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Take a ride with the hitchhiker ants: A systematic review

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Trabalho de Conclusão de Curso apresentado ao Curso de Graduação em Ciências Biológicas da Universidade Federal de Juiz de Fora como requisito à obtenção do título de Bacharel em Ciências Biológicas.

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RESUMO

Caroneiras são as menores operárias de formigas cortadeiras que frequentemente são observadas nas trilhas de forrageamento sobre os fragmentos que estão sendo carregados por operárias forrageiras. Diversos estudos foram realizados para entender qual seria a função dessas operárias e, conseqüentemente, quais os motivos para se exporem a potenciais perigos. A fim de possibilitar uma visão ampla e comparativa sobre a ocorrência, função e fatores desencadeadores desse comportamento realizamos uma revisão sistemática, feita em duas bases de dados, Web of Science (WOS) e Scopus, seguindo o Protocolo PRISMA, que nos permitiu comparar o resultado de 12 artigos. O país mais produtivo em relação a artigos publicados com caroneiras foi o Brasil, enquanto a revista com maior número de publicações foi *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA*. As espécies mais investigadas foram *Atta cephalotes* e *Atta sexdens*. Das funções atribuídas às caroneiras: “Defesa contra parasitóides” foi a mais citada, o que coincide com o fator “Presença de forídeos”, o mais citado como desencadeador do comportamento de caroneira. O fato do Brasil estar na liderança de países mais produtivos indica um empoderamento dos pesquisadores brasileiros sobre a investigação de importantes espécies nativas. O estudo envolvendo caroneiras e suas funções ainda é precário haja vista o baixo número de artigos sobre o assunto, sendo necessária a avaliação deste comportamento em outras espécies de formigas cortadeiras, permitindo o aprimoramento do conhecimento sobre as funções, fatores que desencadeiam esse surpreendente comportamento e como esses diferentes fatores interagem entre si.

Palavras-chave: Caroneiras, Formigas cortadeiras, Comportamento Animal.

ABSTRACT

Hitchhikers are minor workers of leaf cutting ants often observed on the foraging trails over the fragments that were being carried by foraging workers. Several studies began to be carried out to find out what is their function and, consequently, what are the reasons for exposing themselves to potential hazards. In order to enable a broad and comparative view about the hitchhikers occurrence, function, and factors there are most cited as triggers of this behaviour, we provide a systematic review, made in two databases: Web of Science (WOS) and Scopus, following the PRISMA protocol, which allowed us to compare the result of 12 papers. The most productive country in relation to published articles with hitchhikers was Brazil, while the journal with most publications was *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA*. The species mainly investigated were *Atta cephalotes* and *Atta sexdens*. Of the functions attributed to the hitchhikers: "Defense against parasitoids" was the most cited, what coincides with factor "Phorids presence", the most cited one as trigger of the hitchhiker behavior: The most productive country result indicates an empowerment of brazilian researchers over the investigation of important native species. The study involving hitchhikers and their functions is still very precarious and needs more research involving a wider range of species allowing us to improve the knowledge about the functions, what factors trigger this amazing behavior and how these different factors could interact with each other.

Keywords: Hitchhiker, Leaf cutting ants, Animal behavior.

SUMMARY

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1. INTRODUCTION

The eussocial mode of life is one of the characteristics responsible for the ecological success of the ants due to its extremely high level of organization and cooperation among the members of a colony (Dupuis and Harrison 2017). In leaf-cutter ants, workers which belong to different physical and/or age castes execute different tasks simultaneously (Wilson 1980a; Forti et al. 2004; Camargo et al. 2007; Mehdiabadi and Schultz 2009). While major workers usually protect their nestmates from predators and assist during the cutting of leaves, medium-sized workers act by foraging leaf fragments, cutting and transporting them back to the colony. Minor workers perform a series of tasks inside the nest such as clipping plant material into smaller fragments, crushing and molding them into moist pellets, and finally incorporating them in the fungus garden. Also they are responsible to care for larvae and eggs (Hölldobler and Wilson 2011)

However these minor workers are often observed on the foraging trails and over the fragments that were being carried by forager workers and, since these workers did not cut or carry leaf fragments, studies began to be carried out to find out what is their function, consequently, what are the reason for exposing themselves to potential hazards (Feener and Moss 1990; Linksvayer et al. 2002; Vieira-Neto et al. 2006). Due to the habit of “hitchhiking” in the leaf fragments that are being carried, these are called “hitchhikers”.

Upon leaving the nests, the workers are exposed to a series of potential hazards such as parasitoid insects, desiccation and predation. The loaded workers are more exposed to these risks while cutting and carrying leaf fragments back to the colony, since they are slow-moving and are using their jaws to fix and load the fragments, which turn them unable to defend themselves from possible parasitoids. Given that tasks outside the nest increase mortality risk by exposing workers to predators and pathogens, allocation of older workers to external labor seems to be adaptively advantageous to colonies (Hölldobler and Wilson 1990).

