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REVIEW ARTICLE

# Interactions among attending ants, brown-citrus aphids, and ladybugs in plants of *Citrus sinensis*

## Interações entre formigas atendentes, afídeos dos cítricos e joaninhas em plantas de *Citrus sinensis*

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*In memoriam*

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## Abstract

Attending ants promote colony survivorship and reproduction of aphid colonies, mainly by protection against natural enemies. However, very few papers are about the assessment of the effect of attending ants directly on individuals of aphids without the presence of other organisms. In this article, a review of the main papers that had assessed the effect of the attendant ant *Camponotus punctulatus* (Formicidae) on the table of life of the brown-citrus-aphid *Toxoptera citricidus* (Hemiptera: Aphididae) that grows in plants of *Citrus sinensis* (Rutaceae) without the presence of natural enemies. The ant behavior in the presence of adults and immature individuals of the ladybug *Cycloneda sanguinea* (Coleoptera: Coccinellidae) in colonies kept on *Poncirus trifoliata* was also evaluated. Nymph survivorship, adult total fertility, reproductive and post-reproductive period were not affected by the attending ants. The elevation of mean and daily fecundity of the aphids attending on the first days has great importance in the population growth. Ant behavior does not depend on the ladybug sex, nor on the colony size, so that ladybug larvae are more tolerated than adults in the aphid colonies. We registered that the behaviour of the aphids is similar independently of their sex and colony size, whereas ladybug larvae are more tolerated than their adults in aphid colonies.

**Keywords:** survivorship, fecundity, table of life, population growth.

## Resumo

As formigas atendentes aumentam a sobrevivência e a reprodução das colônias de afídeos, principalmente pela proteção contra os inimigos naturais. Entretanto, são raros os trabalhos que avaliam o efeito das formigas atendentes diretamente sobre os indivíduos sem a presença de outros organismos. Neste artigo, é feita uma revisão dos principais trabalhos que avaliaram o efeito da formiga atendente *Camponotus punctulatus* (Formicidae) sobre o pulgão *Toxoptera citricidus* (Hemiptera: Aphididae) mantido em plantas de *Citrus sinensis* (Rutaceae) na ausência de inimigos naturais. Também foi avaliado o comportamento dessas formigas na presença de adultos e imaturos de *Cycloneda sanguinea* ((Coleoptera: Coccinellidae) em plantas de *Poncirus trifoliata*. O aumento da fecundidade média e diária de pulgões atendidos nos primeiros dias tem papel importante no crescimento populacional. Neste trabalho, observamos que o comportamento dos afídeos (*T. citricidus*) é semelhante independentemente do seu sexo e do tamanho das colônias de formigas (C. *punctulatus*), sendo que as larvas de joaninhas (*C. sanguinea*) são mais toleradas do que os adultos das joaninhas nas colônias de pulgões.

**Palavras-chave:** sobrevivência, fecundidade, tabela de vida, crescimento populacional.

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## Presentation

Citrus culture [*Citrus sinensis* (L.) Osbeck (Rutaceae)] has been targeted by many pests and diseases, which under favorable developmental conditions can bring about irreversible damage (Carvalho *et al*., 1991). Among insect species that can impair citrus cultures there are the aphids (Hemiptera: Aphididae) which can cause direct damage, such as generalized withering, leaf wrinkling and development paralysis (Cushman and Addicott, 1991). Indirect damages include compromised photosynthetic and respiratory rate of the plant resulting from the development of saprophyte fungi and transmission of phytopathogenic viruses (Dixon, 2004). One of the main species of aphids which spread through citrus cultures in Brazil is the *Toxoptera citricidus* (Kirkaldy 1907) (Hemiptera: Aphididae), one of the main vectors on "tristeza do citrus" causative agent.

