Foraging Activity Rhythms of *Dinoponera quadriceps* (Hymenoptera: Formicidae) in Its Natural Environment

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**ABSTRACT.** This study characterizes the foraging activity of the queenless ant *Dinoponera quadriceps* (Kempf) (Hymenoptera: Formicidae) in its natural environment by testing the hypotheses that foraging activity presents both daily and seasonal rhythmic variations, and that these rhythms are related to environmental variables. Four colonies of *D. quadriceps* were observed in an area of secondary Atlantic forest in northeastern Brazil. Data collection was performed over 72 h every three months during an annual cycle. Both daily and seasonal foraging activity rhythms of *D. quadriceps* colonies were related to environmental factors, but colony differences also explained part of foraging variations. Foraging activity of *D. quadriceps* colonies was predominantly diurnal independently of season. In the early dry season, the colonies had two activity peaks, one in the morning and another in the afternoon, with a decrease in foraging at midday; however, during the rest of the year, foraging activity was distributed more evenly throughout the daylight hours. The daily rhythm of foraging activity was likely determined by an endogenous circadian rhythm year-round, but in the dry season, temperature and relative humidity also influenced daily foraging activity, with a negative effect of temperature and a positive effect of relative humidity. On a seasonal scale, foraging activity peaked in the early dry season and suddenly declined at the end of this season, increasing again at the late rainy season. The seasonal rhythm of foraging was negatively related to relative humidity and positively related to prey availability.

**Key Words:** Ponerinae, daily rhythm, seasonality, environmental factor, queenless ant

Environmental changes over time occur in any habitat. Some changes in environmental conditions occur regularly in predictable cycles, paralleling daily and seasonal variations. Such variations create an selective pressure for the evolution of behavioral and physiological cycles in animals (Tauber et al. 1986). Most insects exhibit daily and seasonal activity cycle (Saunders 2002). Inside the nest, ants alternate moments of activity and rest, leading to rhythmic variations in activity levels in the colony as a whole by the interaction of workers (Cole 1991, North 1996). However, activities outside the nest, such as foraging, are influenced by many abiotic factors. Temperature, humidity, and light intensity are among the major abiotic factors that affect the temporal pattern of foraging in ants (Retana et al. 1988, North 1996, Pol and Lopez de Casenave 2004, Dunn et al. 2007, Domisch et al. 2009).

Ants are poikilotherms; thus, temperature and humidity fluctuations can affect the energy costs of foraging activity (Traniello 1989). The influence of these factors on foraging activity depends on the climatic characteristics of the environment inhabited by the species, its maximum and minimum limits of tolerance and its behavior. In boreal vegetation zones, the activity intensity in the species *Formica aquilonia* (Yarrow) generally increases with the air temperature (Domisch et al. 2009), whereas in a secondary Amazon rainforest area, temperature has a negative relationship on the activity rhythm of *Dinoponera gigantea* (Perty) (Fourcassié and Oliveira 2002). In the desert, the harvester ants *Pogonomymyx pronotalis* (Santschi) and *Pogonomymyx rastratus* (Mayr) exhibit temporal changes in the activity on the surface that are associated mainly with fluctuations in soil temperature. Nevertheless, within the limits tolerated by the species, temperature is sometimes not a good predictor for daily or seasonal activity fluctuations. In this case, other biotic and abiotic factors, such as light intensity, predation, and food availability, could better explain foraging variations (Pol and Lopez de Casenave 2004). In *Camponotus sylvaticus* (Olivier), when temperature is within the limits of tolerance of the species, light intensity is the most important factor influencing the beginning and end of foraging activity (Retana et al. 1988).

The foraging activity of ants is also influenced by the availability of food (Peeters and Crewe 1987, Cogni and Oliveira 2004, Medeiros et al. 2012). The foraging activity of *Dinoponera quadriceps* (Kempf) (Formicidae: Ponerinae) in the Caatinga of northeastern Brazil was positively related to the availability of potential prey (Medeiros et al. 2012). *Ophthalmopone berthoudi* (Forel) activity decreases in the dry months of winter when environmental conditions reduce the nocturnal activity of termites, its exclusive prey (Peeters and Crewe 1987). In *Gnamptogenys moelleri* (Forel), the number of ants leaving the nest is higher in summer when prey availability is also higher. This is also when the colonies have more larvae to feed, but the worker population of the colonies is similar in size to the worker populations in the winter (Cogni and Oliveira 2004).

The species respond differently to these multiple factors controlling the daily pattern and intensity of foraging activity, resulting in temporal segregation that likely contributes to the reduction in competitive interactions between them (Briese and Macauley 1980). Sympatric species of *Myrmecia* (Fabricius) exhibit this temporal segregation in foraging activity, which may have evolved to avoid competition. Their foraging schedules vary from strictly diurnal in *Myrmecia crassula* (Taylor) to diurnal and crepuscular in *Myrmecia tarsata* (Smith) to crepuscular and nocturnal in *Myrmecia nigripes* (Mayr) and *Myrmecia pyriformis* (Smith). As an adaptation to foraging in lower luminosity conditions, the eyes of workers in crepuscular and nocturnal species have larger lenses and photoreceptors, increasing their optical sensitivity (Greiner et al. 2007).