One of the biggest threats to foragers is phorids flies. Phorid flies are one of the most diverse groups of insects, and a lot of species are parasitoids of leaf-cutting ants (Weber, 1972; Disney, 1994). Some studies have shown that, even with a low number of real attacks, the presence of phorids on the trail delays the speed with which ants collect and transport leaf fragments (Orr, 1992; Feener & Brown, 1993; Tonhasca, 1996; Bragança et al., 1998).

Several hypotheses have been raised and five non-exclusive hypotheses are recurrent in explanations about the function of hitchhikers: defense (Feener and Moss 1990), leaf preparation for entry into the nest (Camargo et al. 2003; Griffiths and Hughes 2010), energy conservation (Feener and Moss 1990; Linksvayer et al. 2002), sap feeding (Stradling 1978; Linksvayer et al. 2002) and avoid traffic jams on the trail (Hastenreiter, et al. 2018).

In this study we provide a systematic review about the hitchhikers in order to enable a broad and comparative view about the hitchhikers occurrence and function, and also which factors are most likely to explain the occurrence of the behavior of hitchhikers and the stimuli that promote their recruitment.

2. MATERIAL AND METHODS

Data collection was made following the PRISMA protocol (Moher et al., 2015, adapted from Moher et al., 2009), which allowed us to establish the selection criteria, definition of search strategies, assessment of the studies, and the extraction of data relevant to our question.

To localize the studies related to the occurrence, triggering factors, and function of hitchhikers, we made searches in the Data Basis Web of Science (WOS) and Scopus using the search code:((leaf-cutting* ant OR leafcutter ant* OR Attini OR Atta OR Acromyrmex) AND hitchhiker).

The articles obtained in the research were examined and selected when they comprised studies with leaf-cutting ants that evaluate the hitchhiker function, which was our eligibility criteria. From these articles we extracted data about: (i) studied species, (ii) the function of the hitchhiker, and (iii) factors related as triggers of the occurrence of hitchhikers.

Once the data were collected, we used the bibliometrix package (Aria & Cuccurullo, 2017) of the software R (version 4.0.3) to obtain the metrics related to: (a) country distribution and (b) frequency of articles by journals and their impact factor.

3. RESULTS

Initially we found 16 articles on Data Basis Web of Science (WOS) and 12 articles on Scopus totalizing 28 articles. Furthermore, one more article was added by searching on the references of these 28 articles, totalizing 29 papers. The search in both databases revealed the same papers and thus after the duplicate removal, the number of examined papers was 12 (Figure 1).

