Neighbor Colonies Affect Level of Foraging in the Generalist Ant Pheidole oxyops (Hymenoptera: Formicidae)

Authors: Assis, Diego Santana, Rodrigues Camargo, Giovanni Abrami, Barrios, Katty, Tannure-Nascimento, Ivelize C., and Do Nascimento, Fabio Santos

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Neighbor colonies affect level of foraging in the generalist ant *Pheidole oxyops* (Hymenoptera: Formicidae)

Diego Santana Assis[1], Giovanni Abrami Rodrigues Camargo[1], Katty Barrios[1], Ivelize C. Tannure-Nascimento[2], and Fabio Santos do Nascimento[1,*]

Abstract

Pheidole oxyops Forel (Hymenoptera: Formicidae) is a generalist ant that can display passive and active forage strategies. Moreover, this species can forage actively for a variety of food resources from plant debris to dead arthropods. In this study we tested whether abiotic factors (e.g., daytime, temperature, and residual soil accumulation), as well as neighboring colonies, could influence the patterns of foraging activity. Forage activity was observed in morning, afternoon, and evening sessions. Also, we recorded the frequency of individuals, direction, and ground surface temperature during foraging events. Our results showed that forage direction was not affected by residual soil accumulation and neighboring *P. oxyops* colonies. The rate of departures from nests decreased as ground surface temperature increased, but nest exits increased significantly with the occurrence of nearby *P. oxyops* colonies. We observed also that *P. oxyops* appeared to maximize forage activities during the evening period that would reduce their exposure to potential predators, competitors, and any adverse effects associated with direct solar radiation.

Key Words: abiotic factors; sit-and-wait foraging; active foraging; passive foraging

Resumen

Pheidole oxyops Forel (Hymenoptera: Formicidae) es una hormiga generalista que puede presentar dos tipos de estrategia de alimentación, activa y pasiva. Esta especie busca activamente fragmentos de plantas y artrópodos muertos. En este estudio probamos si los factores abióticos (e.g., hora del día, temperatura, y suelo residual acumulado) y las colonias adyacentes podrían influir en los patrones de actividad de alimentación. El flujo de colectores se registró en los períodos de mañana, tarde y noche. Además, registramos la frecuencia individual, la dirección y la temperatura del suelo durante los eventos de alimentación. Nuestros resultados mostraron que las direcciones de las rutas de alimentación no se vieron afectadas por la presencia de colonias vecinas o la acumulación de suelo residual. La temperatura del suelo, la hora del día y la presencia de colonias vecinas influyeron significativamente en la frecuencia de alimentación. La frecuencia de las salidas de los nidos aumentó significativamente cuando había más colonias vecinas cercanas, pero disminuyó a medida que aumentó la temperatura de la superficie del suelo. Además, en la tarde las hormigas no mostraron preferencias claras por las rutas. Las actividades de búsqueda de alimento fueron significativamente más frecuentes durante la noche. Los resultados nos permiten concluir que las colonias maximizan sus actividades en relación con el entorno externo, reduciendo los costos de alimentación en períodos más cálidos y competidores potenciales.

Palabras Clave: factores abioticos; estrategia de coleta; busca activa; busca pasiva

Several factors can affect food gathering by ants (Carroll & Janzen 1973; Traniello 1989). Some factors such soil and air temperature, diel period, as well as proximity of other ant species can limit foraging dynamics (Asfiya et al. 2016). For example, *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae) changes recruiting velocity when it is competing with other species (Yitbarek et al. 2017), whereas *Ocymyrmex barbiger* Emery (Hymenoptera: Formicidae) decreases searching time but increases walking velocity when soil temperature is very high (Marsh 1985).