In Brazil there are few studies on the assessment of ant attendance on the aphid life table which may be affected by other organisms, such as ants (Peña-Martinez, 1992; Lazzari and Lazzaratto, 2005). As part of the Hemiptera, the aphids excrete the honeydew, a protein-rich exudate, a rich source of food for many ants (Takeda *et al*., 1982; Vökl *et al*., 1999). Many species attend aphid colonies for the honeydew; in exchange, they carry out certain services in a mutualistic interaction. Mutualistic ants promote benefits for the attending Hemiptera, such as protection against natural enemies and the resulting survival increase, fecundity increase and decrease of the generation gap (Vökll *et al*., 1999; Vökll, 1997). Although the ant-hemiptera interaction is known as mutualistic, mutualism is conditioned to space and time variations, which possibly make the participant costs higher than the benefits under some circumstances.

## The aphid problem

The aphids are an important group of insects for agriculture worldwide because of their distribution, and direct and indirect damages (Peña-Martínez, 1992). Direct damage results from their feeding on plants, nutritious substances removal and liberation of toxins from their saliva, which brings about generalized withering, leaf wrinkling, and paralysis of their development (Godfrey *et al*., 2000). Indirect damages include photosynthetic and respiratory rates compromised as a result from the development of saprophyte fungi, such as the genus *Capnodium* (Peña-Martínez, 1992; Godfrey *et al*., 2000), besides transmission of phytopathogenic viruses (Nault, 1997).

More than 4,700 aphid species were reported (Remaudière and Remaudière, 1997), out of which around 190 are plant-virus transmitters (Nault, 1997), with many species capable of transmitting more than one virus (Eastop, 1983). Out of the more than 700 viruses that attack plants, about 50% are transmitted by Hemiptera belonging to the suborders Auchenorrhyncha and Sternorryhncha (van Regenmortel *et al.*, 2000).

The brown-citrus aphid, *T. citricidus*, is connected to two significant diseases of citrus culture, "tristeza do citrus" and enation of the citrus woody gall (Roistacher and Bar-Joseph, 1987; Carvalho *et al.*, 2001). The "tristeza do citrus" is among the main diseases of world citrus culture resulting from the "*Citrus tristeza virus"* (CTV) (Roistacher, 1991; Marroquín *et al.*, 2004). According to Roistacher and Bar-Joseph (1987), *T. citricidus*, *Aphis gossypii* Glover 1877, and *Aphis spiraecola* Patch 1914 are the main CTV vectors.

A third disease, the citrus sudden death (CSD), has been disseminated across Brazil since 2001 (Bassanezi *et al.*, 2003; Roman *et al.*, 2004). Its symptoms and distribution pattern of attacked plants are similar to those of the "tristeza do citrus", and that is why suggestions exist that CSD is caused by a mutation of the tristeza virus from the region, or a newly introduced virus (Müller *et al.*, 2002).

## Biology of *Toxoptera citricidus*

The brown-citrus aphid has a Chinese origin, the same origin of the citrus (Rocha-Peña *et al.*, 1995). Its introduction in South America happened either in Brazil or in Argentina in the 1930s when these regions were increasing their citrus production (Rocha-Peña *et al.*, 1995). Currently, it has been found in various South American countries such as Bolivia (Timmer *et al.*, 1981), Peru (Roistacher, 1988), Uruguay, Chile, and Colombia, besides Brazil (Rocha-Peña *et al.*, 1995). There are records of *T. citricidus* even in forest regions, as the Peruvian Amazon (Ortiz, 1981), and the Atlantic Forest (Lazzari and Lazzarotto, 2005).

Host plants of *T. citricidus* are generally restricted to the genus *Citrus*, although there are reports of the occurrence of other Rutaceae species. The Rutaceae can be colonized when there is no availability of young branches in citric plants, or when the winged forms are being displaced to other citrus plants, and they only land on these supposed hosts (Michaud, 1998).

According to Souza-Silva and Ilharco (1995), *T. citricidus* is among the main species of aphids that infest citric orchards in Brazil. In surveys conducted in *C. sinensis* orchards in southeast Brazil over two years about half of the collected individuals belonged to *T. citricidus* (Primiano, 2005). In some orchards, this species represented more than 80% of the total of collected individuals.

