchiaro, M. Winklhofer, H. Dutra, P.S. Oliveira, D.M.S. Esquivel, E. Wajnberg, 2005. Comparative magnetic measurements on social insects. Journal of Magnetism and Magnetic Materials, 289: 442-444.

Frier, H.J., E. Edwards, C. Smith, S. Neale & T.S. Collet, 1996. Magnetic compass cues and visual pattern learning in honeybees. Journal of Experimental Biology, 199: 1353-1361.

Gould, J.L., 2008. Animal navigation: the evolution of magnetic orientation. Current Biology, 18: R482-R484. DOI: http://dx.doi.org/10.1016/j.cub.2008.03.052.

Gould, J.L., J.L. Kirschvink & K.S. Deffyes, 1978. Bees have magnetic remanence. Science, 201: 1026-1028. DOI: http://dx.doi.org/10.1126/science.201.4360.1026.

Gould, J.L., J.L. Kirschvink, K.S. Deffeyes & M.L. Brines, 1980. Orientation of Demagnetized Bees. Journal of Experimental Biology, 86: 1-8.

Hepworth, D., R.S. Pickard & K.J. Overshott, 1980. Effects of the periodically intermittent application of a constant magnetic field on the mobility in darkness of worker honeybees. Journal of Apicultural Research, 19: 179-186.

Hsu, C.Y. & C.W. Li, 1994. Magnetoreception in honeybees. Science, 265: 95-96. DOI: http://dx.doi.org/10.1126/science.265.5168.95.

Hsu, C.Y., 2002. Magnetic remanence in common hornet (*Vespa affinis*). Journal of Minghsin Institute of Technology, 28: 181-186.

Hsu, C.Y., 2004. The process of iron deposition in the common hornet (*Vespa affinis*). Biology of the Cell, 96: 529-537. DOI: http://dx.doi.org/10.1016/j.biolcel.2004.05.001.

Ishay, J. & D. Sadeh, 1975. Direction finding by hornets under gravitational and centrifugal forces. Science, 190: 802-804. DOI: http://dx.doi.org/10.1126/science.1198099.

Ishay, J.S., Z. Barkay, N. Eliaz, M. Plotkin, S. Volynchik & D.J. Bergman, 2008. Gravity orientation in social wasp comb cells (Vespinae) and the possible role of embedded minerals. Naturwissenschaften, 95: 333-342. DOI: http://dx.doi.org/10.1007/s00114-007-0334-z.

Jander, R. & U. Jander, 1998. The light and magnetic compass of the weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae). Ethology, 104: 743-758.

Jardine, M., 2010. Sunscreen for the young earth. Science, 327: 1206-1207.

Johnsen, S. & K.J. Lohmann, 2005. The physics and neurobiology of magnetoreception. Nature Reviews Neuroscience 6, 703-712. DOI: http://dx.doi.org/10.1038/nrn1745.

Kirschvink, J.L., A.K. Kirschvink & B. Woodford, 1992. Magnetite biomineralization in the human brain. Proceedings of the National Academy of Sciences USA, 26: 7683-7687.

Kisliuk, M. & J. Ishay, 1977. Influence of an additional magnetic field on hornet nest architecture. Experientia, 33: 885-887.

Korall, H., T. Leucht & H. Martin, 1988. Bursts of magnetic fields induce jumps of misdirection in bees by a mechanism of magnetic resonance. Journal of Comparative Physiology A, 162: 279-284.

Kuterbach, D.A. & B. Walcott, 1986. Iron containing cells in the honeybee (*Apis mellifera*). I. Adult morphology and physiology. Journal of Experimental Biology, 126: 375-387.

Lindauer, M. & H. Martin, 1968. Die Schwereoientierung der Biene unter dem Einfluss des Erdmagnetfelds. Zeitschrift fur vergleichende physiologie, 60: 219-243.

Lohmann, K.J. & S. Johnsen, 2000. The neurobiology of magnetoreception in vertebrate animals. Tins - Trends in Neurosciences, 23: 153-159.

Lucano, M.J., G. Cernicchiaro, E. Wajnberg & D.M.S. Esquivel, 2006. Stingless Bee Antennae: a magnetic sensory organ? BioMetals, 19: 295-300. DOI: http://dx.doi.org/10.1007/s10534-005-0520-4.

Martin, H. & M. Lindauer, 1977. Der Einfluβ des Erdmagnetfeldes auf die Schwereorientierung der Honigbiene (*Apis mellifica*). Journal of Comparative Physiology A, 122: 145-187.

Martin, H., H. Korall & B. Forster, 1989. Magnetic field effects on activity and ageing in honeybees. Journal of Comparative Physiology A, 164: 423-431.

Oliveira, J.F., E. Wajnberg, D.M. Esquivel, S. Weinkauf, M. Winklhofer, M. Hanzlik, 2010. Ant antennae: are they sites for magnetoreception? Journal of the Royal Society, Interface 7: 143-152. DOI: http://dx.doi.org/10.1098/rsif.2009.0102.