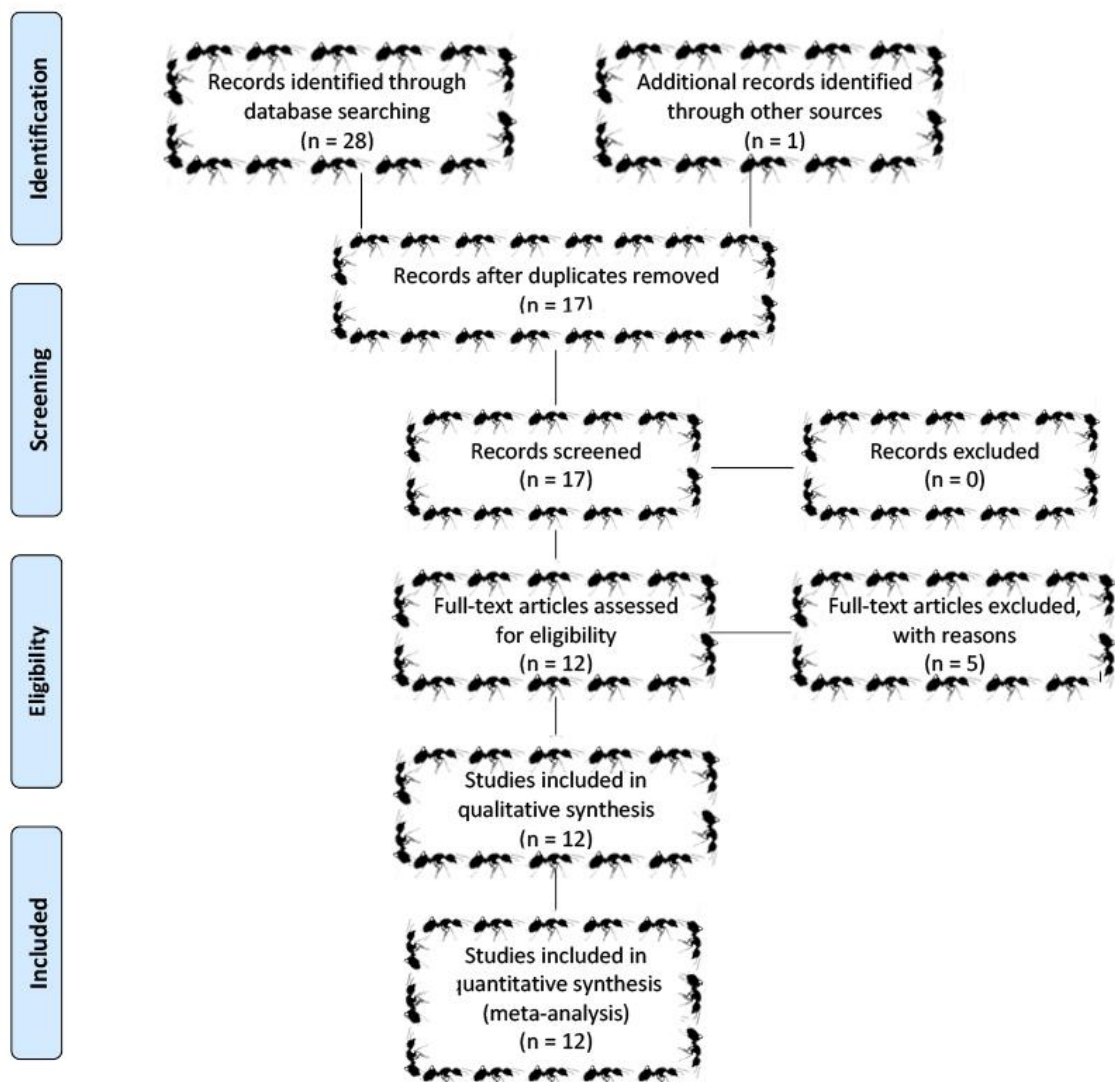


Figure 1 - Prisma flowchart showing the selection process of the publications studies on hitchhiker behavior. Database searches returned 28 possible data sources. Figure adapted from PRISMA (Moher et al., 2009).

The most productive country in relation to articles with hitchhikers was Brazil with 6 of 12 (50%) publications, followed by the UK with 2 of 12 (16.7%) publications and Argentina, Germany, Panama, USA with 1 of 12 (8.3%) publications each (Figure 2).

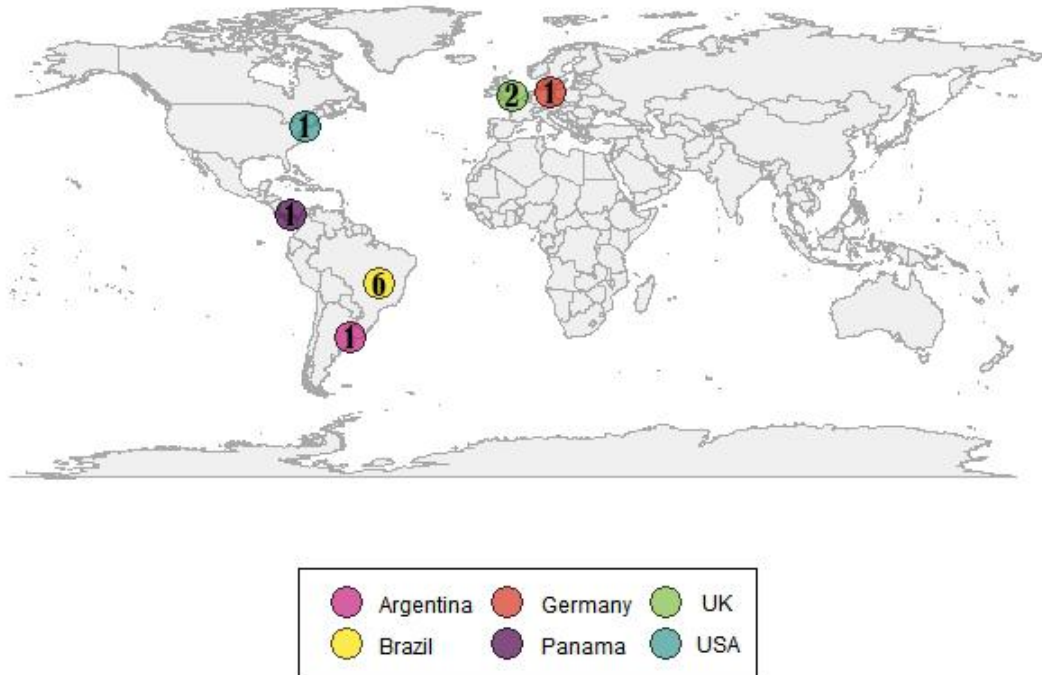


Figure 2 - Distribution and number of publications related to the theme hitchhiker considering the authors' affiliation over the world.

About the journals, we verified that *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* whose impact factor is 1.696 published 3 of the 12 articles analyzed (25%), while *BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY* with impact factor of 2.277 published 2 of 12 articles analyzed (16.7%). The other journals published one article each (Figure 3).



