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Seasonal Patterns of the Foraging Ecology of *Myrmelachista arthuri* Forel, 1903 (Formicidae: Formicinae)

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Abstract

Temporal dynamics of foraging activity, diet and habitat are key for understanding the bioecology of ants. These patterns are poorly studied in many Neotropical species, such as those belonging to genus *Myrmelachista*. In the present work, we investigate the foraging behavior and diet of *M. arthuri* and describe aspects of their food-searching behavior. We recorded the dynamics of workers exiting and entering nests built in the twigs of native Atlantic forest trees during the cold/dry and warm/wet seasons. Food items carried by workers were also counted and identified. *Myrmelachista arthuri* foraged throughout the day, but worker activity became more intense as temperature increased and moisture declined, regardless of the season, and especially in the afternoon. This species had a generalist diet: 92% of the food items were live or dead arthropods or their remains, and a small proportion consisted of plant materials, such as seeds. Arthropod fragments, mostly of *M. arthuri* workers, represented the largest proportion of the diet, followed by whole Collembola individuals. Food items did not vary between seasons, the number of items was higher in the cold/dry season. The results of this work contribute to the understanding of *M. arthuri* biology, especially related to foraging dynamics.

Introduction

Ants form an abundant and diverse insect group that is essential for ecosystem structure, especially in the tropics (Del-Claro et al., 2002; Del-Claro & Torezan-Silingardi, 2009; Mertl et al., 2009). Each species has inherent foraging dynamics, which are essential for colony success (Hölldobler & Wilson, 1990). These dynamics are particularly important in the context of ecosystems, because they directly influence trophic relationships (Dátillo et al., 2009; Elisei et al., 2012). Foraging success is influenced primarily by temperature, but also by predation, inter- and intraspecific competition, colony development stage, resource availability, spatial orientation, and relative humidity (Carroll & Janzen, 1973; Fowler et al., 1991; Belchior et al., 2012; Brito et al., 2012; Lima & Antonialli-Junior, 2013).

The ant genus *Myrmelachista* is exclusively Neotropical and arboreal (Kempf, 1972; Longino, 2006), including 56 species and 13 subspecies (Antwiki, 2017). Ants in this genus are rarely observed on plants or in the leaf litter, despite being diurnal and abundant in forests (Silvestre et al., 2003; Longino, 2006). *Myrmelachista* ants are generally small, but are specialized in terms of resource exploitation and niche colonization (Silvestre et al., 2003). Some species are associated with myrmecophytes. These ants use plants as shelter and feed on extrafloral nectaries; in return, the host plant receives protection against herbivores and parasites (Frederickson & Gordon, 2009). Ants in this genus may

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also feed onanimal-derived proteins (Nakano et al., 2013) or honeydew from scale insects (Longino, 2006).

Myrmelachista colonies are usually big, polydomous and/or polygynous and occupy dead branches or live tree stems (Frederickson, 2005; Longino, 2006; Frederickson & Gordon, 2009; Nakano et al., 2012; Nakano et al., 2013), making it difficult to study the biology of the species. In this work, we describe how *M. arthuri* foraging patterns and diet vary between different seasons of the year, in addition to reporting other aspects of its natural history.

Material and methods

Collection area, nests and species

The study was conducted in Parque Municipal Leon Feffer (23°31'49" S; 46°13'26" W). The park is located within the urban matrix of Mogi das Cruzes (São Paulo state, Brazil) (Fig 1), but it has patches of native Atlantic forest within an exotic vegetation matrix (PMMC, 2017). According to Köppen's classification, the climate is mesothermal with a dry winter (Cwb). Annual precipitation is between 1300 and 1700 mm (Minuzzi et al., 2007; Pagani, 2012).

Observations were carried out in an area of approximately 2784 m², where 12 nests were found: 11 of these were inside live stems of two locally common tree species, *Alchornea triplinervia* (Spreng) (9 nests) and *Mimosa bimucronata* (de Candolle, O. Kuntze) (2 nests); the last nest was in a partially suspended dead stem. This nest was chosen as a reference distance from other nests (Fig 1). Twigs were collected from the leaf litter in the study area to search for colonies of this species.