Some authors assert that the queenless ant genus *Dinoponera* (Roger) is nocturnal (Hölldobler and Wilson 1990, 2009), but this does not seem to be a feature shared by all species of this genus. Foragers of *Dinoponera longipes* (Ermey) seem to be mainly nocturnal but are also...
active during the day (Morgan 1993). In D. gigantea, a bimodal distribution was observed in the daily pattern of activity, with higher foraging intensity at dawn and dusk. However, the study was based on observations between 6:00 a.m. and 6:00 p.m., not reflecting the complete daily cycle (Fourcassie and Oliveira 2002). The authors assume that some activity also occurs during the night. In Dinoponera lucida (Emery), foraging activity is diurnal (Peixoto et al. 2010). Studies with D. quadriiceps have demonstrated that this species exhibits intense diurnal foraging as well as nest maintenance (Araújo and Rodrigues 2006, Azevedo et al. 2014), although it is possible to find workers moving around in the forest at night.

*D. quadriiceps* is endemic to northeastern Brazil, found mainly in areas of Atlantic forest and Caatinga (Kempf 1971, Paiva and Brandão 1995). Colonies of *D. quadriiceps* nest in the soil (Paiva and Brandão 1995), and their workers forage individually (Araújo and Rodrigues 2006). *D. quadriiceps* workers mainly carry dead organic matter of animal origin, particularly arthropods, to the nest. Only rarely does the capture of live animals occur. Small fruits and seeds are also collected by the workers, but their diet is mainly composed of animal food items that are difficult to predict in terms of spatial and temporal distribution (Araújo and Rodrigues 2006). This study aimed to characterize the foraging activity rhythm of *D. quadriiceps* colonies in their natural environment by testing the hypotheses that foraging activity presents both daily and seasonal rhythmic variations and that these rhythms are related to environmental factors. According to the scarce literature about this species and others that are closely related, a predominantly diurnal foraging activity, with an annual peak in the rainy season when temperature is lower and air humidity is higher, is expected.

**Materials and Methods**

**Colonies.** Four colonies of *D. quadriiceps* were observed in a secondary Atlantic forest area in the Floresta Nacional de Nísia Floresta (06°05′ S, 35°12′ W), Instituto Chico Mendes de Conservação da Biodiversidade, northeastern Brazil. The same colonies were observed throughout the study and had the same conditions of vegetation and luminosity. The colonies were located at distances ranging from 15 to 35 m from one another. Each colony had one to three nest entrances that do not appear to have underground connections because workers move from one to another on the soil surface. The nest entrance with the highest movement of workers in previous observations in each colony was chosen for data collection because it was not possible for one observer to monitor all the entrances.

The workers were marked individually before each data collection using a colored plastic tag with a different alphanumeric combination for each individual affixed to the thorax with adhesive based on cyanoacrylate ester, a technique based on Corbara et al. (1986). In total, 453 workers were marked from all four colonies (colony I: 54; colony II: 131; colony III: 105; and colony IV: 163), and 304 workers were observed throughout the study (colony I: 35; colony II: 94; colony III: 57; and colony IV: 118).

**Data Collection.**

**Behavioral Observation.** Data collection was performed during continuous 72-h cycles every 3 months during an annual cycle. The observations were always performed during the full moon to remove any confusion between a possible influence of moon phase variation and the influence of seasons. The observations occurred on 19–22 November 2010, 18–21 February 2011, 15–18 May 2011, and 13–16 August 2011. A group of observers took turns in pairs to cover the 72 h of observation. Each colony was observed continuously for 20 min/h. The four colonies were observed during the same days. During the night-time observations, flashlights with a red light were used to minimally interfere with the activity of workers.

During the observations, all workers leaving or entering the nest that were individually identified were recorded (adapted from Retana et al. 1990). Any worker was considered to have left the nest only when it moved more than 15 cm away from the nest entrance. Records of workers that left the nest carrying sand or waste and returned within 2 min were considered to be conducting nest maintenance activity and were removed from the analysis. Workers that took more time to return, or that left the nest and returned without removing any material from the nest, were considered to be engaged in foraging activity based on previous studies with this species which showed that *D. quadriiceps* workers spend around 90–95% of extra-nest time engaged in foraging activity (Araújo and Rodrigues 2006, Azevedo et al. 2014). When the workers returned with food, the characteristics of the food item were also recorded. The efficiency rate of foraging was calculated as proposed by Giannotti and Machado (1992): (number of workers returning to the nest with food × 100)/total number of workers returning to the nest. Food items carried by the workers were not collected during the 72 h of observation to avoid interference with the colonies.

After the 72 h of observation, the food carried by the workers of each colony was collected for 20 min every hour over 12 h, from 5:30 a.m. to 5:30 p.m. in each month of observation. The collection of food was only performed during the light phase based on the results of food retrieval from the first observation. All food collected was preserved in 70% alcohol and later identified, measured, and weighed in the laboratory.