The brown-citrus aphid feeds only on sprouts, young leaves and flower buds in their host plant (Michaud, 1998). Due to management techniques, such as irrigation, fertilization and prunning, besides climate aspects, sprout occurrence for long periods of time can be induced and, therefore, *T. citricidus* may occur along the year (Bassanezi *et* *al.*, 2003). Well-nourished plants'appeal for aphids results mainly from nitrogenated fertilization that makes high rates of nitrogen available in the phloem (Klingauf, 1989).

In Puerto Rico, the brown-citrus aphid displays peaks of incidence during the spring and half autumn, a time of budding flow, with another possible peak in the summer (Michaud and Browning, 1999). A similar situation happens in Brazil, with two yearly populational peaks, one in the spring and another one in the autumn, although those peaks may also occur in the winter and in the summer (Primiano, 2005).

Aphids go through sexual and asexual reproduction, although in tropical and subtropical regions they are viviparous only. Therefore they reproduce through telitokous parthenogenesis, which means that females give birth to females (Blackman, 1987; Michau, 1998), characterized by offspring genetically identical to their mother, thus producing clones (Blackman, 1987; Carvalho *et al.*, 1991).

In experiments carried out in a plant house in Argentina, aphid cohorts showed a 28-and-48-day-long nymph-adult cycle, with a survivorship rate up to 80%. Daily fecundity encompassed six nymphs, whereas the total fertility ranged from 73 to 81 nymphs per female (Galatoire, 1983).

Tsai (1998) compared the effect of brown-citrus aphids in eight hosts, at 25 $^{o}$C ± 1°C. Nymph survivorship was higher in *Citrus aurantium* (Rutaceae), ranging among species from 41.6 to 93.5%, whereas development time of nymph-adult ranged from 5.9 to 7.2 days, quicker for aphids grown in *Citrus*. The total fertilization varied from 17.7 to 58.8 nymphs per female, and adult longevity fluctuated from 14.6 to 22.8 days.

Temperature was also a significant factor in the life table of *T. citricidus*, and for most insects as well. In a study conducted in Florida, by Tsai and Wang (1999), the life history of the aphids was analysed at eight temperatures (8, 10, 15, 20, 25, 28, 30, and 32°C). The immature development time ranged from 63.1 days at the lowest temperature to 5.5 days at 30°C, with a survivorship rate ranging from 81 to 97%, with the minimum temperature of 32°C. Adult longevity varied between 6 and 6.5 days, at 10 and 32°C, respectively. Fertility was higher for females kept at 20°C, which produced 52.5 nymphs, whereas only 7.5 nymphs were generated at 32°C. The reproduction net rate found by the authors ranged from 33.13 to 41.08 at 15 and 25°C, respectively, similar to the ones for females grown in *C. aurantium* in Japan, of 44.30, and 35.79 to 15.2 and 24.9°C, respectively (Komazaki, 1982). The highest intrinsic increasing rates were similar: 27°C found by Komazaki (1982) and 28°C found by Tsai and Wang (1999).

## Attending ants of *Toxoptera citricidus*

Because of honeydew liberation by the aphids, many ant species use this component as a feeding resource. In the citrus, many ant species were noticed being attended by some ant species. Brazilian reports of ant-aphid interactions are rare, mainly when the *T. citricidus* aphid is considered. In a "*Poncã"*/tangerine organic orchard, in Seropédica, RJ, Rodrigues *et al.* (2006) noticed the attendance of the brown citrus aphid colony by many ant species, *Camponotus rufipes* (Fabricius 1775) among them as the most often seen species, occurring in about half of the observations.

A survey by Morais (2006), in an organic orchard of *Citrus deliciosa* Tenore, var. Montenegrina, in Rio Grande do Sul, showed that the most often occurring ant species were *Camponotus punctulactus* Mayr 1868, identified by Diehl-Fleig (2011), and the *Camponotus* group *crassus*.

