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Research Article

Foraging Activity and Trophic Spectrum of Red Ant *Pogonomyrmex barbatus* Smith, 1858, in Productivity-Contrasted Microenvironments

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Foraging strategies can be influenced by many factors such as abundance, availability, and toxicity of the resources. In arid zones, the distribution and productivity of plants also act as additional factors that affect foraging strategies. Twenty colonies of *Pogonomyrmex barbatus* ants were studied in an arid zone of central Mexico to evaluate the trophic niche breadth in two sites with contrasting productivities in terms of their diversity and amount of resources during two seasons. The results suggest that when the resources are abundant as in the rainy season, the trophic niche breadth is reduced in sites with high productivity and, in the same sites, the trophic niche breadth increases when the resources are limited as in the dry season. In contrast, the trophic niche breadth is similar in both conditions of resource availability (i.e., rainy and dry seasons) at sites with low productivity. During the dry season, populations of *P. barbatus* showed a similar foraging behavior in sites with high and low productivity. Thus, the particular characteristics of a site can significantly affect the foraging strategies of the ants in those environments.

1. Introduction

Food options for organisms are often influenced by several resource characteristics such as availability, distribution, toxins content, palatability, and acceptance, and by the behavior and biology of the organisms, including life cycle, tolerance to environment changes, and feeding habits restrictions [1, 2]. Gordon [3] enumerated the mechanisms behind diet modification in ants in relation to changes in the foraging area: an increase in territory results in higher levels of resources, cost in territory defense, risk of predation, and energy used for gathering and transporting the resources [1, 3]. Other factors that may affect the availability or not of the resources in ant foraging areas include localization, because physical conditions can be very important in the colony development; food availability; intensity of biotic interactions such as inter- and intraspecific competition [4, 5].

According to the optimal foraging theory (OFT), organism must develop cost-effective strategies to obtain more resources and energy by using mechanisms favored by natural selection, resulting in a positive impact on the species fitness [2]. In the case of ants, which are highly diverse and abundant [6], foraging mechanisms involve three general patterns: hunting (including predation and granivory), rewards (e.g., exploitation of extrafloral nectaries, elaiosomes, and homopteran secretions), and defense for discovered resources [7]. Depending on the ant species, cognitive plasticity (learning) and the use of visual signals are important foraging mechanisms, as observed in *Ectatomma ruidum* (Roger, 1860) and *E. tuberculatum* (Olivier, 1792) [8], and in *Pogonomyrmex* sp., whose learning is related to site fidelity [7].

In arid ecosystems, primary production occurs in pulses attributable to rainy seasonal patterns [9] that produce a high environmental heterogeneity as result of the unequal distribution of humidity in time and space [10]. These seasonal patterns are relevant because little modifications in the ecosystem's components, such as precipitation, can influence variations in other elements, thus generating various microhabitats with different productivities, composition and abundance of primary producers, primary consumers, and predators [11–13].

Resource abundance is an indicator of productivity in terms of energy availability. Organisms modify their feeding behavior in relation to food availability in the habitat. In the case of resource scarcity, several important coincidences in the diet of species have been recorded, increasing the competition for food [14]. In contrast, feeding specialization occurs under conditions of food abundance [2, 15].

Although the arid zones have been regarded as sites with low ant diversity, recent investigations have revealed a remarkably high diversity and abundance [6, 16, 17], together with highly variable interactions and trophic habits, as influenced by time. These reports indicate that ants play relevant roles in various ecosystem processes, including nutrient recycling and redistribution of resources [18].

The aim of the this study was to examine the foraging strategies of *Pogonomyrmex barbatus* (Smith, 1858) in relation to habitat productivity by attempting to answer the following question: how does the trophic spectrum of *P. barbatus* influence habitat productivity in a semiarid zone? We assumed that productivity would be directly related to the diversity and abundance of food [11, 19, 20], allowing a direct relationship between productivity and resources diversity and abundance. Our hypothesis was that, under relatively high productivity, the feeding habits of *P. barbatus* would be more specific, whereas in habitats with relatively low productivity, the feeding habits would follow a generalist behavior. High and low productivities in a habitat are defined in this study as a function of the plant species richness and food abundance.