Workers from each marked *M.arthuri* nest were molecularly characterized (GenBank accession nºKY212125). Voucher specimens were deposited in the Entomological Collection Padre Jesus Santiago Moure at Federal University of Paraná (PR, Brazil) and University of Mogi das Cruzes (SP, Brazil).

Worker foraging activity

Worker foraging activity was observed between October 2014 and April 2016 during the cold/dry (April-July) and warm/wet (January-October) seasons (Minuzzi et al., 2007). Worker activity was monitored in four nests, weekly, from 7:00 to 17:00, for a total of 16 observation days (i.e., 160 hours, or 80 hours per season).Every hour, the number of workers leaving and entering the nest was recorded with a manual counter for 10 minutes. Temperature and relative air humidity at each observation period were also recorded.

Diet

The diet of *M. arthuri* was studied in 12 nests in the cold/dry (August and September) and warm/wet (February and March) seasons. Once every 15 days, six nests were monitored, to avoid disrupting nest development. Observations were carried out by a single person for one hour, after 12:00, for a total of 120 hours. Food items carried to the nest by workers were manually collected and preserved in 80% ethanol. These items were sorted according to origin (plant or animal). Animal-derived items were identified to order using Triplehorn and Johnson (2011). If the food item was an ant, it was identified to species using Suguituru et al. (2015).

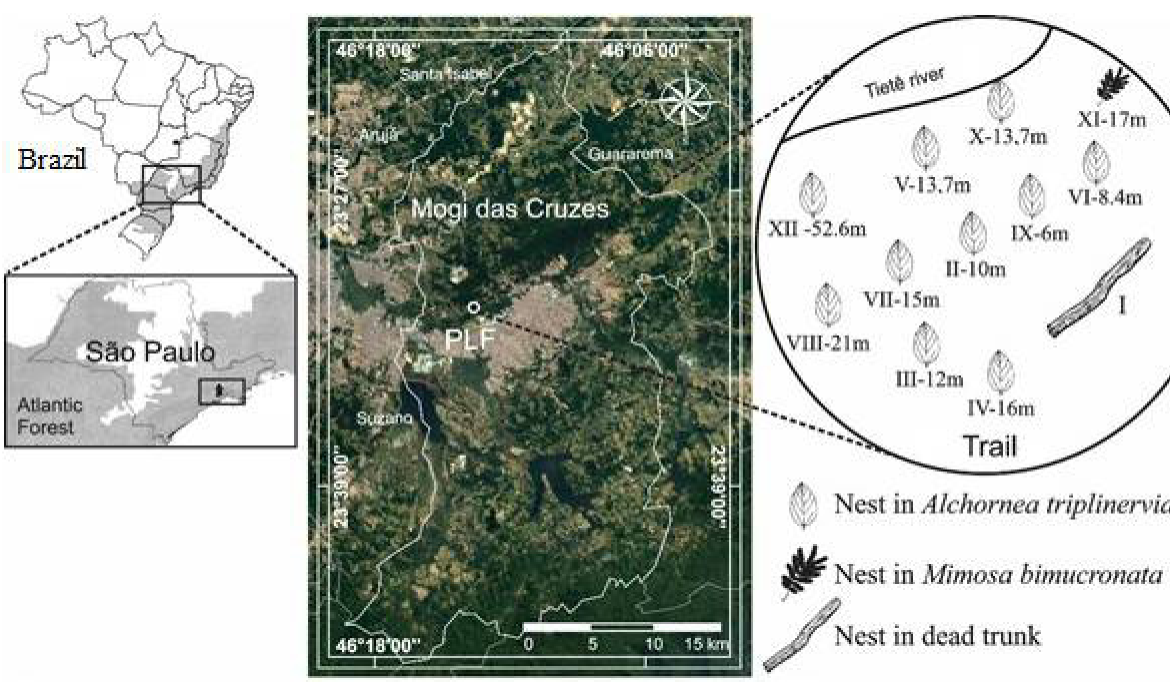

Fig 1.Map showing the location of Parque Municipal Leon Feffer (PLF) in the municipality of Mogi das Cruzes (São Paulo state, Brazil) and approximate spatial distribution of *M. arthuri* nests (I-XII), including the distance (in meters) to the reference nest (I, nest in dead stem). Illustration by L. Menino.