Native of southern South America, *C. punctulatus* nidifies on the ground, although being found in tree stratum zone. Generally, the nests are conspicuous and show an outer portion in conical shape (Folgarait *et al.*, 2002). Nest density in rice growing areas in Argentina may achieve 1,800 nests per hectare, depending on how long the cultivated area had remained abandoned (Folgarait *et al.,* 2002). In Rio Grande do Sul, another ant species, *Camponotus fastigatus*, shows density ranging from 116 to 1,274 nests per hectare, also depending on the time that the area remained without cultivation (Diehl *et al.*, 2005). In natural areas from Argentina, density is lower, achieving 23 nests per hectare (Folgarait *et al.,* 2002). Nests showed size variation over time and, if mature, they reached around 1.0 m high and 2.0 m wide in Argentina (Gorosito, 2007). According to Diehl *et al.* (2005), *C. fastigatus* nests are up to 0.6 m high and 1.0 m wide, in Santo Antônio da Patrulha.

*Camponotus punctulatus* is omnivorous, feeding mainly on honeydew and insects (Gorosito, 2007). It is regarded as a pioneer species which rapidly invades agricultural fields (Folgarait *et al.,* 2007), as well as *C. fastigatus* (Diehl *et al.*, 2005). It shows mature monoginic colonies although many queens had been found in still not finished nests (Folgarait *et al.,* 2002).

## Ant-aphid interaction

Interactions between two species show a static classification, that is, they fit one category only, such as predation, competition, or mutualism (Cushman and Addicott, 1991). Mutualism has many times been defined as an interaction between two mutually benefic species (Krohne, 1998; Begon *et al.*, 1999). For a long time the ant-hemiptera interaction has been used as an example of a mutualistic relationship. However, new studies have shown that this relationship, mainly for the aphids, has resulted in not previously known costs, possibly oscilating from mutualism to predation over time and throughout the space (Offenberg, 2001).

Besides, the ant-partner relationship is generally seen as based on a trophic interaction only, something known as trophobiosis, according to original studies by Wasmann (Hölldobler and Wilson, 1990). Trophobiosis is widely used in ant references, which tends to simplify, and even mask, the complex association between the ants and their many partners. These associations, in general, are far from being symbiotic or even trophic only. Mutualism should be understood as a way of mutual exploitation resulting from evolutionary adaptations, as well as costs and benefits for each partner in the interaction (Stadler and Dixon, 2008).

Mutualistic conditions may be discused by considering three aspects. The first aspect is linked to the variation of ecological "problems" which mutualistic partners undergo, as the case when the ants benefit their partners when their predator shows high abundance (Cushman and Whithman, 1989). The second aspect involves variations of the possible "solutions" that mutualistic partners can provide for the problems, as the distinctive ability of two ant species to defend the attended aphid. The last aspect is that being conditioned may be connected to the availability variation of the mutualistic partners, such as distances between partner colonies (Cushman and Whithman, 1989).

The large abundance of ants together with their high activity in the various habitats results in a significant amount of associations between them and other organisms, such as the aphids, with varying optional and mandatory interactions (Hölldobler and Wilson, 1990; Rico-Gray and Oliveira, 2007). The aphids feed on the phloem that is usually rich in sugars and poor in nitrogen. Therefore, they have to ingest a high volume of sap excreted as honeydew (Stadler *et al.*, 2002; Dixon, 2004). Honeydew is a mixture of water, carbohydrates, amino acids and proteins (Buckley, 1987; Völkl *et al.*, 1999), an important food source for many ant species (Hölldobler and Wilson, 1990; Rico-Gray, 1993).

Two studies only report the attending effect of ants on the life of *T. citricidus*. In a Japanese citrus orchard, it was noticed that the ant *Pristomyrmex pungens* Mayr 1866 attended the brown-citrus aphid colonies, thus interfering with their predator behavior (Michaud, 1998). Also in Japan, the brown-citrus aphid made dense colonies in citric budds when they were actively attended by *L. niger* and *P. pungens* ants (Kaneko, 2003).