2. Materials and Methods

2.1. Study Sites. The study was performed at the "Helia Bravo" Botanical Garden (18°27′30′′N, 97°24′50′′W) at 1678 m a.s.l., located in the Zapotitlán Salinas Valley, into the physiographic region of Tehuacán-Cuicatlán, in Puebla and Oaxaca States, Mexico. The weather is generally dry with a rainy period from May to October each year and 400 mm of annual average precipitation, and a dry season from November to April. The annual average temperature ranges from 18 to 22°C. The dominant vegetation consists of xerophytic shrub, as reported by Rzedowski [21], with physiognomic variations related to the local environmental conditions, resulting in different vegetation types [22].

Two sites in the Botanical Garden, each with contrasting productivities based on plant cover, species richness, and productivity, were selected. The first site was named Jardín (18°19.78′N, 97°27.45′W) and showed the highest values of plant cover (116.36%) and species richness ($S = 25$), when compared to those of the second site named Llano (18°19.54′N, 97°27.26′W), which is located in a zone with high erosion (plant cover = 45.54%; species richness = 16). The distance between the sites, estimated with a Garmin 60 C GPS, was 600 m in a linear direction, although a hill was located between the two sites. Species similarity between the two plant communities was estimated as 12.2% by using the Renkonen similarity index. The availability of resources at the Jardín site, according with a preliminary study by Guzmán-Mendoza [23] was 2,252 seeds of different species, 175 remains of vegetal material (branches, leaves, and parenchymal tissue of leguminous pods), and 1,379 objects of animal material (insects, exuviae, spiders, and caterpillars) per 600 m^2. At the Llano site, the available resources included 12,760 seeds, 470 plant material remains, and 1,004 animal materials per 600 m^2. The amount of resources differed in relation to the site; thus, the Llano site possessed a greater variety of resources (Jardín: $\chi^2_{0.05,12} = 634.46$, $P < 0.0001$; Llano $\chi^2_{0.05,12} = 5663.86$, $P < 0.0001$), and season (rainy season: $\chi^2_{0.05,12} = 1141.14$, $P < 0.0001$; dry season: $\chi^2_{0.05,12} = 4805.67$, $P < 0.0001$). The composition of resources (i.e., seeds types and animal composition) was similar in both sites and seasons.

2.2. Foraging Activity of Pogonomyrmex Barbatus. To establish the intensity of foraging activity, the number of ants engaged in searching and gathering resources for an approximated duration of 8 minutes was counted. In each site (Jardín and Llano) were studied ten colonies for a total of 20 colonies studied in the area. In each observation, the colony disk was divided into four quadrants with directions NE, SE, SW, NW, and each quadrant was observed for 2 minutes. The ants leaving or joining the colony was recorded for each quadrant, counting only those that crossed the disk border. All data were analyzed using two-way analysis of variance (ANOVA) to compare the number of ants engaged in foraging between sites and seasons. Significant differences were tested using the least significant differences (LSDs) multiple comparison test [24].

Trophic niche breadth was estimated from the recorded number of ants returning to the nest with objects in their mandibles. Observations were performed for approximately 20 minutes. The objects carried by the ant using their mandibles were removed using entomological forceps and were assigned to one of the categories previously mentioned. To measure niche breadth, Levins index [25] was used to estimate the width, which was used as a measure of distribution of individuals uniformity among resources. The index value is highest when individuals are observed in all resources, and the minimum value is observed when the individuals are present in only one resource [25]. We estimated the diversity

Table 1: Results of two-way ANOVA test for the effect of site, season and interaction on the foragingintensity of *Pogonomyrmex barbatus* at the "Helia Bravo" Botanical Garden, Puebla, Mexico. Significant level $\alpha = 0.05$.