**Measurement of Environmental Factors.** The availability of potential prey throughout the year was estimated by collecting invertebrates using pitfall traps. Six groups of pitfall traps were installed in the forest, 50 m away from the colonies observed to prevent ants from the nests under observation from being captured. Three groups were placed to the east and three to the west of the colonies, arranged in transects of 40-m long, 20 m from one another. The traps remained open in the field for 72 h in each month of data collection. Each group consisted of five pitfall traps arranged in a cross, 1 m away from one other with the four pitfalls of the tips connected to the central pitfall with 15 cm high plastic, forming a sample area of 4 m². The material collected in the pitfalls was preserved in 70% alcohol and later identified in the laboratory. Invertebrates belonging to the following taxa were considered potential prey for *D. quadriiceps*: Blattodea, Coleoptera, Diptera, Hymenoptera, Isoptera, Lepidoptera, Orthoptera, Araneae, Chilopoda, Diplopoda, Oligochaeta, Gastropoda, and pupae and larvae of unidentified Insecta based on food items collected from workers and on the composition of the diet presented by Araújo and Rodrigues (2006).

Immediately after each 20 min of behavioral observation, temperature and relative humidity were recorded with the digital thermometer EMR899HGN Oregon Scientific Inc., Portland, OR (temperature range: −50 to +70°C, humidity range: 2–98%) and luminosity was recorded with the digital photometer MLM-1011 Minipa Eletronics USA Inc., Houston, TX (luminosity range: 1–100,000 lux) both at ~10 cm from the observed nest entrance. Rainfall data from the observation days were obtained from the Empresa de Pesquisa Agropecuária do Rio Grande do Norte (EMPARN).

**Statistical Analysis.** The foraging activity of the colonies was estimated by the sum of the number of records of workers’ departures and returns in each 20 min/h observation. According to the results of Kolmogorov-Smirnov test, we used parametric or nonparametric tests, all of them with a two-tailed level of significance of 5%. The statistical software used was PASW Statistics 18 and R version 2.15.3.

To analyze the daily rhythm, the Wilcoxon signed-rank test was used for differences in foraging activity and food retrieval between the light and dark phases of the day. The Spearman correlation test was used to analyze the relationship between the daily rhythm of foraging activity and food retrieval. The generalized linear model (GLM) was used to analyze the influence of environmental factors on foraging activity and food retrieval daily variation. The models were applied with a quasi-Poisson distribution and log link function and were performed separately for each observation month. Foraging activity and the return with food were the response variables. Taking into account the autocorrelation because of the circadian rhythm, two auxiliary independent variables were added, $H_{\text{rain}} = \cos(2\pi \times \text{Hour}/24)$ and $H_{\text{rain}} = \sin(2\pi \times \text{Hour}/24)$ (van Oudenhove et al. 2011). The other
explanatory variables were colony (four-level factor), temperature, humidity, and luminosity. For colony factor, colony no. 4 was chosen as the reference level because it was the colony with higher foraging activity during most of the time. To detect the occurrence of multicollinearity among the independent variables, we checked the variance inflation factor (VIF), considering values lower than 10 to be acceptable (Field 2009). The full models were simplified by applying an analysis of deviance to remove step-by-step, nonsignificant effects.

For the seasonal analysis, the daily average of the foraging activity, food retrieval, temperature, humidity, and luminosity data were used, obtaining one value for each colony in each day of observation. According to the rainfall data from EMPARN, November was classified as the early dry season (EDS), February as the late dry season (LDS), May as the early rainy season (ERS), and August as the late rainy season (LRS). To compare the dry and rainy seasons, foraging activity and food retrieval were analyzed with paired-sample t-tests (t).

To analyze the variation of foraging activity, food retrieval, prey availability, and number of workers captured in pitfall traps among EDS, LDS, ERS, and LRS, repeated measures ANOVA (F) was used with a post hoc Bonferroni test. When sphericity was violated, the Greenhouse-Geisser correction was used. To analyze prey availability, the total number of potential preys obtained in each group of pitfall traps was included. The Spearman correlation test (r_s) was used to analyze the relationship between the foraging activity and food retrieval and the foraging activity and the number of workers found in the traps. A Pearson correlation test (r) was used to relate the variation in foraging activity with the number of foragers from the colony and the number of foraging trips per worker, as estimated by the daily number of different individuals engaged in foraging activity and the mean daily records of each worker’s foraging activity within each colony, respectively. GLM was used to analyze the influence of environmental factors on foraging activity seasonal variation. The model was applied with a normal distribution (Gaussian family) and identity link function. Foraging activity was the response variable and colony (four-level factor), temperature, humidity, luminosity, rainfall, and prey availability were the independent variables. VIF was taken into account before introducing independent variables in the model. The full model was simplified by applying an analysis of deviance to remove step-by-step not significant effects. The Kruskal-Wallis test (H) was used for differences throughout the year in the size and weight of food carried by the workers. The chi-square test ($\chi^2$), with continuity correction, was used to analyze the diet composition among seasons.