Paz, H., M.A. Vargas, O.A. Forero, J.F. Pabón, J.A. Plaza, 2012. Local distorion of the earth's magnetic field as a proposal for handling the leafcutter ant species *Atta* spp. (Hymenoptera: Formicidae). Ingeniería e Investigación, 32: 28-33.

Pereira-Bomfim, M.G.C., W.F. Antonialli-Junior, D. Acosta-Avalos, 2015. Effect of magnetic field on the foraging rhythm and behavior of the swarm-founding paper wasp *Polybia paulista* Ihering (Hymenoptera: Vespidae). Sociobiology, 62: 99-104.

Sandoval, E.L., E. Wajnberg, D.M.S. Esquivel, H. Lins de Barros & D. Acosta-Avalos, 2012. Magnetic orientation in *Solenopsis* sp. ants. Journal of Insect Behavior, 25: 612-619.

Schiff, H. & G. Canal, 1993. The magnetic and electric fields induced by superparamagnetic magnetite in honeybees. Biological Cybernetics, 69: 7-17.

Schiff, H., 1991. Modulation of spike frequencies by varying the ambient magnetic field and magnetite candidates in bees (*Apis mellifera*). Comparative Biochemistry and Physiology A, 4: 975-985. DOI: http://dx.doi.org/10.1016/0300-9629(91)90325-7.

Shcherbakov, V.P. & M. Winklhofer, 1999. The osmotic magnetometer: a new model for magnetite-based magnetoreceptors in animals. European Biophysics Journal, 28: 380-392. DOI: http://dx.doi.org/10.1007/s002490050222.

e-ISSN 1983-0572

Skiles, D.D., 1985. The geomagnetic field: its nature, history and biological relevance, p. 43-102. *In:* Kirschvink, J.L., D.S. Jones & B.J. MacFadden, (Eds.). Magnetite Biomineralization and Magnetoreception in Organisms. A new biomagnetism. New York, Plenum Press, 682p.

Stokroos, I., L. Litinetsky, J.J.L.Van der Want & J.S. Ishay, 2001. Keystone-like crystals in cells of hornet combs. Nature, 411: 654.

Towne, W.F. & J.L. Gould, 1985. Magnetic field sensitivity in honeybees, p. 385-406. *In*: Magnetite Biomineralization and Magnetoreception in Organisms. A new biomagnetism. Kirschvink, J. L., Jones, D.S. & MacFadden B.J. (Eds). Plenum Press – New York and London. 704 p.

Válková, T. & M. Vácha, 2012. How do honeybees use their magnetic compass? Can they see the North? Bulletin of Entomological Research, 102: 461-467. DOI: http://dx.doi.org/10.1017/S0007485311000824.

Wajnberg, E., D. Acosta-Avalos, L.J. El-Jaick, L.G. Abraçado, J.L.A. Coelho, A.F. Bakusis, P.C. Morais & D.M.S. Esquivel, 2000. Electron Paramagnetic Resonance Study of the Migratory Ant *Pachycondyla marginata* abdomens. Biophysical Journal, 78: 1018-1023. DOI: http://dx.doi.org/10.1016/S0006-3495(00)76660-4.

Wajnberg, E., D. Acosta-Avalos, O.C. Alves, J.F. Oliveira, R.B. Srygley & D.M.S. Esquivel, 2010. Magnetoreception in eusocial insects: an update. Journal of the Royal Society Interface, 7: S207-S226. DOI: http://dx.doi.org/10.1098/rsif.2009.0526.focus.

Wajnberg, E., G. Cernicchiaro & D.M.S. Esquivel, 2004. Antennae: the strongest magnetic part of the migratory ant. BioMetals, 17: 467-470. DOI: http://dx.doi.org/10.1023/B:BIOM.0000029443.93732.62.

Walcott, B., 1985. The cellular localization of particulate iron, p. 417-438. *In*: Kirschvink, J.L., D.S. Jones & B.J. MacFadden (Eds.). Magnetite biomineralization and magnetoreception in organisms: A new biomagnetism. New York, Plenum Press. 682p.

Walker, M.M. & M.E. Bitterman, 1985. Conditioned responding to magnetic field by honeybees. Journal of Comparative Physiology A, 157: 67-71. DOI: http://dx.doi.org/10.1007/BF00611096.

Wiltschko, W. & R. Wiltschko, 2006. Magnetoreception. BioEssays, 28: 157-168.

Received in: 03.v.2015
Accept in: 10.vii.2015

****

Suggested citation:

Pereira-Bomfim, M. da G.C., W.F. Antonialli-Junior & D. Acosta-Avalos, 2016. Magnetoreception in Social Wasps: An Update. EntomoBrasilis, 9 (1): 01-05.
Available in: doi:10.12741/ebrasilis.v9i1.526