Data analysis

Pearson correlation tests were used to evaluate the correlation between foraging frequency (worker exit and entrance) and temperature and humidity. Foraging activity was compared between seasons and times of day using Student's t-tests. A Mann-Whitney test was used to analyze the variation in food item abundance between seasons. A G test was used to compare the two food sources (animal- vs. plant-derived) between seasons. All analyses were preceded by the Lilliefors test to verify data normality. The software BioEstat 5.0 (Ayres et al., 2007) was used for all of the tests, and the significance level was set at 0.05.

Results

Workers constantly exited and entered *M. arthuri* nests through holes along tree stems (Fig 2A). The trails used to walk on the surface of stems were well-marked (Fig 2B) and had a clear and distinctive color on live trees (Fig 2C). Workers used these trails to reach the leaf litter, but no nests were found in fallen twigs. No alates were observed during the study. Only one mtDNA haplotype was found in workers from each of the 12 nests through DNA sequencing.

Fig 2. A. Nest in a dead *M. bimucronata*stem; **B.** Foraging trail on a live *A. triplinervia*stem; **C.** Foraging trail on a live *M. bimucronata*stem. Arrows indicate worker entrance and exit holes. Identification of plant species by R.J. Almeida-Scabbia.

Foraging occurred throughout the day and was more intense in the afternoon (entering nest: t = 10.92, df = 1;p< 0.0001; leaving nest: t = 11.01, df =1; p< 0.0001) and during the cold/dry season (Fig 3).

Foraging was also correlated with temperature and relative air humidity in the cold/dry season (temperature: r = 0.52; p < 0.0001; humidity: r = -0.55; p < 0.0001) and in the warm/wet season (temperature: r = 0.31; p < 0.0001; humidity: r = -0.13; p = 0.0132) (Fig 4).

By the end of the observation period, workers had collected a total of 336 food items, 92% of animal origin and 8% of plant origin. Regardless of season, intraspecific predation was the most frequent food source (47%), followed by transportation of arthropod remains (24.1%), fragmented plant material (5.1%), and whole individuals of Collembola (4.2%) and Diptera (3.6%) (Fig 5).

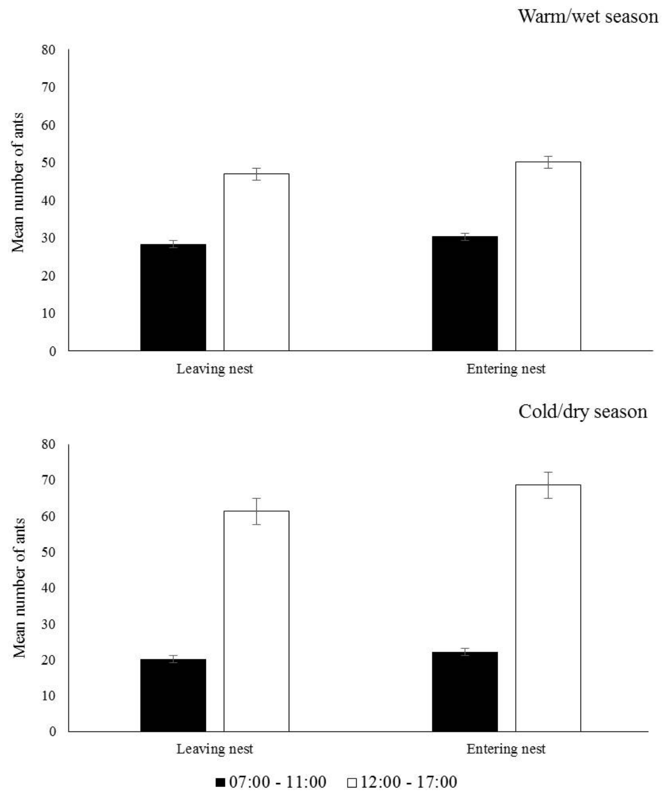

Fig 3. Average number of *M. arthuri*workers leaving and returning to the nest at different times of day and seasons. Vertical lines: standard deviations.