Results

Daily Rhythm. Colonies of D. quadriceps were continuously active, exhibiting no periods of inactivity. However, foraging activity varied during the day and was very low during the dark phase. Foraging activity was predominantly diurnal regardless of the season (Fig. 1). The number of workers involved in foraging activity was significantly higher during the light phase than during the dark phase throughout the year (EDS: z = -6.8, N = 144, P < 0.01; LDS: z = -4.0, N = 144, P < 0.01; ERS: z = -4.1, N = 144, P < 0.01; LRS: z = -7.9, N = 144, P < 0.01). In November, the EDS, the colonies had two activity peaks, one in the morning and another in the afternoon, with reduced foraging in the middle of the day (Fig. 1A), whereas in other months, foraging activity was distributed more evenly throughout the light phase of the day (Fig. 1B–D).

Food retrieval followed the same pattern of foraging activity, with a positive correlation between them (EDS: r_s = 0.55, N = 288, P < 0.01; LDS: r_s = 0.59, N = 288, P < 0.01; ERS: r_s = 0.40, N = 288, P < 0.01; LRS: r_s = 0.64, N = 288, P < 0.01). However, food retrieval was more restricted to the light phase (EDS: z = -4.9, N = 144, P < 0.01; LDS: z = -3.7, N = 144, P < 0.01; ERS: z = -2.6, N = 144, P < 0.01; LRS: z = -7.1, N = 144, P < 0.01), consistent with the times of highest foraging activity (Fig. 1).

Regarding the influence of environmental factors on the daily rhythm of activity of D. quadriceps, temperature, humidity, and light intensity effects varied depending on the season (Fig. 2). The best statistical model for the daily pattern of foraging activity in the EDS included the effect of the hour, temperature, humidity, and colony (Table 1). Differences among colonies explained part of the variability in foraging data. In the model, colony no. 1, 2, and 3 were compared with colony no. 4, the reference level of the factor. The endogenous circadian oscillations represented by the two variables $H_{cos}$ and $H_{sin}$ also had a

![Fig. 1. Daily variation in the number of workers involved in foraging activity and food retrieval in colonies of D. quadriceps in the (A) EDS, (B) LDS, (C) ERS, and (D) LRS. The median, first, and third quartiles and nonoutlier range of the data are presented. The bars at the top of each graph represent the light phase (white) and the dark phase (black).](https://i.oxford.university/library/academic/oup.com/journals/doi/10.1093/2381843/26/2019/3/1)
significant influence. Temperature had a negative significant effect and humidity had a positive significant effect on foraging activity. In the LDS, the best model included the effect of the hour, humidity, and colony. Humidity continued positively influencing daily foraging fluctuations, but temperature effect was not significant. In ERS and LRS, the best models included only the effect of hour and colony. There was no effect of light intensity on daily pattern of foraging activity.

For food retrieval, the best statistical models in the early and the LDS included the effect of hour, humidity, and colony (Table 2). As well as foraging, food retrieval was also positively affected by relative humidity. Differences among colonies also explained part of the variability in food retrieval data that was likely affected by endogenous circadian oscillations too. In the ERS, the best model included only the effect of hour and colony. In the LRS, the best model included the effect of hour, light intensity, and colony. There was a negative effect of light intensity on food retrieval in the LRS. Temperature did not help explain food retrieval daily variations.

Seasonal Rhythm. The foraging activity ($t = 1.9$, $N = 24$, $df = 23$, and $P = 0.06$) and food retrieval ($t = 0.5$, $N = 24$, $df = 23$, and $P = 0.64$) did not differ significantly between the dry and rainy seasons. However, with a more detailed analysis that took into account the month of collection (EDS, LDS, ERS, or LRS), it was possible to show that variation occurs in foraging activity throughout the year. The following results concerning seasonal variation refer to differences between these four stages of the year.

Colonies of *D. quadriceps* exhibited seasonal variation in foraging activity ($F = 7.6$, $N = 12$, $df = 3$, and $P < 0.01$), with peak activity at the EDS that dropped sharply at the end of this season. The low level of activity persisted throughout the ERS, tending to increase during the LRS (Fig. 3A). The variation in foraging activity was positively related to the daily number of different foragers from the colonies ($r = 0.71$, $N = 48$, and $P < 0.01$) but it was not related to the number of foraging trips performed by each worker ($r = 0.23$, $N = 48$, and $P = 0.11$). A similar pattern of seasonal variation was observed for the number of *D. quadriceps* workers captured in pitfall traps ($F = 10.9$, $N = 6$, $df = 3$, and $P < 0.01$) (Fig. 3B). The number of workers found in the traps was positively related to the foraging activity observed in the colonies ($r_s = 0.50$, $N = 48$, and $P < 0.01$). Despite the seasonal foraging activity, food retrieval did not vary significantly throughout the year ($F = 2.1$, $N = 12$, $df = 1.6$, and $P = 0.16$) (Fig. 3C), although there was a positive correlation between foraging activity and food retrieval ($r_s = 0.60$, $N = 48$, and $P < 0.01$).

