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Multilevel factors affecting the route decision for foraging in the generalist ant *Pheidole oxyops*

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Abstract: *Pheidole oxyops* Forel, 1908 is a generalist ant, which forages actively for plant debris to dead arthropods. In addition, its nest has an entrance that allows the ants gather resources passively by capturing falling preys into the nest. Our objective was to verify if different day periods, temperature and residual soil accumulation (ground pile in the side of nest entrance) could influence the patterns of foraging activity. Foraging activities were registered in the morning, afternoon and twilight. We measured direction and vector of trails, air temperature and humidity during foraging events. Our results showed that foraging routes are independent of residual soil accumulation and other nearby nests. However, air temperature and the time daily period are significant factors to foragers' exits. Higher air temperatures influenced negatively the exits. In the period of the afternoon, the ants do not show any preference for routes, different from the morning and twilight. In addition, foraging activities were significantly more frequent during twilight period. Leaving the nest at twilight could allow ants foraging in an environment with less exposition to potential predators and competitors. Moreover, it may be also related to opportunism to hunt other nocturnal insects.

Keywords: Multilevel Factors, Sit-and-wait foraging, Active foraging

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1. Introduction

Ants display several forms to gather resources, i.e., foraging strategies [1,2]. These strategies range from solitary to group/mass recruitment [3]. In the individual foraging strategy, the individual leaves the nest, find the resource, gather it, and take back to the colony alone [2,4]. While, in the group/mass recruitment one individual finds the food item and communicates it to the colony, and other ants leave the colony to collect the food item [5]. According to Bernstein [6], foraging can be classified into three basic forms: 1) individual foraging: solitary searching and resource obtaining independently of other ants from the colony; 2) mass recruitment: solitary searching, but resources are collected with help of several ants; and 3) group foraging: each ant gather the resource in solitary way, however, they follow colony trails. These three basic forms of foraging are considered active forms [6].

Ants can also demonstrate another type of foraging strategy, a passive one, the trap-building [7]. Trap-building can be considered a passive form of foraging and is commonly called "sit-and-wait" [7]. Some ant species expend energy and/or time both building the traps and searching for a suitable place to build the nest traps [7]. Even some ecologists that classified species within "active" or "sit-and-wait" categories that it is possible that these species do not use only one foraging strategy during their lifetime [8].

Some abiotic factors can influence the foraging strategy in ants [5]. For example, *Wasmannia auropunctata* changes the recruiting velocity when it is competing with another species [9]. The species *Ocymyrmex barbiger* decreases the time for searching and increases walking velocity when soil temperature was very high [10]. In *Formica schaufussi*, the rate of oxygen consumption can be an important factor to prey selection [11]; and several abiotic factors can affect the foraging dynamics in *Pheidole megachephala* [12].

In the *Pheidole* genus, considered by a lot of authors as a hyperdiverse genus of ants [13], and within the genus, *Pheidole oxyops* shows both strategies of foraging, active and passive [14,15]. This species is a generalist ant that forages from vegetal parts (leaves, flowers, fruits) to dying arthropods [14,15]. It is a very common ant in Brazilian Southeast, occurring in the Atlantic Forest, Brazilian Savanna (Cerrado), plantations and anthropic environments [14]. *P. oxyops* presents recruitment by group [16], in which one ant, generally a scout, finds a resource and goes back to the nest and communicates it to the other ants [16]. This foraging strategy allows the ants to reduce the energy waste in the search for food, and velocity of the collection after colony recruitment [2]. For *P. oxyops* a different way to get resources is the nest structure [15]. Its nest has an entrance in the format of pitfall-trap [14,15,17] (Figure 1). This species is an excellent model to study foraging ecology. First, because the species has both foraging strategies, active and passive; second, these ants can be considered an excellent organism model to the study of cooperative transport of food items [16,18].

In this study, our objective was to verify if different daily periods, temperature, residual soil accumulation (ground pile in the side of nest entrance) and luminosity could influence the colony foraging activity. In addition, we tested the efficacy of the nest entrances as natural pitfall traps. Furthermore, we addressed some discussion about ecological and evolutionary aspects of foraging of *Pheidole oxyops*.

2. Materials and Methods

In each experiment, we observed 15 colonies of *Pheidole oxyops* at Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo. The municipality of Ribeirão Preto has annual average temperature of 21.9ºC, altitude 546m, with annual precipitation of 1508mm [19].