In the cold/dry season, ants carried 19 types of food, while 17 types were carried in the warm/wet season. The number of collected resources differed between seasons (U = 24.50, df = 1, p= 0.003). In the cold/dry season, 222 items were collected, compared to 114 in the warm/wet season (Table 1). The most frequently collected items in the cold/dry season were *M. arthuri*workers, arthropod remains, whole springtails (Collembola) and fragmented plant material. Collection of plant-derived items increased in the warm/wet season compared to the cold/dry season (G = 6.73, df = 1, p = 0.0094) (Fig 6). There was also a drastic reduction in the capture of whole springtails in the warm/wet season.

Discussion

The nesting strategy of *M. arthuri* is similar to the strategy used by other species of this genus, as reported by Longino (2006), since nests were observed in live or dead tree stems. However, there were no nests inside fallen twigs in the leaf litter. Similarly, in a large study of *Myrmelachista*

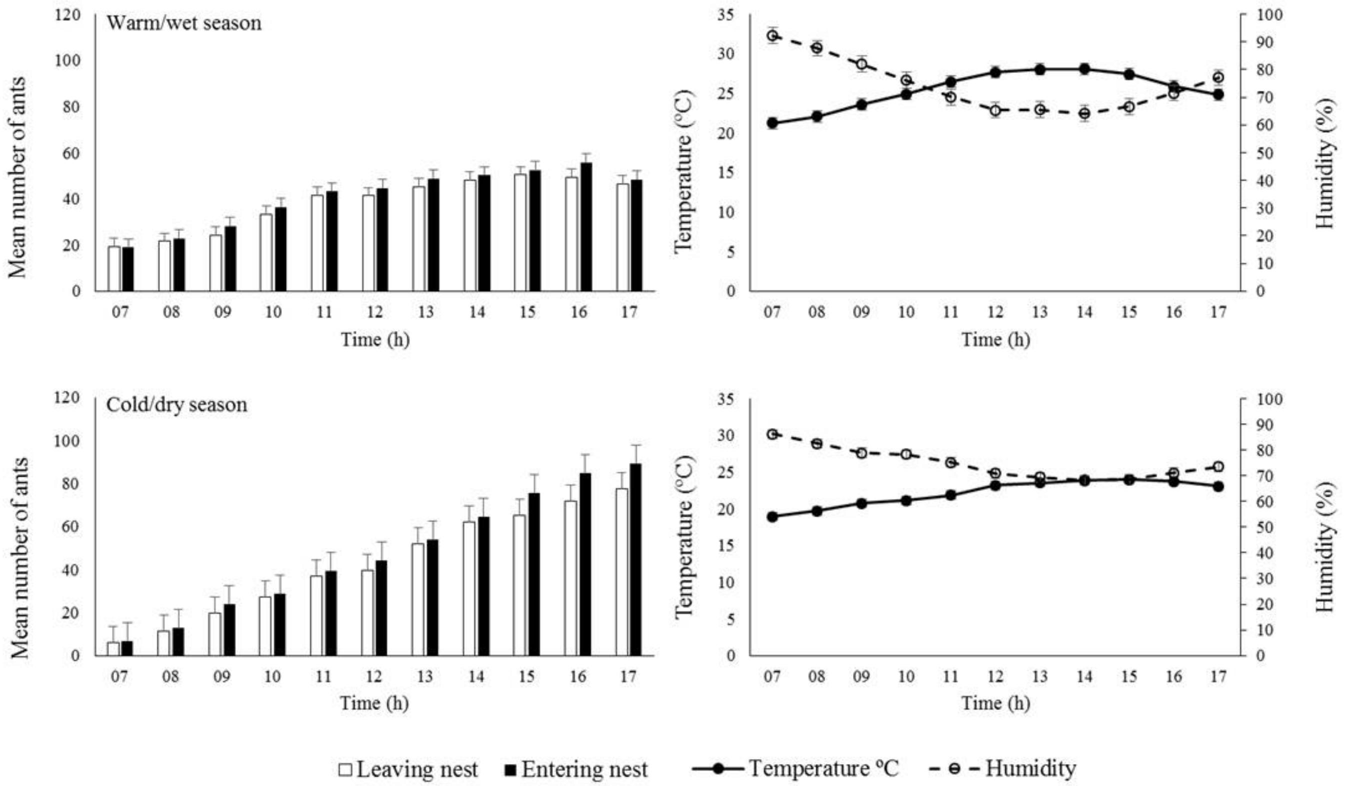

Fig 4. Daily and seasonal variation of the foraging activity of *M. arthuri*. Vertical lines: standard deviations.