Analyzing the activity of workers during each phase of the day (light or dark), it was observed that foraging activity at night did not vary significantly throughout the year ($F = 1.7$, $N = 12$, $df = 3$, and $P = 0.18$). The seasonality of foraging activity was mainly because of the variation of this activity during the light phase of the day ($F = 10.4$, $N = 12$, $df = 3$, and $P < 0.01$) (Fig. 4).

The best statistical model for the seasonal variations in foraging activity included the effect of colony, daily mean humidity, and prey availability (Table 3). Differences among colonies explained part of the variability in foraging data. Humidity had a significant negative influence and prey availability had a significant positive influence. Daily mean temperature, daily mean luminosity, and daily rainfall did not help explain seasonal variations of foraging data.

The availability of prey in the environment did not show any significant seasonal variation ($F = 1.2$, $N = 6$, $df = 3$, and $P = 0.33$). Similarly, neither the size nor the weight of the food that was captured by workers differed significantly throughout the year ($H = 3.5$, $N = 121$, $df = 3$, $P = 0.33$; $H = 5.8$, $N = 120$, $df = 3$, and $P = 0.12$).
Table 1. Final GLMs investigating the effects of biotic and abiotic variables on the daily variation of foraging activity of *D. quadriceps* in secondary Atlantic forest

| Season | Estimate (±SE) | t-value | P-value |
|--------|---------------|---------|---------|
| EDS (Intercept) | 2.8032 (±0.9523) | 3.17 | <0.01 |
| *H*<sub>cos</sub> | -1.3105 (±0.1828) | -7.17 | <0.01 |
| *H*<sub>sin</sub> | 0.2722 (±0.0868) | 3.14 | <0.01 |
| Temperature | -0.116 (±0.0519) | -2.23 | <0.05 |
| Humidity | 0.0271 (±0.0113) | 2.4 | <0.05 |
| Colony no. 1 | -0.1645 (±0.1623) | -1.01 | 0.31 |
| Colony no. 2 | -0.1845 (±0.1604) | -1.15 | 0.25 |
| Colony no. 3 | -0.7976 (±0.1884) | -4.23 | <0.01 |
| LDS (Intercept) | -6.6642 (±0.9484) | -7.03 | <0.01 |
| *H*<sub>cos</sub> | -0.7957 (±0.0971) | -8.19 | <0.01 |
| *H*<sub>sin</sub> | -0.5209 (±0.0881) | -5.91 | <0.01 |
| ERS (Intercept) | 0.0949 (±0.1032) | 9.64 | <0.01 |
| Colony no. 1 | -0.03 (±0.2377) | -0.13 | 0.9 |
| Colony no. 2 | 1.1701 (±0.1955) | 5.98 | <0.01 |
| Colony no. 3 | 1.0346 (±0.1984) | 5.22 | <0.01 |
| LDS (Intercept) | 0.9949 (±0.1013) | 9.64 | <0.01 |
| Colony no. 1 | -0.10678 (±0.204) | -5.23 | <0.01 |
| Colony no. 2 | -0.2486 (±0.1553) | -1.6 | 0.11 |
| Colony no. 3 | -0.5683 (±0.204) | -1.86 | <0.05 |
| LRS (Intercept) | 1.1708 (±0.0923) | 12.69 | <0.01 |
| *H*<sub>cos</sub> | -0.781 (±0.085) | -9.19 | <0.01 |
| *H*<sub>sin</sub> | 0.2754 (±0.0797) | 3.45 | <0.01 |
| Colony no. 1 | -0.7689 (±0.1532) | -5.02 | <0.01 |
| Colony no. 2 | -0.7768 (±0.1536) | -5.06 | <0.01 |
| Colony no. 3 | -0.4426 (±0.1378) | -3.21 | <0.01 |

EDS, early dry season; LDS, late dry season; ERS, early rainy season; LRS, late rainy season.

Table 2. Final GLMs investigating the effects of biotic and abiotic variables on the daily variation of food retrieval of *D. quadriceps* in secondary Atlantic forest