To compensate for the variety of factors that may affect foraging behavior, ants have developed different strategies (Carroll & Janzen 1973; Traniello et al. 1984; Hölldobler & Wilson 1990). These strategies range from solitary to group/mass recruitment (Bonabeau 1997). According to Bernstein (1975), forage behavior can be classified into 3 basic forms: (1) individual foraging, i.e., solitary searching and resource obtaining independently of other ants from the colony; (2) mass recruitment, i.e., solitary searching, but resources are collected with help of several ants; (3) group foraging, i.e., each ant gathers the resource in a solitary way but they follow colony trails. *Pheidole oxyops* shows active and passive foraging strategies and uses the colony entrance as a pitfall trap (Fowler 1979, 1987). This species is also a generalist ant species that forages for vegetable parts (e.g., leaves, flowers, fruits) and dying arthropods (Fowler 1979, 1987). Their nests have an entrance of approximately 9.35 cm diam that are perpendicular to the ground with chambers connected by a unique main channel (Forti et al. 2007). In some cases, *P. oxyops* can decorate the nest entrance with feathers (Gomes et al. 2019) and other objects such as shells, petals, and seeds (D. S. A. and G. A. R. C., personal observation). This behavior

may increase the rate of passive capture of food items for this species (Gomes et al. 2019).

Pheidole oxyops is an ideal model for the study of forage ecology, first because the species possesses active and passive foraging strategies, and second because these ants may be considered a model for cooperative transport of food items (Czaczkes & Ratnieks 2011; Czaczkes et al. 2011). In this study, we tested the following 3 questions: Can neighboring *P. oxyops* colonies affect direction and exit rate of foraging workers of an adjacent conspecific colony? Do the ants of this species forage uniformly in all directions? Can temperature and other abiotic factors influence foraging *P. oxyops* exit rate?

Materials and Methods

We observed 15 colonies of *P. oxyops* on the campus of Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, São Paulo, Brazil (21.1671944°S, 47.8552500°W), approximately 2.7 ha. The municipality of Ribeirão Preto, São Paulo State, is located in southeastern Brazil, in the Brazilian savanna biome. Ribeirão Preto has an annual mean temperature of 21.9 °C, altitude 546 m, with an annual precipitation of 1,508 mm (Climate-Data.org 2017). The study was conducted from Jul 2016 to Apr 2017.

To evaluate foraging direction, we recorded the frequency of workers that naturally exited the colonies to forage for three 20 min per d period per colony for a total of 60 min per colony. The d periods were as follows: morning (8:00 to 9:00 A. M.), afternoon (12:00 to 2:00 P. M.) and evening (5:00 to 6:30 P. M.). During these times we were able to record data from 3 to 4 colonies in 8 cardinal directions at 45° intervals starting from north 0°.

Ground surface temperature was measured 0 to 5 cm from the soil surface with a thermohygrometer Minipa® MT-242 (Joinville, Santa Catarina State, Brazil) at the colony entrance. We used ground surface temperature because it is an interface between atmosphere and lithosphere and is not influenced by wind (Luo et al. 2018). The position of the soil mound deposited immediately outside the colony entrance was referenced using a compass, and the distance between the closest colonies of *P. oxyops* also were recorded (Fig. SM2 in the supplementary material provided online at http://purl. fcla.edu/fcla/entomologist/browse). Food resources brought to the colony over a 10 min per d period per colony were categorized as arthropods, vegetable (flowers, leaves, or fruits), non-arthropod, and others (empty shells, feathers, etc.; Fig. SM1).

STATISTICAL ANALYSIS

To evaluate the route uniformity of forager exits we used Rayleigh's test (Pewsey et al. 2013). Rayleigh's tests the uniformity of data to verify if the ants leave the colony to forage in a direction equally. To test the influence of discard pile and closest colonies on the preference of colony exit route, we used a circular model ('c-c') (Pewsey et al. 2013).

To analyze the explanatory variables preference of "d period," "local ground temperature," and "nearby colonies," we used generalized linear mixed models using the package 'lme4' (Bates et al. 2007). We used generalized linear mixed models because the models are more flexible, and we have data from several sources (in our case several colonies) distributed in a non-normal dataset (Bolker et al. 2009). For the models, we used the variable 'exits from colony' as a response variable with 'colony' as a random factor; for all models we used Poisson error distribution. Also, we performed a post-hoc test using general linear hypothesis test using false discovery rate correction (Hothorn et al. 2008). The post-hoc test was used to determine differences in times of d.

To evaluate the preference in the type of resource collected by the ants, we used a G-test (also known as likelihood ratio test) (Woolf 1957). This test compared the observational data with the expected ratios (Woolf 1957; Macdonald 2014). Our null hypothesis was equal rate of preference of food items (1 per sum of each item). To perform the G-test, we used the package RVAideMemoire (Hervé 2017). All analyses were performed in the R software v.3.4.3 (R Foundation for Statistical Computing 2016), and the package 'circular' (Agostinelli & Lund 2013).