2.1. Foraging: directions, period and abiotic factors

To evaluate foraging direction and day period, we counted the number of workers that naturally exited the colonies to forage and their coordinates (cardinal and collateral points), during 20 minutes. In total, eight directions with a 45º interval for each point, for example: North: 0º [interval: 22.5º - 337.5º]. We observed the colonies during 3 days three times per day: morning (8-9 h), afternoon (12-14 h) and twilight (17-18:30 h). Moreover, to assess the influence of the abiotic factors, we registered air temperature with hygrometer Minipa® MT-242. In addition, the geographical coordinates of the colonies nearby, for the subsequent study of the influence of other nests on the foraging routes. Furthermore, we marked the position of the ground pile and the presence of the luminosity incidence (natural or artificial) on the colony entrance.

2.2. Type of foraging resource

We observed the types of resource brought to the colony for 10 minutes per day period. During the observations, the resources taken to the nests were categorized in arthropods, vegetal parts (flowers, leaves or fruits), non-arthropods (other invertebrates) and others (empty shells, feathers, etc.), as reported in previous study [14].

2.3. Quantity of dry mass of arthropod

To infer the total mass of arthropods we used 48 mini pitfall traps to simulate the colony entrance. We installed the traps within an area of 137.01 m^2. Each mini pitfall trap had 8.5 cm of perimeter and we left them in the field for 24 hours. In each one, we put a saline solution with detergent (to break the water superficial tension), preventing the prey to escape [20]. Then, we dried the sampled individuals in a drying oven for five minutes on 100 ºC. After, we weighed arthropods in a precision balance, we analyzed each pitfall trap content separately. Then, we used the formula DryWeight + DryWeight*70% to access the approximated weight of the insects that fall in *P. oxyops* colonies, that is because the insects have approximately 70% of water in their bodies [21].

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2.4. Statistical analysis

To evaluate the fidelity of exit directions from the nest we used the Rayleigh's test [22] we used the package 'circular' [23] in R software v.3.3.1 [24]. To test the influence of discard pile on the preference of colony exit we did a circular model [22], using number of exits from the nest as a response variable, and the preference route and the position of discard pile from the colony entrance as explanatory variable. To analyze the preference of day period, local temperature and luminosity on the colony entrance we used a linear mixed model (LMM) using the package 'lme4' [25] in all analyses we use the variable 'Colony' as a random factor. In all models, we used the total of exits for each colony. We fit the models using AIC values [26]. All analyses were performed in the R software v.3.3.1 [24].

To analyze the weight and composition of the pitfall traps, we used a linear model to the weight, and a PerMAnova analysis to the composition [27]. In the linear model, we used the weight of each pitfall as a response variable, and the sampled day as an explanatory variable.

3. Results

3.1. Uniformity in foraging routes

Pheidole oxyops showed a tendency to forage in specific directions during the morning (Rayleigh Statistic = 0.078; $p < 0.001$) and twilight period (Rayleigh Statistic = 0.075; $p < 0.001$). However, in the afternoon period there was no tendency for specific routes (Rayleigh Statistic = 0.042, $p = 0.1$), the ants left the colony without a specific direction (Figure 2). Moreover, in all the cases, the position of discard pile also had no influence in the foraging route (rho = 0.298, $p = 0.161$), the workers normally passed over the discard pile to forage.

3.2. Influence of environmental factors on foraging activities

There was difference in the day period of activities, ants showed a higher frequency of nest exits on the twilight ($F = 0.050$, $p < 0.001$, $R^2_{LMM(m)} = 0.293$, $R^2_{LMM(c)} = 0.571$, AIC = 32.422) (Figure 3). However, the air temperature had influence on the exits from the colonies ($F = 10.022$, $p = 0.003$, $R^2_{LMM(m)} = 0.157$, $R^2_{LMM(c)} = 0.451$, AIC = 45.268) (Figure 4). We also did a model to verify if the air temperature, in the environment, was different between the periods (Morning x Afternoon: $p < 0.001$; Morning x Twilight: $p = 0.17$; Afternoon x Twilight: $p < 0.001$ – Supplementary Material S1). In addition, the luminosity on the colony entrance had no influence in the exits of foraging ($F = 1.204$, $p = 0.279$, $R^2_{LMM(m)} = 0.028$, $R^2_{LMM(c)} = 0.168$, AIC = 46.827) (Figure 5).