| Season | Estimate (±SE) | t-value | P-value |
|--------|---------------|---------|---------|
| EDS (Intercept) | 10.0995 (±1.4751) | -6.85 | <0.01 |
| *H*<sub>cos</sub> | -2.6158 (±0.4034) | -6.48 | <0.01 |
| Humidity | 0.12 (±0.0191) | 6.28 | <0.01 |
| Colony no. 1 | 0.0908 (±0.3556) | 0.25 | 0.8 |
| Colony no. 2 | 0.9095 (±0.2962) | 3.07 | <0.01 |
| Colony no. 3 | -0.6619 (±0.4297) | -1.86 | <0.01 |
| LDS (Intercept) | -11.3292 (±1.7404) | -6.51 | <0.01 |
| *H*<sub>cos</sub> | -1.2814 (±0.1908) | -6.72 | <0.01 |
| *H*<sub>sin</sub> | 0.617 (±0.1658) | 3.72 | <0.01 |
| Humidity | 0.1122 (±0.0202) | 5.56 | <0.01 |
| Colony no. 1 | 1.3067 (±0.3906) | 3.35 | <0.01 |
| Colony no. 2 | 1.6301 (±0.3779) | 4.31 | <0.01 |
| Colony no. 3 | -0.458 (±0.5379) | -0.85 | 0.39 |
| ERS (Intercept) | -0.9369 (±0.2063) | -4.54 | <0.01 |
| *H*<sub>cos</sub> | -0.4979 (±0.2232) | -2.23 | <0.05 |
| Colony no. 1 | -3.3576 (±1.108) | -3.03 | <0.01 |
| Colony no. 2 | -1.7482 (±0.5266) | -3.32 | <0.01 |
| Colony no. 3 | -0.6286 (±0.3374) | -1.86 | 0.06 |
| LRS (Intercept) | -0.4231 (±0.1632) | -2.59 | <0.01 |
| *H*<sub>cos</sub> | -1.8611 (±0.225) | -8.27 | <0.01 |
| *H*<sub>sin</sub> | 0.5486 (±0.1322) | 4.15 | <0.01 |
| Light intensity | -0.0006 (±0.0002) | -2.89 | <0.01 |
| Colony no. 1 | -1.4338 (±0.3011) | -4.76 | <0.01 |
| Colony no. 2 | -0.9315 (±0.2273) | -4.1 | <0.01 |
| Colony no. 3 | -0.605 (±0.1991) | -3.04 | <0.01 |

EDS, early dry season; LDS, late dry season; ERS, early rainy season; LRS, late rainy season.

Fig. 3. Mean (±SE) number of (A) workers per hour involved in foraging activity, (B) workers caught in pitfall traps, and (C) workers her hour returning to the nest with food throughout the year in *D. quadriceps*. EDS, early dry season; LDS, late dry season; ERS, early rainy season; and LRS, late rainy season. Error bars with different letters above them are significantly different (ANOVA and Bonferroni a posteriori test, *P* < 0.05).

Discussion

The daily pattern of foraging activity of *D. quadriceps* colonies in this study was predominantly diurnal and was most influenced by their likely endogenous circadian rhythm and by colony differences. The effect of other factors, such as temperature, relative humidity, and light intensity, is varied according to the seasons. The same was observed for food retrieval. Colony differences in the intensity of foraging activity most likely reflect differences in colony population size, with more activity in larger colonies with more foragers and more individuals to feed. This colony effect does not mean differences in the timing of foraging, but rather in the level of activity at a given time. Independently of colony differences, daily variations of foraging and consequently of food retrieval were likely determined by an endogenous circadian rhythm year-round. Despite most studies about foraging in ants focus on the effect of abiotic factors, mainly temperature, the endogenous...
circadian rhythm has an important role for foraging schedules in many ant species. In *Ectatomma tuberculatum* (Olivier), the rhythm of extraneast activity exhibited in the field persists in laboratory constant conditions, indicating that it is not simply a response to field temperature and light/dark cycles but a rhythm that is internally controlled (McCluskey 1987). In *Camponotus compressus* (Santschi), foragers display locomotor activity rhythm that synchronizes with 24-h light/dark cycles and free runs in continuous darkness (Sharma et al. 2004). The influence of circadian rhythm on foraging was also found in *Tapinoma nigererrinum* (Nylander) in addition to the effects of seasonal rhythm and temperature (van Oudenhove et al. 2011). *Linepithema humile* (Mayr) exhibits a circadian activity pattern of foraging independent of temperature (Enzmann et al. 2012).

In the EDS, temperature and relative humidity also affected the daily foraging pattern of *D. quadriceps* colonies. Temperature had a negative effect, and relative humidity had a positive effect on foraging. The effects of these abiotic factors explain the occurrence of two foraging peaks during the day in the EDS. Workers reduced foraging activity in the middle of the day because of high temperature and low relative humidity that were above 30°C and below 60%, respectively. These conditions are likely close to the tolerance limits of the species and become restrictive for foraging. In the LDS, because temperature was lower than in EDS, foraging activity was not limited by temperature. Despite the positive effect of relative humidity, foraging activity was distributed more evenly throughout the light phase of the day. During the rainy season, with lower temperature and higher relative humidity, neither temperature nor humidity influenced daily foraging variations. Foraging activity was also distributed more evenly throughout the light phase of the day when compared with the bimodal pattern exhibited in EDS.