Stadler and Dixon (1999) studied the attendance by *L. niger* ant in the biology of *Aphis fabae cirsiiacanthoides* Scopoli 1763 in the plant *Cirsium arvense* (L.) Scopoli (Asteraceae) over four generations, and they assessed development time (nymph to adult), dry body and gonads weight, number of ovarioles, number of immature and mature embryos, the size of the most developed embryo, and the mean rate of relative growth (MRGR), but ant attendance to aphids resulted in a negative effect. Development time was higher and *per capita* offpsring production was lower. Except for the number of ovarioles, all the other assessed parameters were negatively affected by ant attendance. A different situation occurred in the field. Ant attendance did not affect the development of *Aphis fabae cirsiiacanthoides* colonies, although it positively affected colony size of another aphid, *Symydobius oblongus* (Von Heyden 1837), in *Betula pendula* Roth. (Betulaceae) (Stadler and Dixon, 1999).

Fitness increase due to attendance was 23.5% for *M. fuscoviride*, 5.4% for *B. cardui,* and null for *A. fabae*. The optional species underwent a higher cost when attended in lower quality plants compared to the mandatory myrmecophila. It suggests that aphids are apt to search for high quality sites, becoming more impaired when limited to ant-attended colonies (Stadler *et al.*, 2002).

The effect of alternative food sources (protein and carbohydrate) and the consequent effect of the *L. niger* attendance in *A. fabae* biology, in *Vicia faba* L. (Leguminosae) were assessed by Offenberg (2001). Many combinations of alternative sources of sugar and protein were offered to ants. They accepted the honey solution in place of the honeydew, which led to a decrease of the attendance rate and to an interaction change, since the ants started to prey the brown-citrus aphids, regardless the availability of an additional protein source. This changing induction of a mutualistic association for an antagonist, according to the authors, might applied as a control method in situations where the presence of the ant-hemiptera association results in high cost for the host plant.

Yao *et al.* (2000) assessed in the field the attendance effect of the ant *Formica yessensis* Wheeler 1913 on the biology of the aphid *Tuberculatus quercicola* (Matsumura), in *Quercus dentata* Thunberg (Fagaceae). In the system where aphids were created with no predators, the ants affected them negatively. They showed a decrease in body width, in femur length of the last leg pair, as well as in number of embryos. There was a different system situation where aphids were created with no predators the ants affected them negatively. The brown-citrus aphids showed survivorship and longevity increase due to protection against natural enemies.

Other authors assessed the effect of ant attendance on parasitized hemiptera. There were situations when the ants removed the parasitized aphids, thus decreasing parasitism (Vinson and Scarborough, 1991; Stechmann *et al.*, 1996). In other cases, the ants do not interfere with the parasitized individuals, indirectly promoting protection for the primary parasitoid against predators and hyperparasitoids (Völkl, 1992; Cudjoe *et al.*, 1993; MacKauer and Völkl, 1993; Novak, 1994). These observations suggest that different ant species associated with the same hemiptera have diverse effects (Kaneko, 2003).

## Ant-aphid-ladybeetle interaction

A complex of syrphids and coccinellidae carries out the biological control of brown citrus-aphids, whereas parasitoids show small importance (Michaud, 1999; Michaud and Browning, 1999). The contribution of these two groups of enemies varies between seasons, although compared field data point to ladybeetles as more effective to eliminate *T. citricidus* colonies (Michaud, 1999). Compared to other species of ladybeetles, *Cycloneda sanguinea* is regarded as the best option due to their short development time and reproductive characteristics (Michaud, 2000), and also for their good development even at low temperatures (Cardoso and Lázzari, 2003). Therefore, it is the optimum candidate to control *T. citricidus* populations in southern Brazil.

When cases of an association between ants and brown-citrus-aphid are considered, the ants usually protect the attended hemiptera against natural enemies'attack, a protection that becomes more intense as closer they are to the attended colonies (*ownership behaviour*). The ants react aggressively to the presence of coccinelidae's larvae and adults, by following them, removing or killing them (Bach, 1991; Jiggins *et al.*, 1993; Itioka and Inoue, 1996; Sloggett, 1998; Sloggett and Majerus, 2003). As a result, these predators supposedly avoid ant-attended colonies (Sloggett and Majerus, 2003). Such fact resulted in a recommendation for the ants to be removed from the system when the control of attended hemiptera populations is the goal (Hanks and Sadof, 1990; Reimer *et al.*, 1993; Vanek and Potter, 2010).