3.3. Food preference in active foraging

Pheidole oxyops foragers had a significant preference to search for arthropods (Figure 6). However, they also collected vegetable parts (flowers, leaves and fruits) and non-arthropods [snails, nematodes]), but in lower frequency. The proportion of arthropods collected was 66.27%, plants were collected in smaller proportion (flower = 1.57%; fruit = 9.02%; leaves = 17.65%), non-arthropods was 0.39% and others (such as feathers and shells) were collected 5.10%.

3.4. Passive capture inference

In the artificial pitfall traps we found hymenopterans, coleopteran, dipterans, termites and arachnidan. The efficiency of passive capture showed that colonies obtained 0.027 ± 0.006g day^{-1} in average. The temperature had no influence in the gathered weight ($F = 2.163$, $df = 46$, $p = 0.145$), however has a significant influence in the faunal composition inside the pitfalls (*pseudo*-$F = 4.877$, Permanova $p<0.05$).

4. Discussion

The foraging strategy used by ants depends on several spatiotemporal factors [28]. Abiotic factors such as air temperature [12] and humidity [29], and biotic factors as competition [30] and predation [31,32], and intrinsic factors as colony size [33] shape the foraging strategy used by ants. These strategies involve a trade-off between energy waste [34], mortality risk [32] and value of the resource. Probably, the environment exerted a huge pressure on *Pheidole oxyops* colonies, favoring nests with huge entrance, making it possible to forage in different ways, both actively and passively. In addition, these strategies may be complementary to each other increasing the colony fitness.

In the afternoon period, the lower frequency in ants' exits from the colony (in all directions) can reflect that colonies may have higher demands for resources [29,35]. This situation represents a trade-off of resource energy/risk [36,37], because the mortality risks for foraging in this period of the day are higher [32]. Besides that, the non-uniformity in the foraging directions in this case could suggest that in higher temperatures the energetic cost of following a specific direction is higher than in low temperatures. For instance, in higher temperatures individuals are less selective than in lower temperatures, because in high temperatures the energetic costs for searching may not compensate the value of the resource [11]. *P. oxyops* may forage in all directions in higher temperatures to maximize the resource location, and decrease the energetic/metabolic waste.

Contrary to what was expected, the ground pile had no influence on the directions or the frequency of exits from the colony. Some ant species can use visual cues for location of colonies and foraging trials [38], as *P. oxyops* forage in several directions; the ground pile could be working as a visual landmark to colony entrance [38,39]. For example, the species *Cataglyphis bicolor* and *Catalyphis fortis* could use geometric forms (triangles) or materials (oil barril) to find the colony. Beyond that, ants respond to distance from the object modifying their velocity, farther the landmark faster the ant move [38].

The preference for foraging in the twilight period may be related to the lower sun exposition and, therefore, a lower risk of water loss different from those occurring in high temperatures [36,40]. Also, could be related with the higher predation risk[31,41]. Because the temperatures in the morning and twilight are lower than in the afternoon, this might increase the frequency of exit of scouts/foragers ants from the colony. For instance, in *Pheidole megacephala* the temperature was a limiting factor to exits from the nest to forage [12]. In higher temperatures, ants experience physiological changes, for example, the respiratory and metabolic rates increase [42,43] These physiological changes could increase the ants' mortality [44]. Probably *P. oxyops* foragers evaluate the temperature of the exterior and reduce the frequency of exits of the colony.

P. oxyops is a generalist ant, even having a preference for high protein food sources [14]. The protein resource is essential to the correct development of the brood and the queen of *Pheidole* genus [45]. Our results corroborate previous data of Fowler [14], on the preference of protein resources by *P. oxyops*. However, we did not record seed foraging, despite that; the seeds are also sources of protein [46]. Maybe in the forest the individuals shift its foraging behavior, by consuming seeds, in order to avoid competition and possible mortality risk of foragers [14].

The foraging behavior and strategy are shaped by natural selection [31]. According to Morehead and Feener [47] there are two ways that natural selection optimize the organism's foraging efforts: 1) acting on the morphology and, 2) on the behavior. In the morphology case, specifically, natural selection shaped the colony's entrance structure, in a way that maximized the cost/benefit of foraging strategy. Like some organisms, that have some specializations in foraging strategies, *P. oxyops* uses both active and passive strategies to forage. Trap building by animals could be considered as an 'extended phenotype' [7]. We propose that the nest of *P. oxyops* is, in this way, an extended phenotype of the species. Because it enables species to extend the ways to gather resources and increase the fitness of the colony. In addition, complementing the demand for resources.