A similar effect occurs in some species of desert ants, such as *Cataglyphis bombycina* (Roger), *Ocymyrmex robustior* (Stitz) (Wehner and Wehner 2011), *P. pronotalis*, *P. rastratus* (Pol and Lopez de Casenave 2004), and *Melophorus bagoti* (Lubbock) (Schultheiss and Nooten 2013), and in some species from semiarid environments, such as *O. berthoudi* (Peeters and Crewe 1987). All these species change from a unimodal to a bimodal pattern of foraging, decreasing foraging activity in the middle of the day in the hottest days or months. In *D. lucida*, a slight reduction in foraging activity is observed around midday, just when the temperature is higher, but temperature conditions between 16 and 31.5°C do not seem to be a limiting factor for ant activity outside the nest (Peixoto et al. 2010). *D. gigantea*, during light phase observations, exhibited a bimodal pattern in the LDS in the Amazon rainforest, but changes in the daily pattern throughout the year because environmental conditions, as were observed in *D. quadriceps* and the species mentioned above, has not been investigated. In *D. gigantea*, the decrease in foraging activity in the middle of the day also coincides
with the time when the temperature exceeds 30°C (Fourcassié and Oliveira 2002). Pachycondyla veranea (Forel) exhibits a sharp drop in foraging at temperatures between 29 and 32°C, interrupting foraging at temperatures above 33°C, but the low humidity of 34% on some days was not a limiting factor for the foraging activity of this species (Chagas and Vasconcelos 2002). Consistent with our results from D. quadriceps, the daily foraging activity of Odontomachus chelifer (Latreille) was negatively related to temperature in the warm season but not in the cold season (Raimundo et al. 2009).

According to the characteristics of change in foraging daily pattern throughout the year, D. quadriceps is similar to the group of ant species that are intolerant to heat, such as some Mediterranean species (Messor capitatus (Latreille), Pheidole pallidula (Nylander), T. nigrerrimum, and Tetramorium semilaeve (André)) (Cros et al. 1997, Cerdá et al. 1998). Cros et al. (1997), studying Mediterranean ant communities, have distinguished two groups of species: those tolerant to heat, which are diurnal and slightly modify their daily pattern of activity throughout the year, such as Cataglyphis cursor (Fonscolombe), Camponotus foreli (Emery), and Aphaenogaster semilis (Mayr), and those intolerant to heat, which go from diurnal to crepuscular or nocturnal at high temperatures and exhibit peak activity at temperatures below 30°C, such as M. capitatus, P. pallidula, T. nigrerrimum, and T. semilaeve. In Mediterranean communities, ants intolerant to heat are dominant and exhibit risk-averse behavior, foraging at temperatures very distant from their maximum critical temperature. Heat-tolerant species are subordinates and have the propensity to engage in risky behavior, foraging very close to the maximum critical temperature and at increased risk of mortality (Cerdá et al. 1998, Cerdá 2001).

Analyzing the fluctuation of foraging activity in a seasonal scale, D. quadriceps colonies exhibited seasonal variation in foraging activity despite that the Atlantic forest is one of the Brazilian biomes that, like the Amazon forest, has the lowest seasonal changes in vegetation compared with Cerrado and Caatinga (Formigoni et al. 2011). O. chelifer, another Ponerinae ant species, also exhibits seasonal variation in foraging activity in the Atlantic forest of southeastern Brazil (Raimundo et al. 2009). However, the peak of foraging activity in D. quadriceps was not directly related to the dry and rainy seasons, but to transitions between them. The foraging activity began to increase in the LRS and reached its maximum in the EDS. This pattern occurred mainly because of the variation of activity during the light phase. In a study conducted in the Caatinga, D. quadriceps also exhibited peak foraging activity in the LRS and EDS, even though the rainy season begins earlier (Medeiros et al. 2012). Nevertheless, the seasonal variation of the foraging activity of D. quadriceps that was recorded in the Caatinga by Medeiros et al. (2012) was much higher than that reported here in the Atlantic forest. Barrow and Parr (2008), comparing three types of semi-arid tropical habitats, demonstrated that temporal variation in the ant assemblages may differ among habitats because of higher or lower seasonal fluctuations in environmental conditions.

The number of workers captured in pitfall traps exhibited seasonal variation directly related to the foraging activity of the observed colonies, proving that the use of traps to estimate foraging activity adopted in many studies (Dunn et al. 2007, Barrow and Parr 2008, Medeiros et al. 2012), is indeed appropriate. However, direct observation of the colonies permits the collection of more detailed data and was therefore adopted in this research.

A positive correlation was found between the seasonal foraging activity of D. quadriceps and the daily number of different foragers in each colony, whereas no correlation was found with the estimated number of foraging trips per worker. In a previous study with D. quadriceps, the number of individuals engaged in foraging activity varied seasonally, with an increase in the number of foragers during the dry season (Medeiros and Araújo 2014), the same period during which the peak of foraging activity occurs. Therefore, the increase in foraging activity occurs by increasing the number of foragers in the colony and not the number of foraging trips of each worker.