As pointed by Sloggett and Majerus (2003), the ant-aphid interaction has no simple consequence on the coccinelidae. Factors intrinsic to mutualism, such as the involved species, the distance between colonies of attended hemiptera and ant colonies, the characteristics of the host plant, and even climatic conditions can affect attendance, hence distribution of the hemiptera's natural enemies in relation to the ants (Buckley, 1987; Bristow, 1991).

The coexistence of hemiptera predators and ants can be classified in two kinds depending on the relationship length (Sloggett and Majerus, 2003). Some species of predators optionally coexist with ants, a situation when coexistence is mediated by prey availability. In general, predators and parasitoids avoid sites with attended hemiptera, by favoring non-attended colonies, which represent a less risky resource to be obtained. However, under certain conditions, feeding on hemiptera can be preferred, because when non-attended colonies are scarce, the relative value of the attended colonies becomes higher. This situation is not uncommon, since hemiptera-attended colonies tend to persist longer, as occurring with aphids by the end of the summer, in temperate regions (Mahdi and Whittaker, 1993).

The secong kind of coexistence lasts longer and makes up a mandatory relationship, or a near-mandatory relationship (Sloggett and Majerus, 2003). Some species of predators and parasitoids are myrmecophilous, always occurring in one or more ant species over part or all their lives (Völkl, 1997; Sloggett, 1998). As such, ants are essential to the natural enemy's habitat, and prey usually occurs near the ants (Sloggett and Majerus, 2003). In certain cases, myrmecophilous predators are favored: both by a decrease of the intra-guild pressure and the acquisition of a space free from these prey natural enemies (Völkl, 1992, 1996). Therefore, the mutualistic association between hemiptera and honeydew- collecting ants favors these hemiptera's natural enemies whose populational survivorship and persistence may be key to the natural control of the hemiptera populations at landscape level (Liere and Perfecto, 2008).

Regardless the coexistence degree between coccinelidae and hemiptera ants, ladybeetle tolerance to ants partly results from their defensive ability (Majerus *et al.*, 2007). Coccinelidae use many mechanisms to manage ant aggressivity (Majerus, 1994). These mechanisms can be behavioral, physical or chemical, some of them occurring only at specific life stages, whereas others occur either at the immature stage or at the adult stage (Völkl, 1996; Sloggett *et al.*, 1998; Lohman *et al.*, 2006; Majerus *et al.*, 2007).

Most ladybugs display defensive behaviors as a reaction to ant attacks. It is yet unknown whether these behaviors represent an evolution as a specific reaction to ant aggression. Another possibility is whether they are part of the general defense against predators and parasitoids, although they are better developed in the coccinelidae, which frequently find ants (Sloggett, 1998). Larvae, in general, run away or even throw themselves from the plants, whereas adults, besides their ability to react as the larvae, can fly (Itioka and Inoue, 1996). As an lternative reaction to flight, the adults display a clamp down behavior by retracting their legs under their body, closer to the chest and solidly hanging to the substratum (Jiggins *et al.*, 1993; Majerus, 1994). Such behavior provides a better protection for the Chilocorinae, which show a very flat ventral portion and maybe that is why they also adopt lateral movements by approaching their body to the substratum at the side under ant attack (Jiggins *et al*., 1993; Sloggett, 1998).

Defensive behavior is seen in prepupae and many coccinelidae's pupae, which, as a reaction to tactile stimulus, repeatedly raise their body end portion, a behavior known as pupal flicking (Majerus, 1994). When this movement is carried out, the joints of the abdominal segments work as a contact trap, able to capture and damage antennae and other pieces of ants when the pupa is touched, although the movement *per se* triggers ant hindrance (Eisner and Eisner, 1992). Evolutionarily, there are clues to their major function that are associated to protection against parasitism (Disney *et al*., 1994).

The physical defense of ladybug eggs and immature individuals is little effective against ant attacks. The egg chorion is relatively thin, as well as the larvae exoeskeleton, both easily drilled by ants. Nevertheless, many coccinelidae larvae display a thorn-covered body that provides some protection against ants (Sloggett, 1998).