Variation source	Square sum	F value and probability
Sites	3971.0	$F_{0.05(1)1} = 1.135$; $P = 0.293$
Seasons	68967.4	$F_{0.05(1)1} = 19.719$; $P = 0.001$
Site ∗ season	18409.1	$F_{0.05(1)1} = 5.263$; $P = 0.027$

Table 2: Results of multiple comparison LSD tests for ant foraging during dry and rainy season in two sites, Jardín and Llano. $\alpha = 0.05$. LlR: Llano rainy; LlD: Llano dry; JR: Jardín rainy; JD: Jardín dry. Distinct letters indicate significant differences.

Site-season	Difference average	Probability	Confidence intervals (95%)	
LlD_a				
LlR	120.09	<0.05	171.05	69.12
JD_a	21.90	>0.05	72.87	29.05
JR	60.18	<0.05	111.14	9.21
LlR				
JD	98.18	<0.05	47.21	149.14
JR	59.90	<0.05	8.94	110.87
JD_b				
JR_b	38.27	>0.05	89.23	12.69

of resources by using the Shannon index and compared the results obtained in both communities [25]. The comparisons were made between sites and seasons. Data analyses were performed using SPSS 12.0 software (SPSS INC. 2003 SPSS for Windows rel. 12.0, Chicago IL, USA).

3. Results

3.1. Foraging Intensity. There were differences in the number of ants engaged in foraging in both sites and seasons. During the rainy season, the Llano colonies showed a higher number of foraging ants (average ± se = 53.5 ± 22.73) than the Jardín colonies (20.65 ± 18.96). During the dry season, the observed pattern was reversed: the Jardín colonies were more active (15.07 ± 9.73) than the Llano colonies (6.59 ± 7.17; Table 1). The results of ANOVA test showed significant differences in the site and season, and the LSD multiple-comparison test, LSD reveled that ants were more active during the rainy season, regardless of site (Table 2). The lowest values in activity for both sites (Figure 1) were recorded during the dry season. However, the foraging activity in Jardín was similar during both seasons (MD = 38.2, $P = 0.137$). Nevertheless, in Llano, the season significantly influenced the foraging ant activity (Table 2).

3.2. Trophic Niche Breadth. Similar to the study by Guzmán-Mendoza [23], the heterogeneity of available resources was similar in both sites ($t_{0.05,17.97} = 0.66$, $P = 0.52$), despite the greater abundance of seeds recorded in Llano. The comparison of trophic niche breadth showed that the Jardín colonies exhibited a stronger generalist approach than the Llano colonies ($t_{0.05,44} = 4.96$, $P < 0.0001$, Table 3). However, both sites showed that more seeds were used as a major resource on the basis of the observed number of ants physically carrying this specific resource (Figure 2).

Table 3: Trophic niche breadth of *Pogonomyrmex barbatus* at two semiarid sites with contrasting productivities during the rainy and dry season. JR: Jardín rainy; JD: Jardín dry; LlR: Llano rainy; LlD: Llano dry.

Site-season	Levins standardized index	Shannon diversity index	t value and probability
JR	0.31	0.95	
LlR	0.17	0.81	$t_{0.05(44)} = 4.96$, $P < 0.0001$
JD	0.16	0.76	
LlD	0.14	0.73	$t_{0.05(34)} = 0.713$, $P = 0.48$