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5. Conclusions

In summary, multilevel factors can influence the number of foragers outside the colony, the number of exits from the colony and directions. Despite *P. oxyops* being a generalist ant species, it has a preference to forage dying arthropods. These results show that even considered an ant 'generalist', the colony prefer to forage for protein. In addition, use both strategies of foraging, active and passive, but probably the passive strategy (sit-and-waiting) is complementary, and not the principal way to gather resource. Our results will help future studies on the ecology of foraging of both *P. oxyops* and other ant species. Moreover, these results show important aspects of the behavioral ecology of foraging in generalist ants, showing that even generalist ants have a prey preference.

Supplementary Materials: The following are available online at www.mdpi.com/link, Document S1: Additional Images and Map.

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Conflicts of Interest: The authors declare no conflict of interest

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Figure 1. Nest entrance of *Pheidole oxyops*. The entrance works like as a natural pitfall trap.

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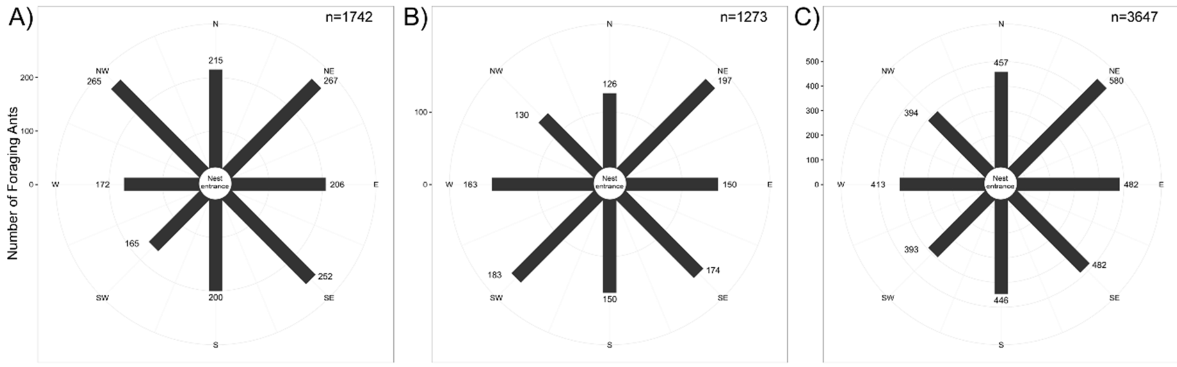

Figure 2. Foraging routes used by *Pheidole oxyops*, in three daily periods: A) Morning, B) Afternoon, C) Twilight. The numbers represents the numbers of exit from the nest in the period.

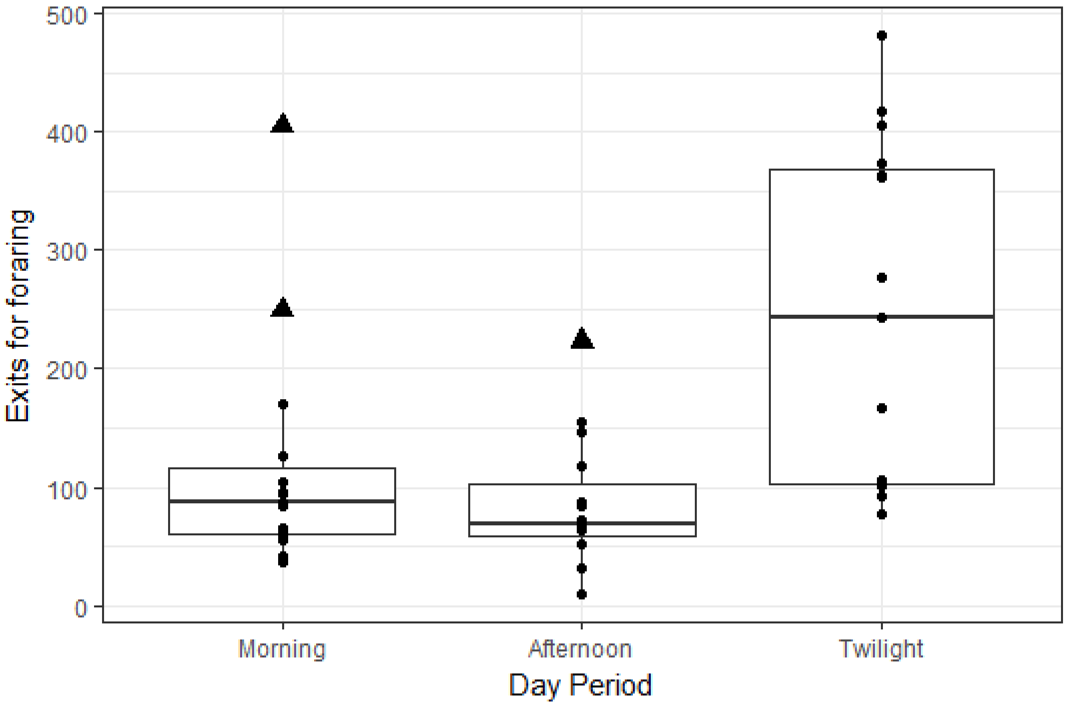

Figure 3. Exit to foraging in the daily periods. Triangles means outliers in the sample.