The presence of waxy filaments on the ventral and dorsal surface of the larvae of some ladybug species also provides protection against ants (Völkl and Vohland, 1996; Liere and Perfecto, 2008). The normal larvae mortality (with filaments) of *Scymnus nigrinus* KUGELANN 1794 and *Scymnus interruptus* (GOEZE 1777) is higher than the larvae whose protection was intentinally removed when attacked by the ants *Formica polyctena* Foerster 1850 and *L. niger*, respectively, although the attack was not avoided (Völkl and Vohland, 1996). However, this protective mechanism is effective for a few ant species only (Bach, 1991; Reimer *et al*., 1993; Liere and Perfecto, 2008).

The coccinelidae pupae exoskeleton is relatively hard and it provides some protection against ant attacks (Majerus *et al*., 2007). Furthermore, except for the Coccinellinae, Sticholotinae, and some species of other subfamilies, the pupae display an additional layer derived from the skin of the last larval stage, either prickly or waxy.

The adult physical defense, the eliter, is effective against ant attacks, and together with the behavioral appendixes withdrawal and their holding to the substratum, they are almost immune to ant bites. Some species still show some hair covering the eliter, which may increase protection (Majerus *et al*., 2007).

As a chemical defense, ladybeetles bleed (*reflex bleeding*), thus extravasating a tibial-femoral linking fluid in the adults and on the dorsal surface of larvae and pupae, with properties the ants dislike (Attygalle *et al*., 1993; Sloggett, 1998; Majerus *et al*., 2007). In various species of ladybugs, the defensive chemical components are synthesized by the individuals themselves (Jones and Blum, 1983). In other species these components result from substances directly gotten from the prey (Witte *et al*., 1990). The bleeding frequency seems to be connected with a lack of the ladybug run away options, such as the flight, that is used as a last option (Majerus, 1994). Some eggs also show defensive chemical components (Godeau, 1997; Sloggett, 1998), although they do not provide total protection against ant attacks (Sloggett, 1998).

## Final considerations

It is already know that aphids change their behavior depending on their receiving or not ant attendance (Rauch *et al.,* 2002). Honeydew excretion rate, in particular, is affected by tactile stimuli. The aphid excretion rate in *Aphis craccivora* KOCH 1854 increased about seven times for the attended individuals (Takeda *et al*., 1982), and in *A. fabae*, there was a two-time increase. These facts suggest that ant attendance stimulates feeding and the resulting rate with honeydew liberation. The feeding rate of the attended aphid *A. fabae* is higher and, therefore, this aphid changes its feeding activity by controlling the suction pump located in its head. Using a different study technique, Rauch *et al.* (2002) could not detect such change for the aphid *M. fuscoviride* when attended by the ant *L. niger*.

The increased feeding rate of the attended aphids does not lead necessarily to a corresponding increase in the *per capita* reproduction rates (Takeda *et al.*, 1982). The fact that the increased feeding and/or excretion rate does not lead to a corresponding increasing reproduction rate might be connected to the fact that the faster the nutrient absorption by the aphids, the faster the honeydew liberation for the ants, without being used by the aphids themselves (Yao *et al.* 2000). On the other hand, there is no indication that the opposite situation does not occur, that is, the higher feeding rate brought about by ant pressure could promote, with enough nutrients, either the liberation of honeydew quantity/quality for the ants, or the use of these nutrients for aphid development and maturational speed of the embryos. Although interaction with ants was not explored, Nevo and Coll (2001) refer to the increase of nitrogenated fertilization in a cotton field as triggering fertility increase and an increase of the growth intrinsic rate of the aphid *A. gossypii*. In addition, the authors detected the plant nutritional status of the progenitors as being more influential in the table of life than the plant status on which the aphid is feeding. This effect was already reported and described as belonging to the aphid biology that represents telescopic generations (Dixon, 1998).

The honeydew is regard as the main feeding source for *Camponotus* species (Retana *et al.*, 1988; Rico-Gray and Sternberg, 1991). Besides the sugars present in the ant honeydew, it also contains amino acids, amids, lipids, sterols, organic acids, auxins, B complex vitamines, salts, and minerals, although not all of the ten essential amino acids are present (Hagen, 1987).