Results

ROUTES AND INFLUENCE OF ENVIRONMENTAL FACTORS ON FORAGING ACTIVITIES

Pheidole oxyops showed a tendency to forage in specific directions during the morning (Rayleigh Statistic = 0.078; $p < 0.001$) and evening periods (Rayleigh Statistic = 0.075; $p < 0.001$). In both periods, the northeast, east, and southeast directions were preferred by the ants. In stark contrast, there was no tendency to follow specific routes in the afternoon period (Rayleigh Statistic = 0.042; $p = 0.100$) where ants exited the colonies without a specific direction (Fig. 1). In all cases, the position of the soil mound had no influence on foraging route (rho = 0.333; $p_{cos(\Theta)} = 0.499$; $p_{sin(\Theta)} = 0.843$) where workers normally passed over the soil mound to forage. In addition, there was no influence of

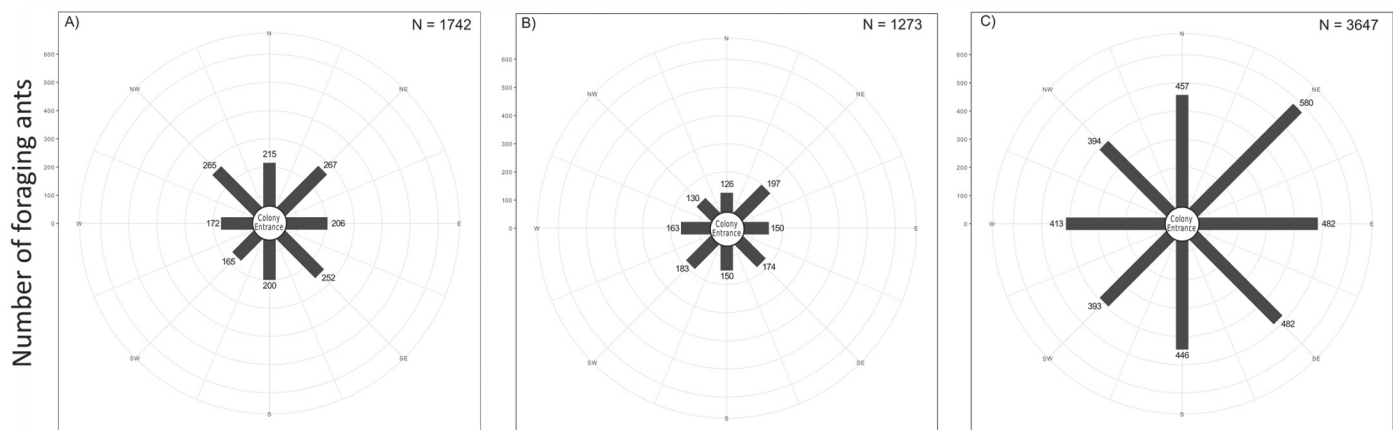

Fig. 1. Foraging route directions used by *Pheidole oxyops*, in 3 d periods: (A) morning, (B) afternoon, (C) evening. Numbers beside lines represent exits from the nest in that period. *N* value represents the total of exits.

neighboring *P. oxyops* colonies on the route of forager (rho = 0.267; $p_{cos(\Theta)}$ = 0.821; $p_{sin(\Theta)}$ = 0.057), nor did they show a route preference. The mean distance of neighboring colonies was 11.5 m. These results can be visualized in Figure SM2 as supplemental material.

All 3 d activity periods were different (χ^2 = 1326.800; *p* < 0.001). In the morning we recorded 1,742 ants ($\bar{x}$ = 116.133; median = 87), in the afternoon 1,273 ants ($\bar{x}$ = 84.867; median = 68), and in the evening 3,647 ants ($\bar{x}$ = 243.134; median = 243). Additionally, the rates of individual exits were 5.807, 4.243, and 12.157 individuals per min, in the morning, afternoon, and evening, respectively. There was a significant difference in the d period of activities, and ants showed a higher frequency of nest exits during the evening period (χ^2 = 1326.800; *p* < 0.001; Intercept: Estimate = 4.608; Z = 31.681; *p* < 0.001; afternoon: Z = −8.511; *p* < 0.001; evening: Z = 25.383; *p* < 0.001; Random effects: Variance = 0.308; SD = 0.555) (Fig. 2a).