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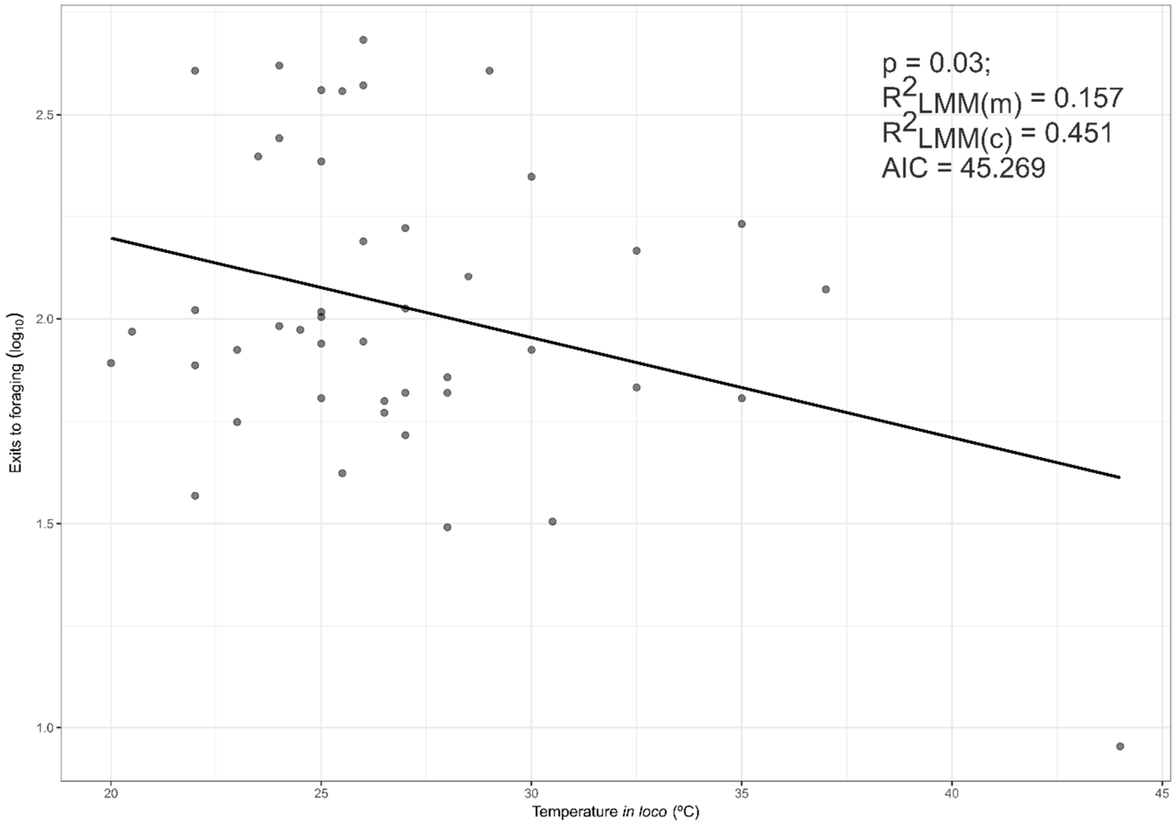

Figure 4. Influence of temperature on the exits to foraging. There is a decreasing in the number of exits with the increase of temperature. The values were extracted from the LMER model.