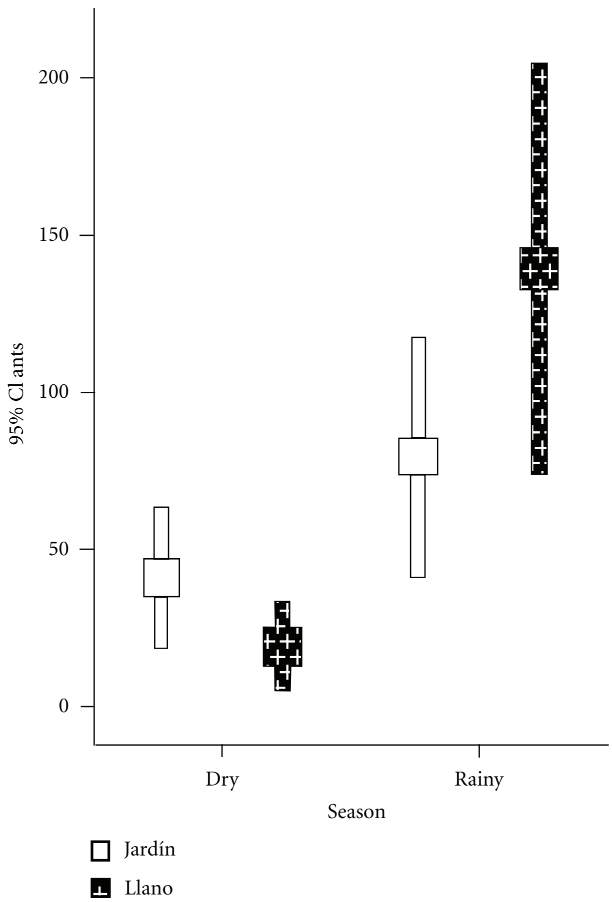

Figure 1: Average foraging activities of active ants at two sites at the Zapotitlán Valley, Puebla, Mexico, with contrasting productivities during two seasons.

Despite the variety of resources available to the colonies, the ants of Jardín mainly foraged on seeds, arthropods, floral structures, leaves and excreta, whereas the Llano ants