species, Nakano et al. (2012, 2013) did not find *M. arthuri* nests in fallen twigs; these authors were only able to find this species in live tree stems or in recently fallen tree stems.

According to Longino (2006), *Myrmelachista* workers rarely leave the nest, and there are no external signs of their presence. In contrast, we observed intense foraging on tree stems by *M. arthuri*, which formed clearly visible trails on the stems where the nests were found. Workers used these trails throughout the day to forage for resources in the leaf litter, mostly in the afternoon. Arboreal ants, such as *M. arthuri*, exploit resources that are rare in the arboreal environment (Delabie et al., 2015), especially resources rich in nitrogen (Begon et al., 2006).

Many species, such as *Pogonomyrmex naegelii* Forel, 1878 and *Camponotus sericeiventris* Guérin, 1838, are more active outside the nest at the warmest times of day (Yamamoto & Del Claro, 2008; Belchior et al., 2012). *Myrmelachista*

Fig 5. Food items collected by *M. arthuri* during foraging. **(A)** flower bud exudate **(B)** Collembola **(C)** remains of Lepidoptera **(D)** remains of Diptera. Images A, C and D by J.P.S. Rosa; B. illustration by D.Y. Kayano.

Table 1. Types of food collected by *M. arthuri* workers along a 120-hour observation period splitbetween two seasons.

Type of food item	Cold/dry season		Warm/wet season		Total	%
	Quantity	%	Quantity	%		
Plant						
Seeds	3	1.4	8	7.0	11	3.3
Fragments*	7	3.2	10	8.8	17	5.1
Animal						
Acari	2	0.9	-	-	2	0.6
Araneae	1	0.5	2	1.8	3	0.9
Coleoptera	6	2.7	3	2.6	9	2.7
Collembola	13	5.9	1	0.9	14	4.2
Diptera	5	2.3	7	6.1	12	3.6
Hemiptera	1	0.5	1	0.9	2	0.6
Hymenoptera						
Micro-Hymenoptera	2	0.9	1	0.9	3	0.9
Atta sexdens	4	1.8	1	0.9	5	1.5
Camponotus rufipes	-	-	1	0.9	1	0.3
Cephalotes atratus	-	-	1	0.9	1	0.3
Cephalotes pusillus	1	0.5	1	0.9	2	0.6
Crematogaster sp.	1	0.5	-	-	1	0.3
Myrmelachista arthuri	114	51.4	44	38.6	158	47.0
Nylanderia sp.	-	-	1	0.9	1	0.3
Pachycondyla striata	1	0.5	-	-	1	0.3
Pseudomyrmex sp.	1	0.5	-	-	1	0.3
Solenopsis sp.	-	-	1	0.9	1	0.3
Isopoda	5	2.3	3	2.6	8	2.4
Isoptera	1	0.5	-	-	1	0.3
Neuroptera	1	0.5	-	-	1	0.3
Arthropoda fragments	53	23.9	28	24.6	81	24.1
Total	**222**	**100**	**114**	**100**	**336**	**100**

*flowers, fruits and seeds

arthuri followed this pattern regardless of the season, although foraging was more intense in the cold/dry season. In this case, the activity pattern was influenced by season and probably related to low food availability, which causes the workers to leave the nest more often (Fowler et al., 1991; Yamamoto & Del-Claro, 2008; Belchior et al., 2012; Lima, 2013).Workers foraged less frequently in the warm/wet season, despite higher energy requirements due to increases in temperature (Lima, 2013) and a late production (Nakano et al., 2013) and greater food availability in the environment (Belchior et al., 2012).