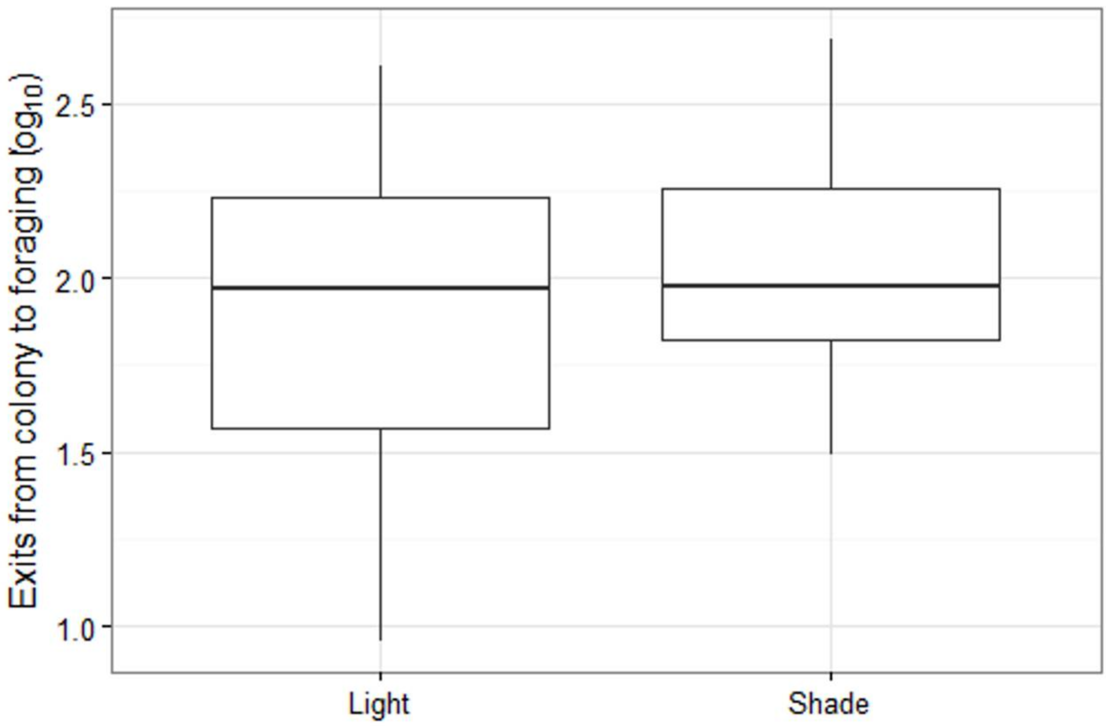

Figure 5. Exits from colony to foraging in presence of light (as natural as artificial) and shade.

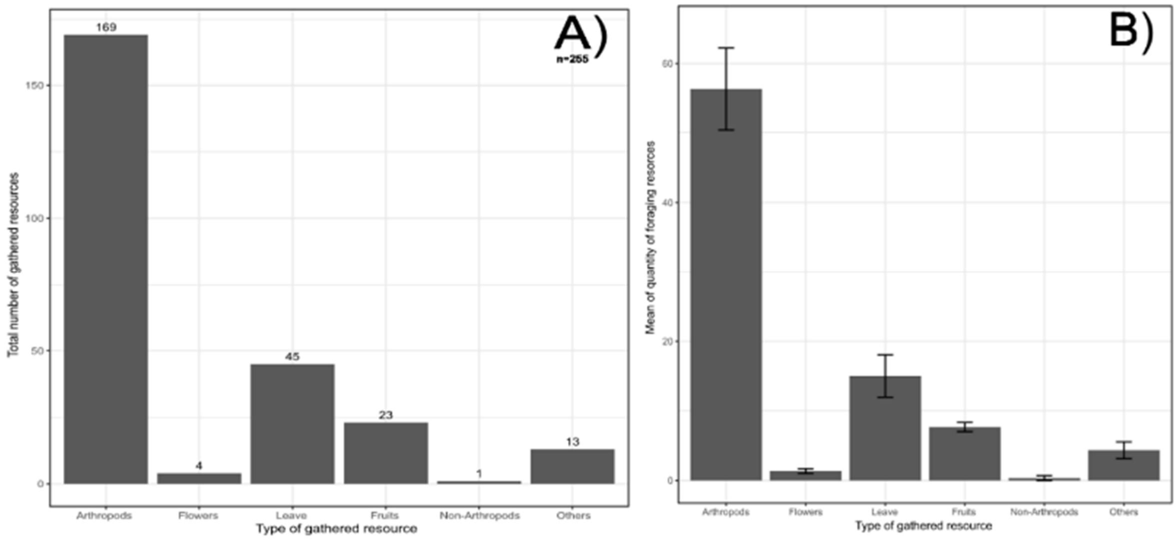

Figure 6. A) Total number of foraging items by *Pheidole oxyops* in the 15 nests; B) Mean of the foraging resources, the error bar means ± SD.