The presence of endosymbionts in species of *Camponotus* is connected with the essential amino acids synthesis, even in ants feeding on diets with no amino acids whatsoever (Feldhaar *et al.*, 2007). An obligatory intracellular symbiont of the *Blochmannia* genus was already found in more than 30 *Camponotus* species (Bolton, 1993; Sameshima *et al.*, 1999; Sauer *et al.*, 2000; Degnan *et al.*, 2004). *Blochmannia* has the ability to synthesize all amino acids, except for arginine, and non-essential amino acids (Zientz *et al.*, 2004; Degnan *et al.*, 2005). There are also clues that this endosymbiont is able to synthesize tyrosine, an amino acid associated with cuticle development and coloring (Hopkins and Kramer, 1992).

In addition, there are findings regarding the inclusion of *C. sanguinea* predator in the interaction (Diehl-Fleig, 2011). The ants partialy protect the aphid from the attack, as was also reported for other interaction (Jiggins *et al.,* 1993). Such protection depends on the ladybug life stage, more noticeable in males than in females. In turn, the first instar larvae are tolerated longer than the adults in aphids. Colonies attended by the ant *C. punctulatus*, spending on the degree of the attendance provided to the aphids. Because the scarcity of Brazilian studies, Diehl-Fleig (2011) conducted laboratory experiments with the aim of assessing if the interation was positive or negative between *C. punctulatus* and *T. citricidus,* in *Citrus sinensis* var. valence in *Poncirus trifoliata* (L.) Raf., through individual (survivorship, fertility, and longevity) and populational parameters (table of fertility life) of the aphid, and through computer simulation of the aphid growth. It was also observed the growth of *C. punctulatus* workers from two colonies, besides larvae and adults of the ladybug *C, sanguinea* during the ant-aphid-ladybug interaction.

Based on scientific literature, a plausible explanatory hypothesis is that the attended aphids are asked by the ants to increase the honeydew liberation rate thus resulting in an increased feeding rate. This increase is possible by the availability of plant nutrients (fertilized before the experiment) resulting in a decrease in the time aphids take to move through the plant as a function of the chemical print left by the ants. The increased release and feeding rate does not deprive the aphids of nutrients; instead, there is an acceleration of the embryo maturation and a resulting increase of mean fertility, followed by a longevity decrease depending on the the attendance strength (Diehl-Fleig, 2011).

In addition to these results about the ant-aphid interaction, there are findings regarding the inclusion of the predator *C. sanguiinea* in the interaction (Diehl-Fleig, 2011). The ants partially protect the aphid from the attack, as was also reported for other interactions (Jiggins *et al.*, 1993). Such protection depends on the ladybug life stage, more noticeable in males than in females. In turn, the first instar larvae are tolerated longer than the adults in aphid colonies attended by the ant *C. punctulatus*, depending on the degree of the attendance provided to the aphids.

Ladybugg tolerance to ant aggressivity is partly dependent on the ladybugg defensive ability (Majerus et al., 2007). The coccinelidae defensive skills can be behavioral, physical, or chemical, depending on the ladybuggs life stage (Majerus, 1994; Diehl-Fleig, 2011). The findings of the Diehl-Fleig's work (2011) provide relevant and unprecedented information about the ant *C. punctulatus*, with the aphid *T. citricidus* interaction in the presence or absence of the predator *C. sanguinea*. The aphid biology can be either changed or preserved as a reaction to the attending ants. Supposedly, this variation is associated with attendance degree. There is a need of other studies for such verification, when the density-dependence relationship among organisms is considered through manipulation of the aphid density by plant, instead of manipulating the ant density based on their colony size. The consideration of the attendance effect on the aphid honeydew quality is interesting, since it would shed light on how the aphids allocate the available food energy in reaction to the ants.

Although ants protect aphids against the *C. sanguinea* male and female adult attack, the *C. sanguinea* larvae are more tolerated. The larvae never reach the aphid colony by flying. Diehl-Fleig (2011) observations showed that they slowly approach the aphids.

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