In addition, the ground soil temperature negatively influenced forager exits from the colonies (Fixed effects: χ^2 = 462.730; *p* < 0.001; Correlation of fixed effects = −0.542; Random effects: Variance = 0.4161; SD = 0.645 (Fig. 2b). Furthermore, the presence of neighboring *P. oxyops* colonies negatively influenced the number of forager exits from the nest (χ^2 = 10.440; *p* < 0.001; Correlation fixed effects = −0.868; Random effects: Variance = 0.180; SD = 0.424) (Fig. 2c).

FOOD PREFERENCE IN ACTIVE FORAGING

Pheidole oxyops foragers had a significant preference for arthropod prey (*G* = 151.47; df = 5; *p* < 0.001) (Fig. 3a, b). Ants also collected vegetable parts (flowers, leaves, fruits) and non-arthropods (snails, nematodes) but at a lower frequency. The proportion of arthropods collected was 66.27%, vegetable parts were collected in smaller proportion (flowers = 1.57%; fruits = 9.02%; leaves = 17.65%), other (such as feathers and shells) was 5.10%; non-arthropods consisted of only 0.39% of collections (Fig. 3a).

Discussion

The foraging strategy used by ants depends on several spatiotemporal factors (Lanan 2014). In *P. oxyops*, ground soil temperature and presence of conspecific neighboring colonies influenced the foraging rate. Other workers also have found that abiotic factors such as air temperature (Asfiya et al. 2016) and humidity (Gordon 2013), including biotic factors such as competition (Sanders & Gordon 2003) and predation (Hunt 1983; Nonacs & Dill 1990), and intrinsic factors such as colony size (Beckers et al. 1989) affect the foraging strategy used by ants. These strategies involve a trade-off among energy expendi-
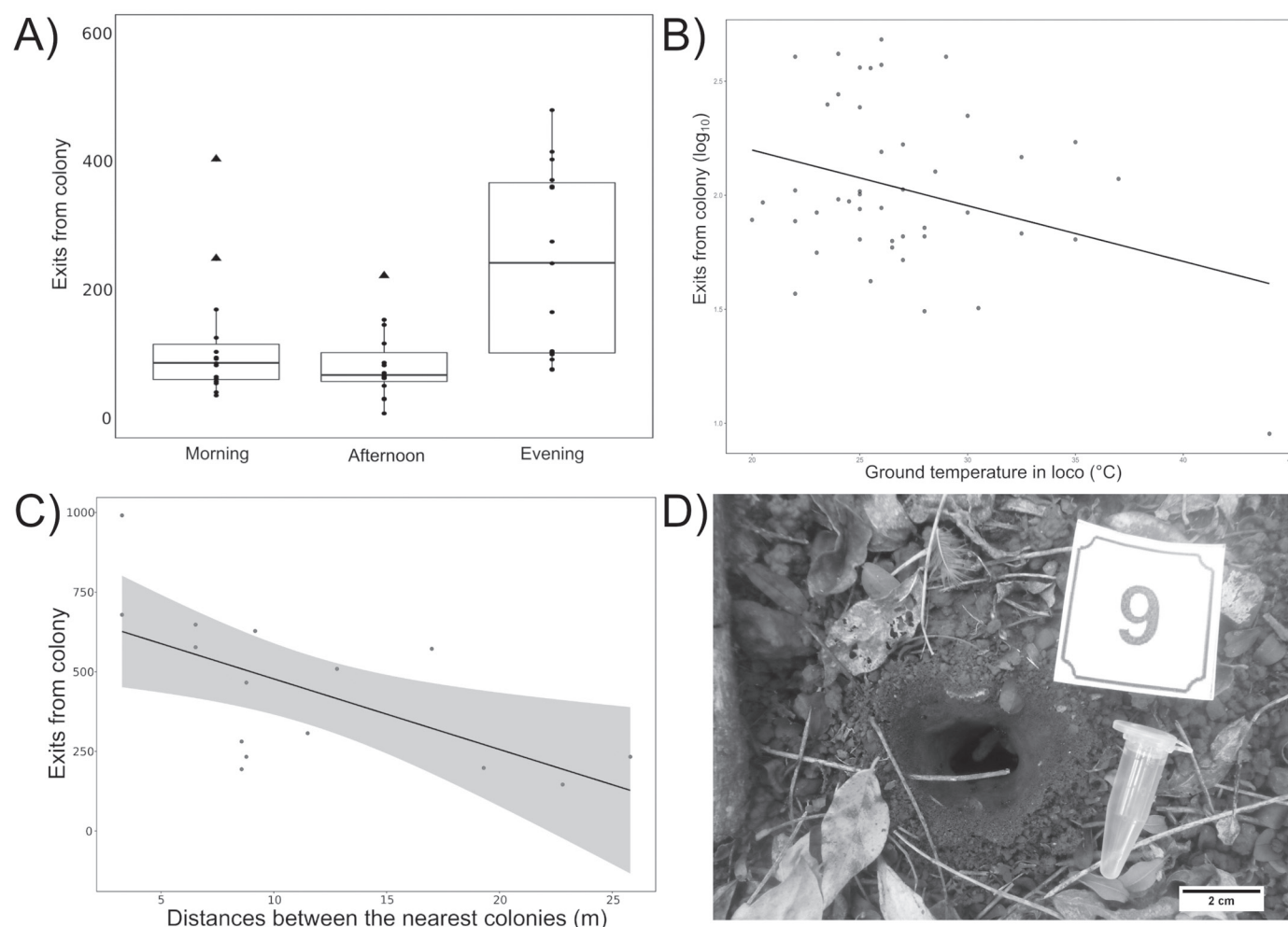