Figure 3 - Word cloud representing the number of publications by scientific journals included in the systematic review. The font size represents the frequency of registers. The colors indicate the impact factor in which each journal is fitted.

The theme of hitchhikers (occurrence and/or function) was mainly investigated for the species *Atta cephalotes* and *Atta sexdens* (12 articles) followed by the species *Atta colombica*, *Atta laevigata* and *Acromyrmex subterraneus*. (Figure 4).

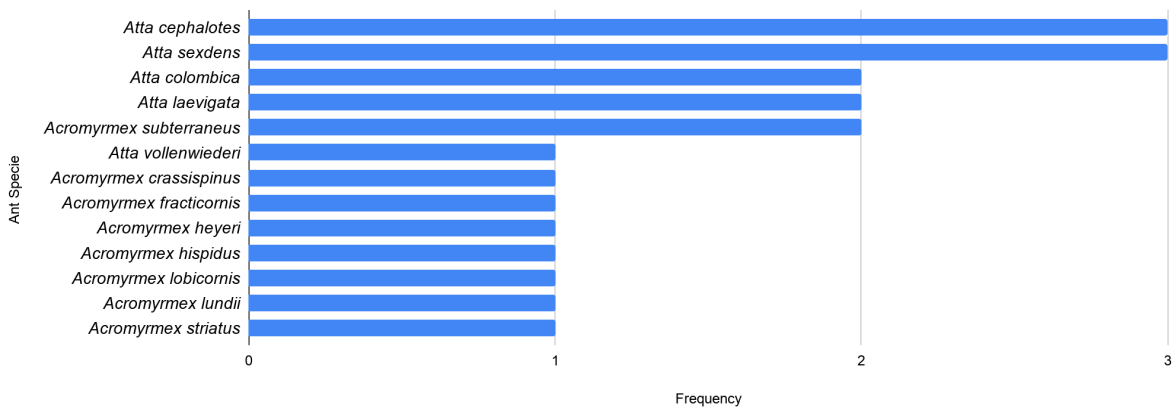


Figure 4 - Frequency of ant species studied in the analysed publications (n=12).

Of the functions attributed to the hitchhikers: "Defense against parasitoids" was the most cited, followed by "Contaminant cleaning", "Energy saving and foraging efficiency", "Sap feeding", "Trichome removal" and "Control of trail traffic" (Figure 5).

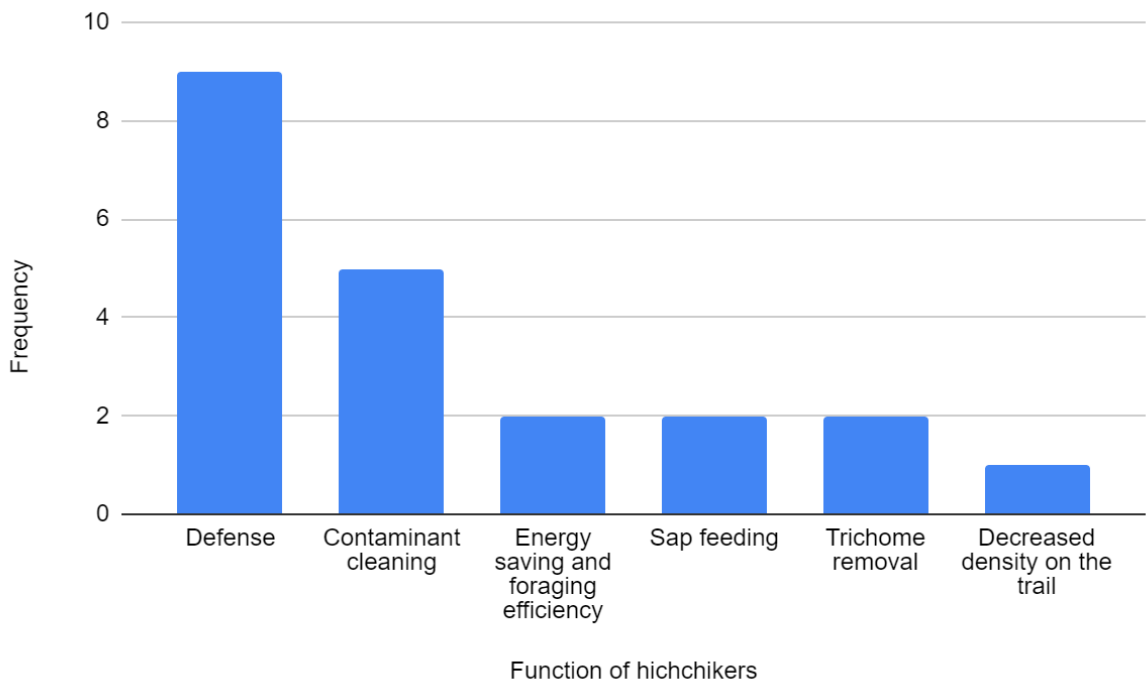


Figure 5 - Frequency of the functions cited for hitchhikers in the analysed publications (n=12).