D. quadriceps colonies increased foraging activity at the time of year with drier environmental conditions that were more favorable for foraging. In wet months, foraging decreased. In Gigantopus destructor (Fabricius), which has strictly diurnal foraging activity, more foragers were observed in the field on sunny days than on cloudy days (Beugnon et al. 2001). In M. bagoti, also diurnal, foraging activity is reduced on cloudy days (Muser et al. 2005). The rain itself is a limiting factor for foraging by increasing the difficulty of movement in the environment, especially under heavy rain. The inhibition of foraging by rain was also observed in D. lucida (Peixoto et al. 2010). Similarly, in Cataglyphis iberica (Emery), rain can cease the activity of the colonies in a few minutes (Cerdá and Retana 1989). The same occurs with M. bagoti, with an interruption of foraging observed once the rain starts (Muser et al. 2005). Intense and long rainfall also causes interruptions of foraging in P. verenea (Chagas and Vasconcelos 2002).

Abiotic factors related to seasonal foraging activity of D. quadriceps in secondary Atlantic forest differed from those in semi-arid Caatinga. In the Caatinga area, seasonal variations in the foraging activity of D. quadriceps are negatively related to temperature and positively related to prey availability (Medeiros et al. 2012). This indicates that the same species can be influenced by different environmental factors depending on the conditions of the habitat it is in. However, prey availability was positively related to seasonal changes in foraging activity in both habitats, although prey availability did not significantly fluctuate throughout the year in secondary Atlantic forest. An increase in food availability increases foraging activity in many ant species. In Pogonomyrmex barbatus (Smith), the rate of successful foragers returning to the nest with seeds used as a food availability measure by workers inside the nest and regulates the rate at which they leave the nest to forage. The combination of the odor of food and the odor of foragers stimulates a foraging increase (Greene et al. 2013). In O. chelifer, which preys on a wide variety of arthropods, foraging activity is higher in the warm and wet season when there is a higher abundance of available prey. The number of returning workers carrying prey into the nest also tends to increase the departure of inactive workers from the nest to forage (Raimundo et al. 2009). In D. quadriceps, Nascimento et al. (2012) demonstrate positive feedback between the incoming food and the activation of new foragers and Azevedo et al. (2014) show that the success in a previous trip negatively influences the time spent by the worker inside the nest before the next foraging trip, with shorter intertrip latency when the worker had captured a prey in the previous trip, and that the percentage of success in the next trip is higher when the previous trip was successful.

Although the foraging activity varied seasonally with changes in relative humidity and prey availability, food retrieval did not vary significantly throughout the year. The number of food items collected and the size, weight, and ratio of items from animal or plant origin and of living or dead prey carried by workers did not exhibit significant seasonal variation, most likely because of low variation in food availability in the environment. The capture of living prey in both seasons was not rare. Living prey was an important portion of the animal items captured by workers, different from the observations by Araújo and Rodrigues (2006).

In this study, seeds and fruits of three plant families, Burseraceae, Dilleniaceae, and Rubiaceae, were carried to the nest by D. quadriceps. Fruits and seeds from Myrtaceae were also observed, and this had been previously recorded by Araújo and Rodrigues (2006). The prevalence of items of animal origin, mainly arthropods, in the diet of this species was confirmed by our results. Although most of their diet consists of items of animal origin, large ponerine ants, such as O. chelifer and Pachycondyla striata (Smith), are the main vectors of seeds in Restinga habitat (Passos and Oliveira 2003).

The efficiency rate of foraging was 26.8%, on average, whereas Araújo and Rodrigues (2006) observed a rate of 76% and Azevedo et al. (2014) observed a rate of 57%. Azevedo (2009) observed the success in obtaining food in 25% of foraging trips of D. quadriceps...
workers, a value close to ours. A low efficiency rate is common for species that feed on insects, such as *C. ibera*, which has an average daily efficiency rate between 15 and 28% (*Cerdá and Retana 1989*). By contrast, a high efficiency rate is common in seed harvesting species, such as *P. rastratus*, *P. mendenoanus* (Cuezzo and Claver), and *P. inermis* (Føre), which have average efficiency ~86% (*Pol et al. 2011*).

*D. gigantea* workers, which have a diet similar to that of *D. quadriiceps*, were successful in only 10% of foraging trips (*Fourcassie and Oliveira 2002*). The differences between the results presented here and those found by *Araújo and Rodrigues* (*2006*) and *Azevedo et al.* (*2014*) may be because of differences in sampling, underlying the importance of studies with longer field observation and taking into account the temporal variation, both seasonal and daily.

Based on the results, we conclude that the foraging activity of *D. quadriiceps* colonies presents rhythmic variations, both daily and seasonal, even in a relatively constant environment such as the Atlantic colonies. *D. quadriiceps* foraging activity was predominantly diurnal and its annual peak occurred in the EDS, with increased activity beginning in the LRS. The foraging activity rhythm of the *D. quadriiceps* colonies was related to environmental factors, but colony differences also explained part of foraging variations. The daily rhythm of foraging activity was likely determined by an endogenous circadian rhythm year-round, but in the dry season temperature and relative humidity also influenced daily foraging activity, with a negative effect of temperature and a positive effect of relative humidity. The foraging seasonal rhythm, however, was negatively related to relative humidity and positively related to prey availability.

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