Most plants flower in the warm/wet season (Yamamoto & Del-Claro, 2008), since workers collected more plant material in this season. So, we can assume they provide better energy gains compared to the other food items. However, the observed reduction in worker activity during the warm/wet season is not common for ants. In *Pogonomyrmex naegelii*, for instance, colony activity is higher after it rains, because workers remove soil particles from the nest and it is easier to capture dead arthropods in the surroundings (Belchior et al., 2012). In addition to transporting more plant-derived items in the warm/wet season, the number of collected items, in general, indicated seasonal shifts of the foraging habits of *M. arthuri*. This is probably related to resource availability and energy content, which vary seasonally (Fowler et al., 1991; Carvalho, 2004; Yamamoto & Del-Claro, 2008).

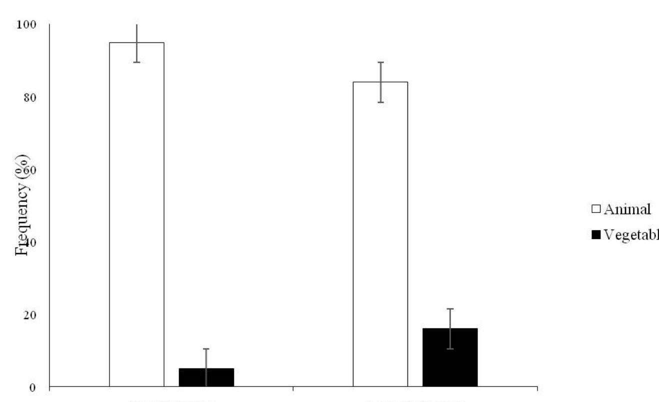

Fig 6. Seasonal variation of the proportion of food types collected by *M. arthuri* workers. Vertical lines: standard errors.

Myrmelachista ants feed on plant exudates (Silvestre et al., 2003), but they may also use seeds and arthropod fragments encountered in the foraging trails, as observed for *M. arthuri*. Nakano et al. (2013) observed workers of this species carrying pieces of cockroaches and termites to the nest, corroborating our observations. However, the high proportion of whole springtail individuals in their diet was unexpected, because *M. arthuri* workers do not have the jaws of ants that specialize on this type of prey (Brandão et al., 2009). Based on the food items transported to the nest, we can conclude that their diet is generalist. Because of diversification, the colony is able to fulfill its nutritional requirements, despite resource scarcity, competition and seasonality (Fowler et al., 1991).

Many ant species, including *M. catharinae* and *M. ruszkii*, expand their colonies to twigs in the leaf litter (Nakano et al., 2012), forming satellite nests. These nests promote territory defense, increase protection of the host plant and improve survival of the colony itself, which has a higher risk of being eliminated by predation or other disturbances when it is concentrated in one spot (Krebs & Davies, 1993; Santos & Del-Claro, 2002; Santos & Del-Claro, 2009). However, although expanding the colony to twigs in the leaf litter is structurally simple and demands small worker investment for colonization, it does not seem to be a strategy adopted by *M. arthuri* (McGlynn et al., 2012). Despite many collection expeditions by Carvalho and Vasconcelos (2002), Nakano et al. (2012), Fernandes et al. (2012) and Souza et al. (2012), this species has never been found nesting in this microhabitat. However, these ants do colonize surrounding trees, which was corroborated by the finding of a single mitochondrial haplotype in all studied colonies.

This is the first study to collect information on the foraging activity and diet of an Atlantic forest *Myrmelachista* species, in addition to describing other behavioral aspects of *M. arthuri*, such as the formation of trails on trees and predation on springtails. This work also expands the list of *Myrmelachista* host plant species (reviewed by Nakano et al., 2013). Based on our data, we can infer that this genus is generalist in relation to the occupation of dead or live tree stems, despite its complex mutualistic interactions with the host tree (Longino, 2006).The knowledge of life history of organisms is fundamental to make appropriate decisions for management and biodiversity preservation. This information helps fill the gaps in knowledge about the biology of an exclusively Neotropical genus with complex behavior.

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