About the factors that are cited as triggers of the hitchhiker behavior, we pointed out: "Phorids presence", which was verified in 41.7% of the papers. Also, it was verified positive relationships between hitchhikers occurrence and "Leaf contamination", "High number of foragers", "Foragers stridulation", "Forager Burden", "Trichomes presence", "Sap presence", "Trail width" and "Day period" (Figure 6).

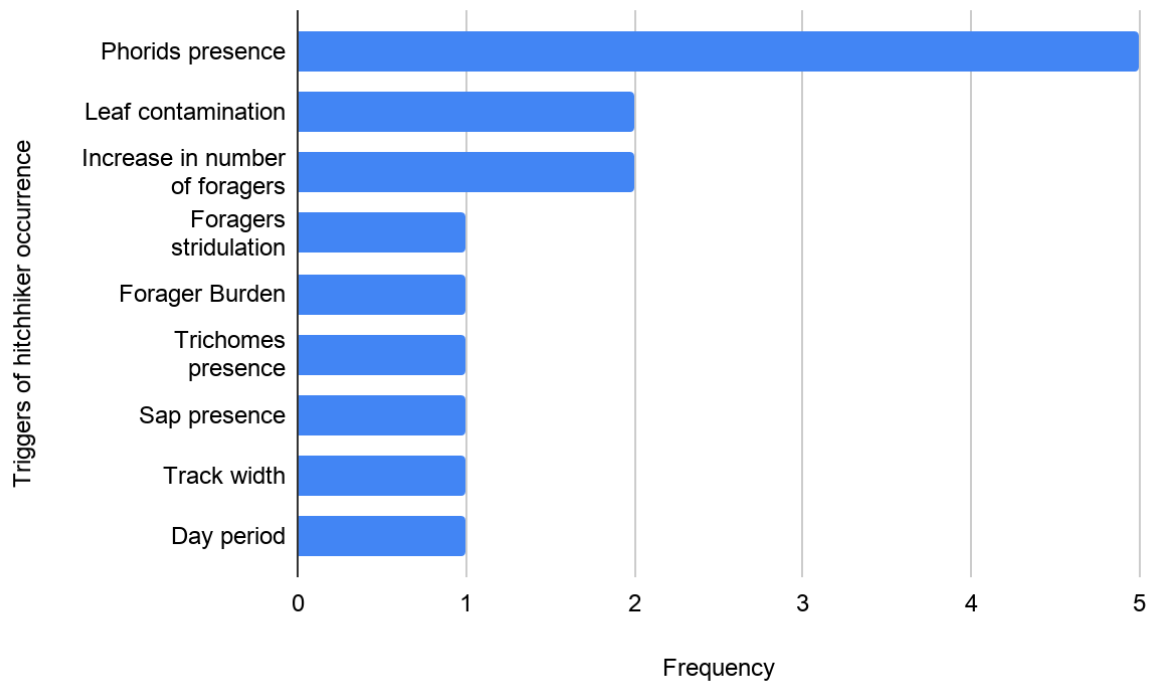


Figure 6 - Frequency of factors cited as triggers of hitchhiker behavior in the analysed publications (n=12).

4. DISCUSSION

The large percentage of published articles that aim to assess the function of hitchhikers relates this behavior to the defense against parasitoid phorids, since they delay the flow of foraging and pose a risk to foraging workers (Braganca, et al. 1998). However, in some studies, the presence of hitchhikers was observed even in the absence of phorids (Linksvayer et al, 2002), indicating that hitchhikers may not only exercise their defense function, but also assist in other tasks such as cleaning of contaminants on the leaves (Linksvayer et al, 2002; Vieira-Neto et al, 2006; Yackulic et al, 2007; Griffiths et al, 2010) and trichome removal (Kitayama et al, 2012; Yackulic et al, 2007).

On the other hand, hitchhiker occurrence is also associated to sap feeding (Vieira-Neto et al, 2006; Hastenreiter et al, 2016), increasing of the foraging efficiency (Yackulic et al, 2007) and avoidance of traffic jams on the trail (Hastenreiter, et al. 2018). In fact, Linksvayer (2002) discards the hypothesis that hitchhikers would leave the colonies exclusively to seek sap and he also rules out the possibility that these ants accidentally become hitchhikers, as they can be isolated over the leaf which is cut by another forager workers.

The hitchhiking behavior is also associated with the task of chemical trail laying made by the minor workers. Some authors suggest that minor workers could take a ride on the transported leaves to save energy while coming back to the colony (Orr, 1992; Evison et al. 2008).