Fig. 2. (A) Number of total foraging exits per d period. Triangles indicate outliers in the sample. (B) Relationship between ground surface temperature and frequency of foraging exits. Values extracted from the Linear Mixed Effect Model. (C) Number of exits from colony and distance between the nearest colonies. (D) Colony entrance with some workers and feathers near entrance.
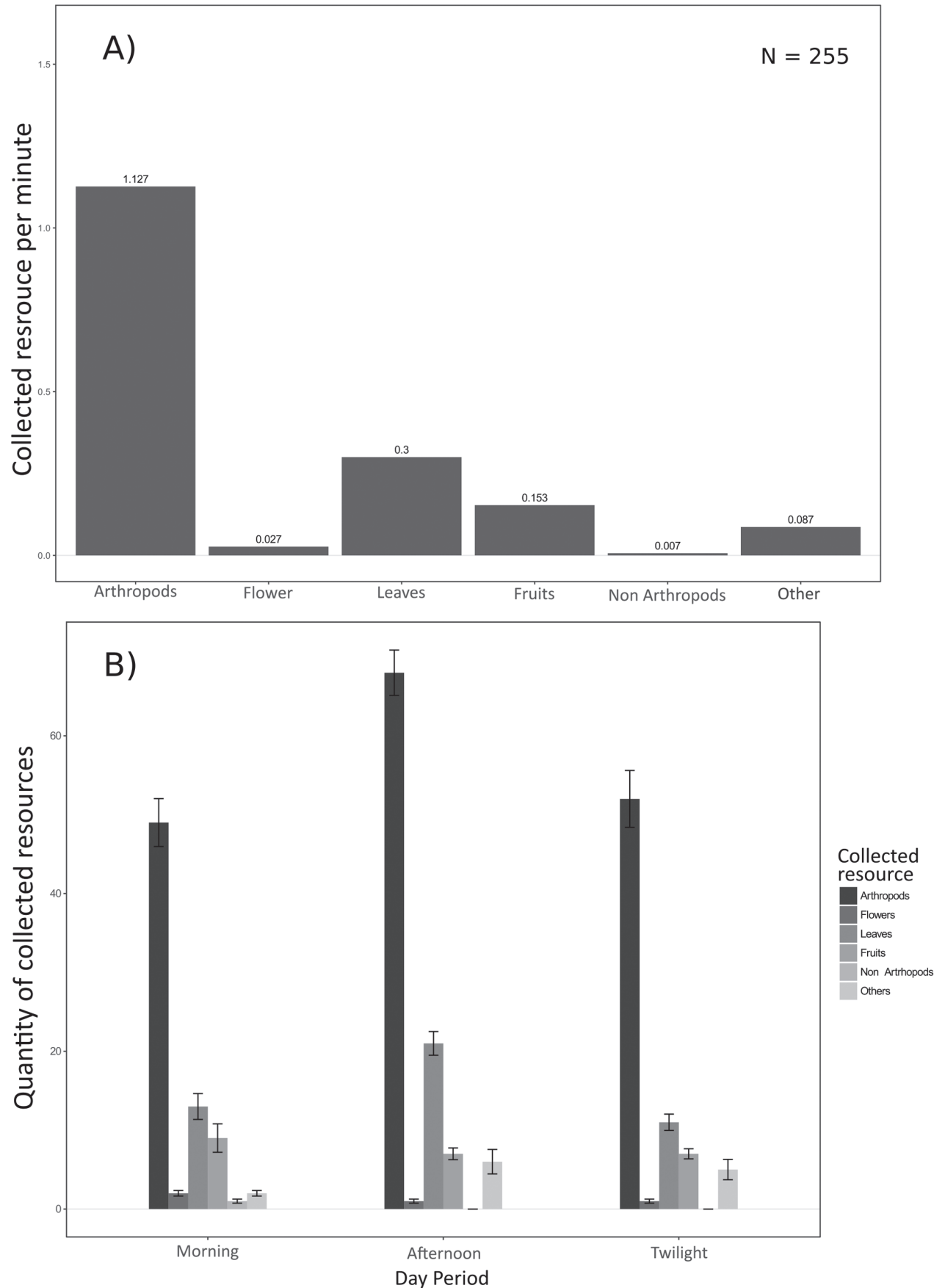
Fig. 3. (A) Frequency of foraging items obtained by *Pheidole oxyops* per min during our observation in the 15 nests; (B) mean quantity of resources obtained by *P. oxyops* during the d periods. Whiskers mean ± SD.