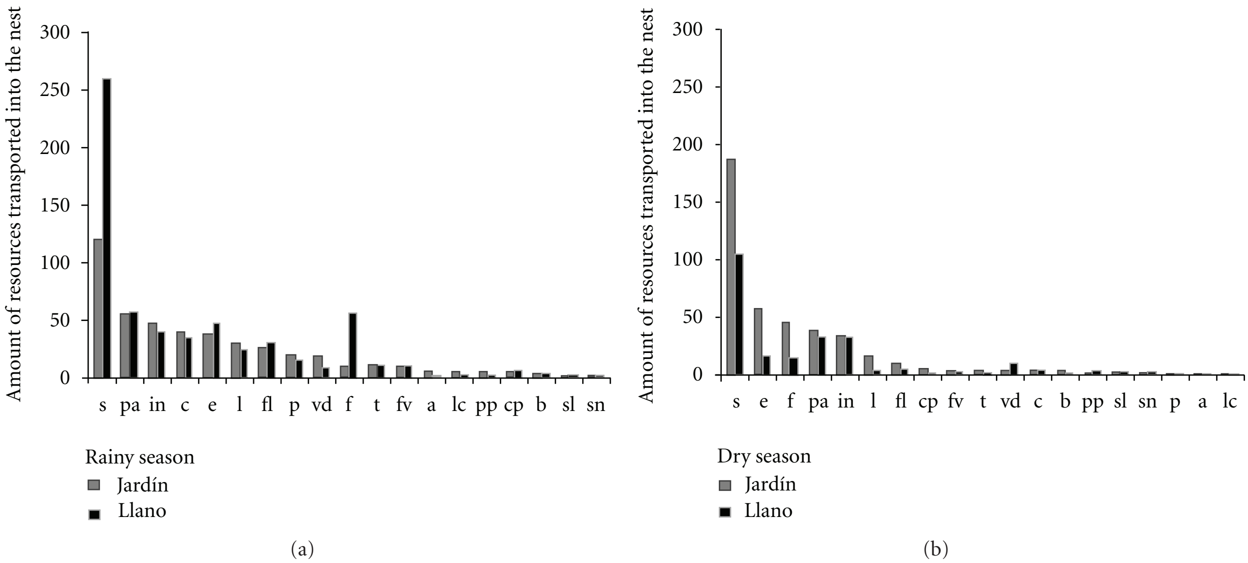

FIGURE 2: Resources removed from the ant mandibles during the rainy and dry season in two contrasting sites at the "Helia Bravo" Botanical Garden at Zapotitlán de las Salinas, Puebla, Mexico. a: algae; b: buds; c: capitate; cp: caterpillars; e: excretes; f: fruits; fl: flowers; fv: fleshy vegetal tissue; in: insects; l: leaves; lc: lichen; p: peels; pa: pieces of arthropods; pp: pupae; s: seeds; sl: soil; sn: snails; t: twigs; vd: vegetal debris.

were more actively focused on seeds, fruits, arthropods, and excreta.

During the dry season, the amount of resources differed at both sites. More resources and heterogeneity were recorded at Jardín than at Llano ($t_{0.05,17.97} = 44.43$, $P < 0.0001$). The comparison between trophic niches breadth values showed no significant differences during this season ($t_{0.05,34} = 0.713$, $P = 0.48$, Table 3).

4. Discussion

Results from counting the number of foraging ants in relation to trophic niche breadth suggest a direct and positive relationship between both variables. A high number of foraging ants indicated a wider range of choices diet, as observed in the Llano site during both rainy and the dry seasons. When resources were limited, some foraging ants invested less time searching for resources, and instead, focused on the most common resources in the area, such as seeds, insect fragments, excreta, and fruits, as shown in Figure 2. This pattern is related to the season, humidity, and temperature conditions. However, other ant species can search for complementary food sources to increase their trophic spectrum and foraging efficiency [7]. On the basis of these results, our study does not completely agree with the optimal foraging theory (OFT) that predicts wide-range diets in low productive environments, as compared to limited-range diets in high productive environments [2]. Although that theory has been tested in different cases [14, 26, 27], evidence for granivory systems are limited [28], and it seems that the behavioral peculiarities of ants related to patterns of foraging for resources, make them to perform somehow away from the predictions of OFT [29].

The number of foraging ants is related to trophic niche breadth, but the patterns of increase or decrease in the number of foraging ants depend on the environmental conditions related to the season, as shown by the recorded humidity and temperature values. Seasonality is an important factor for niche breadth of *P. barbatus* at the two studied sites, and attributable to the availability of resources and time of foraging, which are directly related to the humidity and temperature of the soil surface. In other arid zones, ants belonging to other species of *Pogonomyrmex* genus showed differences in their foraging habits in response to an environmental gradient; some of them preferred the highest temperatures during the day, whereas others showed peak foraging activity during the coldest hours of day [27]. At the Jardín site, the changes number of foraging ants were attributable to abundance of resources, whereas the diversity of resources at the Llano site showed a modified niche breadth; here, a wider trophic niche was observed with higher diversity levels and more forager ants. Thus, ants at the Jardín site under conditions of high abundance and diversity of resources reduced their trophic niche breadth and activity and were more generalists to a greater extent when the diversity of resources was limited. These results suggest that trophic niche breadth is not influenced by resource abundance alone, contrary to the assumption of the OFT [2].

Although differential abundance of resources can modify the niche breadth, as reported in other organisms such as fishes [14], tadpoles [30], and several butterflies species, and other animals present at a site that was in its first stages of succession after perturbation events and in which food was limited [15, 31], these conditions promote species superposition of diets and strong competition for food. Thus, the abundance and diversity of resources can play an important role in the establishment of variations in trophic niches. On the basis of the results of this study, it is possible to identify particularities in resource use according to inherent features of each site.

The results obtained in this study may increase knowledge on the feeding scheme of ants, which are important species because of their abundance and diversity but have been poorly studied in terms of their feeding relationships [32]. Nevertheless, it is necessary to conduct more observations and field experiments to quantify the influence of other parameters on ant diet, such as age, species diversity, and predation, to understand the role of the ants in the food web of arid ecosystems [32, 33].

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