The observation that hitchhikers are the smaller workers was verified in the papers. These minor workers are the most suitable to do this behavior as they are extremely useful as hitchhikers not only because they do not represent an additional weight to forager workers, but also because they are not parasitized by phorids due to the size of their head capsule and jaw, which makes them not viable for the parasitoid (Elizalde & Folgarait, 2012). In fact, previous studies have identified that ant colonies tend to alter their common foraging schedules in response to the attack of phorids and even select the size of workers that go out to forage (Orr 1992), corroborating the efficiency of smaller workers for the role of hitchhikers. .

In the article by Feener and Moss (1990), the authors declare that smaller workers, who can exhibit the behavior of hitchhikers, are the same ones who perform the larvae feeding and other intranidal tasks, and the presence of these smaller workers on the trail can be related to the availability of this caste inside the nest. Another important information is that until the date, there were no observations of hitchhiker behaviour in the genus *Acromyrmex*

and quote several hypotheses as to why this is. Subsequent research, however, claims the presence of hitchhikers in several species of *Acromyrmex* (Elizalde & Folgarait, 2012; Hastenreiter et al, 2016, 2018).

Regarding the recruitment of these minor workers who may be just chemically marking the trail, Roces (1995) reports that the number of hitchhikers is greater in fragments that have been cut by foragers that stridulated and that, during a phorid attack, stridulation is one of the ways the foragers use to warn the minor workers around. Most of the articles analyzed report that the presence of phorids quickly stimulated the recruitment of hitchhikers to exercise a defense role, giving great evidence of this function. However, Linksvayer (2002) demonstrates that there are also hitchhikers at night, a fact that would be uncommon given the daytime habit of the phorid. Yackulic (2007) also reported that there is variation in the number of hitchhikers throughout the day and that at night there was a greater number of hitchhikers on the trail. In addition, nighttime foragers were larger than daytime foragers. If in fact the hitchhiking behavior was stimulated only in the presence of phorids, being related exclusively to defense, there should be no hitchhikers at this time of day, reinforcing the hypothesis of multiple tasks performed by these workers.

Also, Vieira-Neto et. al. (2006), reported that there was no significant increase in the number of hitchhikers due to the presence of phorids, however, the number of observed phorids rarely exceeded one. A valid hypothesis for this low increase in the number of hitchhikers in relation to the presence of phorids, is the way in which different phorid species do their attack. *Neodohniphora erthali* directly attack unladen workers of *Atta laevigata* and *Atta sexdens*, which are leaving the nest (Bragança et al., 2002), what does not allow the hitchhiker occurrence. The same attack pattern is observed in *Apocephalus. attophilus*, which is the most common parasitoid of *A. sexdens* and *A. laevigata* (Erthal and Tonhasca, 2000; Bragança and Medeiros, 2006), but they made their attack while forager workers are cutting leaves (Bragança and Medeiros, 2006). On the other hand, the species that parasitize *A. colombica* usually land on the leaf fragment before attack (Feener and Moss, 1990).

Regarding the impact on the foraging efficiency, Hastenreiter et al., (2016) reported that leaf fragments containing hitchhikers were considerably larger and heavier than fragments without hitchhikers. However, most of these fragments were transported more slowly, so the authors could not state whether the slow transport of these fragments is related to the burden of the forager or due to the presence of hitchhiker.

Reinforcing the hypothesis that hitchhikers also perform the function of removing trichomes, Kitayama (2012) observed that hitchhikers stayed up to 3 times longer in leaf fragments that contained trichomes in relation to smooth fragments.

About the hypothesis of cleaning contaminants from leaves before they enter the colony, Vieira-Neto et al. (2006) observed that the presence of contaminants in the leaves considerably increased the number of hitchhikers in the same leaf fragment. Also, Griffiths and Hughes (2010), observed that when leaves are contaminated with *Metharizium*, the hitchhikers climbed this fragment and the amount of contaminants decreased considerably due to the time that these hitchhikers stayed in the fragment. Also, a high rate of allogrooming within the workers was observed near the nest entrance, corroborating the hypothesis of protection against parasites and other microorganisms.

Additionally, Vieira-Neto et al. (2006) reported that the position and behavior of hitchhikers in the leaf fragment may be strong indications of the function they are performing at that moment. In fresh leaves, with the presence of sap, hitchhikers were more found at the edges of the leaves. When there is no sap, especially in dry leaves, hitchhikers are found in the center of the leaf. In the presence of phorids it was more common to find hitchhikers walking around the fragment and exhibiting alert behavior, with their jaws open. When there are contaminants, hitchhikers were found more in the center of the fragments with their jaws directed towards the substrate; In the absence of contaminants, hitchhikers were found moving around the fragment. The author also points out that there was no visual confirmation of sap feeding by hitchhikers, however its position correlated to the presence of sap in the leaf fragment is a strong indication.