ture (Adler & Gordon 2003), risk of mortality (Nonacs & Dill 1990), and value of the resource.

We also found that *P. oxyops* had a higher intensity of foragers exiting the colony when in the presence of conspecific neighboring colonies. Sanders and Gordon (2003) reported similar results regarding the number of foraging ants leaving the colony as it related to competition between neighboring colonies. Competition in ants may drive ecological adaptations when searching for food resources (Gordon 1988; Sanders & Gordon 2003). For example, Gordon (1988) showed that *Pogonomyrmex barbatus* (Smith) (Hymenoptera: Formicidae) increased the foraging intensity to compete for resources against *Novomessor cockerelli* (Emery) (Hymenoptera: Formicidae). It is probable that there is intense intraspecific competition between neighboring conspecific *P. oxyops* colonies which results in a higher frequency of foraging. Colony density of *P. oxyops* modulates its foraging strategy by varying the number of foragers leaving the colony. Because of this, our results suggest that *P. oxyops* is a density-dependent competitor species. This strategy could increase the success rate during foraging. In a previous study (see Supplementary Material) we reported that *P. oxyops* exhibited lower aggressiveness to conspecific neighbors than to 'stranger' conspecifics. We suggest that in *P. oxyops*, intraspecific competition drives the foraging rates.

We also found that *P. oxyops* preferred to forage during the evening. This behavior may be related to minimizing sun exposure and a lower risk of water loss compared with those ants that forage in higher temperatures (Cerdá et al. 1998; Adler et al. 2007; Jayatilaka et al. 2011). Moreover, temperatures in the evening are lower than in the afternoon, and this may increase the exit frequency of scout and forager ants from the colony (Asfiya et al. 2016). For instance, in *Pheidole megacephala* (Fabricius) (Hymenoptera: Formicidae), temperature was a limiting factor of exiting foragers from the nest (Asfiya et al. 2016). In higher temperatures, ants experience physiological changes; for example, their respiratory and metabolic rates increase (Vogt & Appel 1999; Schilman et al. 2005). These physiological changes could increase ant mortality (Calabi & Porter 1989). Probably the environment exerts a huge pressure on *P. oxyops* colonies, favoring nests with wide entrances (pitfall entrance format) (Fowler 1987), that permits the ants to forage actively and passively (Czaczkes et al. 2011). In summary, we found the abiotic (ground soil temperature) and biotic (conspecific colonies) are factors that can influence the frequency of *P. oxyops* exits from the colony and the directionality of the forage paths. Although this species is considered a generalist, we found it preferred dying arthropods as a food resource and therefore exhibited a preference for a specific type of resource.

Acknowledgments

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