Regarding the hypothesis of avoidance of traffic jams on the trail, Hastenreiter et al. (2018) is the only publication to raise the hypothesis. The authors observed that the number of hitchhikers was greater on narrow trails and associated the raising of the number of hitchhikers with the higher flow of workers along the trail, indicating that the recruitment of hitchhikers is not only due to defense, chemical or nutritional stimuli.

The leading position of Brazil in this research area was a great finding, especially because this leadership is not verified in other topics which involve leaf cutting ants' behavior, despite their high occurrence and economic importance in Brazilian territory. This result indicates an empowerment of Brazilian researchers over the investigation of important

native species. Furthermore, these articles are published in journals with high impact factor, what guarantees a wider audience, including computer scientists which currently have found in the study of social insects behavior a source of inspiration for the design and implementation of novel distributed multi-agent algorithms, known as ant algorithms (Dorigo et al, 1999). These algorithms are applied to solving many complex combinatorial optimization problems, such as the problem of network-traffic optimization and are especially efficient for online optimization of processes, such as telecommunication network routing (Shtovba, 2005).

The study involving hitchhikers and their functions is still very outdated and this can be confirmed with the low number of studies obtained when searching articles in a database. A wide variety of leaf-cutting ant species still does not have studies on the occurrence of hitchhikers and further studies are needed in the area. Also, as noted by several authors, the verification that hitchhikers do not play just defensive roles, but they exhibit a wide range of functions allow us to wonder that this list can still be improved, as well as the investigation about which factors trigger this amazing behavior and how these different factors could interact with each other.

REFERENCES

- ARIA, M. & CUCCURULLO, C. An R-tool for comprehensive science mapping analysis. **Journal of Informetrics**, v. 11, n. 4, p. 959-975, 2007.
- BRAGANÇA, M. A. L.; TONHASCA, A. JR.; DELLA LUCIA, T. M. Reduction in the foraging activity of the leaf-cutting ant *Atta sexdens* caused by the phorid *Neodohrniphora* sp. **Entomologia Experimentalis et Applicata**, v. 89, n. 3, p. 305-311, 1998.
- BRAGANCA, M. A. L., MEDEIROS, Z. C. S. Ocorrência e características biológicas de forídeos parasitóides (Diptera: Phoridae) da saúva *Atta laevigata* (Smith) (Hymenoptera: Formicidae) em Porto Nacional, TO. **Neotropical Entomology**, vol.35, n.3, p.408-411, 2006.
- CEVALLOS DUPUIS, E.; HARRISON, J. F. Trunk trail maintenance in leafcutter ants: caste involvement and effects of obstacle type and size on path clearing in *Atta cephalotes*. **Insectes Sociaux**, v. 64, n. 2, p. 189–196, 2016.
- CAMARGO, R. S.; FORTI, L. C.; DE MATOS, C. A. O.; LOPES, J. F.; DE ANDRADE, A. P. P.; RAMOS, V. M. Post-selection and return of foraged material by *Acromyrmex subterraneus brunneus* (Hymenoptera: Formicidae). **Sociobiology**, v. 42, n. 1, p. 93–102, 2003.
- CAMARGO, R. S.; FORTI, L. C.; LOPES, J. F. S.; ANDRADE, A. P. P.; OTTATI, A. L. T. Age polyethism in the leaf-cutting ant *Acromyrmex subterraneus brunneus* Forel, 1911 (Hym., Formicidae). **Journal Applied Entomology**, v. 131, n. 2, p.139-145, 2007.
- DISNEY, R.H.L. **Scuttle flies: the Phoridae**. London, Chapman & Hall, 467p. 1994.
- DORIGO, M., DI CARO, G., & STÜTZLE, T. Special issue on “Ant Algorithms”. **Future Generation Computer Systems**, v. 16, n. 8, p. 851-956, 2000.
- ELIZALDE, L.; FOLGARAIT, P. J. Behavioral strategies of phorid parasitoids and responses of their hosts, the leaf-cutting ants. **Journal of Insect Science**, v. 12, n. 135,, 2012.
- ERTHAL, M., TONHASCA, A. Biology and oviposition behavior of the phorid *Apocephalus atrophilus* and the response of its host, the leaf-cutting ant *Atta laevigata*. **Entomologia Experimentalis et Applicata**, v. 95, n. 1, p. 71-75, 2000.
- EVISON, S. E.; HART, A. G.; JACKSON, D. E. Minor workers have a major role in the maintenance of leafcutter ant pheromone trails. **Animal Behaviour**, v. 75, n. 3, p. 963–969, 2008.
- FEENER, D. H. MOSS, K. A. G. Defense against parasites by hitchhikers in leaf-cutting ants: a quantitative assessment. **Behavioral Ecology and Sociobiology**, v. 26, n.1, p. 17-29, 1990.
- FEENER, D. H. JR.; BROWN, B. V.. Oviposition behavior of an ant-parasitizing fly, *Neodohrniphora curvinervis* (Diptera: Phoridae), and defense behavior by its leaf-cutting ant host *Atta cephalotes* (Hymenoptera: Formicidae). **Journal of Insect Behavior**, v. 6, n. 6, p. 675–688, 1993.
- FORTI, L. C.; CAMARGO, R. S.; MATOS, C. A. O. D.; ANDRADE, A. P. P. D.; LOPES, J. F. S. Aloetismo em *Acromyrmex subterraneus brunneus* Forel (Hymenoptera, Formicidae),

durante o forrageamento, cultivo do jardim de fungo e devolução dos materiais forrageados. **Revista Brasileira de Entomologia**, v. 48, n. 1, p. :59–63, 2004.

GRIFFITHS, H. M.; HUGHES, W. O. H. Hitchhiking and the removal of microbial contaminants by the leaf-cutting ant *Atta colombica*. **Ecological Entomology**, v. 35, n. 4, p. 529-537, 2010.

HASTENREITER, I. N.; SALES, T. A.; RIBEIRO, L. F.; LOPES, J. F. S. A convenient trip: an analysis of the impact of hitchhiker ants on forager transport rates. **Journal of Insect Behavior**, v. 29, n. 1, p. 37-47, 2016.

HASTENREITER, I. N.; LOPES, J. F. S.; CAMARGO, R. S.; FORTI, L. C. Avoiding traffic jams: Hitchhiking behavior as a strategy to reduce ant workers' traffic on the foraging trail. *Behavioural Processes* v. 157, p. 54-58, 2018.

HOLLOBLER, B.; WILSON, E.O. **The ants**. Harvard: Belknap Press of Harvard University, p. 732, 1990.

KITAYAMA, K.; SOUSA-SOUTO, L.; AQUINO, P. P. U.; TENÓRIO, L. X. Trichome removal by hitchhikers in two leaf-cutting ant species (Hymenoptera: Formicidae). **Sociobiology**, v. 59, n. 3, p. 935-943, 2012.

LINKSVAYER, T. A.; MCCALL, A. C.; JENSEN, R. M.; MARSHALL, C. M.; MINER, J. W.; MCKONE, M. J. The function of hitchhiking behavior in the leaf-cutting ant *Atta cephalotes*. **Biotropica**, v. 34, n. 1, p. 93-100, 2002.

MEHDIABADI, N. J.; SCHULTZ, T. R. Natural history and phylogeny of the fungus-farming ants (Hymenoptera: Formicidae: Myrmicinae: Attini). **Myrmecological News**, v. 13, p. 37–55, 2009.

MOHER, D., SHAMSEER, L.; CLARKE, M. Preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P). **Syst Rev**, v. 4, 1, 2015

ORR, M. R. Parasitic flies (Diptera: Phoridae) influence foraging rhythms and caste division of labor in the leaf-cutter ant, *Atta cephalotes* (Hymenoptera: Formicidae). **Behavioral Ecology and Sociobiology**, v. 30, p. 395–402, 1992.

ROCES, F.; HÖLLOBLER, B. Vibrational communication between hitchhikers and foragers in leaf-cutting ants (*Atta cephalotes*). **Behavioral Ecology and Sociobiology**, v. 37, n. 5, p. 297-302, 1995.

SHTOVBA, S.D. Ant Algorithms: Theory and Applications. **Programming and Computer Software**, v. 31, p. 167–178, 2005.

STRADLING, D. J. The influence of size on foraging in the ant, *Atta cephalotes*, and the effect of some plant defence mechanisms. **The Journal of Animal Ecology**, v. 47, n. 1, p. 173–188, 1978.

TONHASCA JR. A. Interactions between a parasitic fly, *Neodohrniphora declinata* (Diptera: Phoridae), and its host, the leaf-cutting ant *Atta sexdens rubropilosa*. **Ecotropica**, v. 2, p. 157–164, 1996.

VIEIRA-NETO, E. H. M.; MUNDIM, F. M.; VASCONCELOS, H. L. Hitchhiking behaviour in leaf-cutter ants: An experimental evaluation of three hypotheses. **Insectes Sociaux**, v. 53, n. 3, p. 326-332, 2006.

WEBER, N. A. **Gardening ants: the attines**. *Memoirs of the American Philosophical Society* 92: 1–146. 1972.

WILSON, E.O. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*) II. The ergonomic optimization of leaf cutting. ***Behavioral Ecology and Sociobiology***, v.7, n.2, p.157-165, 1980.

YACKULIC, C. B.; LEWIS, O. T. Temporal variation in foraging activity and efficiency and the role of hitchhiking behaviour in the leaf-cutting ant, *Atta cephalotes*. ***Entomologia Experimentalis et Applicata***, v. 125, n. 2, p. 125-134, 2007.