



RESEARCH ARTICLE - ANTS

Litter Surface Temperature: A Driving Factor Affecting Foraging Activity in *Dinoponera lucida* (Hymenoptera: Formicidae)

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Abstract

Dinoponera lucida is a poneromorph ant endemic to the Atlantic Forest of Brazil. The species is classified as endangered in Brazil's Red List due to its peculiar reproductive biology and high habitat fragmentation. Herein, we characterize *D. lucida* foraging activity and response to litter surface temperature in a lowland forest remnant in south-eastern Brazil. The mean flow of workers at nest openings was 3.8 ± 0.6 per hour, mean foraging trip was 14.2 ± 2.2 min, and mean foraging distance was 3.8 ± 0.4 m. The time spent per foraging trip and litter surface temperature were positively correlated. Flow of workers at nest openings was higher with mean temperature of litter surface between 21.0 and 27.0 °C. Our results show that *D. lucida* has a diurnal foraging activity related to habitat temperature. Our data contribute to the knowledge about the ecology of *D. lucida* and support the hypothesis of optimal food foraging regulated by habitat temperature. In addition, the better understanding of *D. lucida* activity patterns can assist on conservation planning of this endangered and endemic ant.

Introduction

Foraging requires appropriate decisions related to the time spent in exploration and choosing the appropriate time to maximize net amount of energy gained, foraging efficiency, and survival, or to minimize the risk of starvation (Emlen, 1966; MacArthur & Pianka, 1966; Ydenberg, 2007). These decisions are subject to constraints that limit viable alternatives, such as time spent and the energy cost of the activity (Emlen, 1966; MacArthur & Pianka, 1966; Perry & Pianka, 1997; Ydenberg, 2007). Decisions may be related

to the time spent searching for food, affecting foraging efficiency, when the increase in time spent does not result in an increase in the amount of food obtained (MacArthur & Pianka, 1966; Norberg, 1977; Pyke, 1984; Perry & Pianka, 1997). The trade-off between costs and benefits does not depend only on the forager's intrinsic factors; external factors (e.g. environmental conditions and prey density) can alter the foraging activity dynamics (Norberg, 1977; Pyke, 1984).

The eight species of *Dinoponera* Roger, 1861 (Hymenoptera: Formicidae: Ponerinae) are endemics to South America (Kempf, 1971; Lenhart et al., 2013), and



called giant ants because reach up to 40 mm (Kempf, 1971; Lenhart et al., 2013; Escárraga et al., 2017). Among these species, *Dinoponera lucida* Emery, 1901 is endemic to Brazil's Atlantic Forest from the states of Espírito Santo, eastern Minas Gerais and southern Bahia (Peixoto et al., 2010; Simon et al., 2020). Currently, only 12% of the area originally covered by Atlantic Forest has forest remnants, mostly small and isolated across the human-altered matrix (Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais, 2019). *Dinoponera lucida* is a forest-specialist and currently recorded only in forest remnants. The area of geographic range of the *D. lucida* was estimated at 156 km² (Instituto Chico Mendes de Conservação da Biodiversidade & Ministério do Meio Ambiente, 2018). Habitat fragmentation causes isolation of populations, since the species is unable to colonize over long distances, leading to a clumped distribution pattern over the geographic range (Instituto Chico Mendes de Conservação da Biodiversidade & Ministério do Meio Ambiente, 2018). New colonies of *D. lucida* are generated by fission of extant colonies, increasing inbreeding and reducing genetic diversity, which has led to local extinctions (Mariano et al., 2008; Campiolo et al., 2015), a genetically fragmented distribution (Mariano et al., 2008; Resende et al., 2010; Simon et al., 2016), and endangered (EN) species status on the Brazilian Red List (Ministério do Meio Ambiente, 2014; Instituto Chico Mendes de Conservação da Biodiversidade & Ministério do Meio Ambiente, 2018). Thereby *D. lucida* conservation is intrinsically linked to the preservation and recovery of the Atlantic Forest and the connection between its forest remnants.

How microclimate affects the ecology of *D. lucida* remains poorly understood. For instance, *D. lucida* responds to regional temperature and rainfall pattern (Simon et al., 2020); populations settle mainly in areas with higher annual mean temperatures, lower annual temperature range and less precipitation during the driest month (Simon et al., 2020).

Microclimatic variables such as temperature, rainfall, and humidity are known to influence the realized niche of insects, and can do so by influencing behavior and foraging strategy (Willmer, 1982; Colinet et al., 2015; Pincebourde & Suppo, 2016; Simon et al., 2020; Welch et al., 2020). *Dinoponera lucida* increase foraging activity in mild temperature associated with high elevations (Peixoto et al., 2010). The pattern of foraging activity of *D. lucida* has an optimal temperature range in areas surrounding the nest (Peixoto et al., 2010). Inside the forest, microclimatic variables are influenced by canopy cover, edge effects, evapotranspiration and other factors related to vegetation and habitat heterogeneity (Magnago et al., 2015; Stangler et al., 2015; Boehnke et al., 2017). Thus, an appropriate approach to assess the foraging activity of *D. lucida* should consider microclimate conditions. *Dinoponera lucida* commonly prey upon epigeic ectotherm taxa, and these prey respond to temperature, which alters its density and availability (May,

1979; Colinet et al., 2015; Pincebourde & Suppo, 2016; Welch et al., 2020). We expect that *D. lucida* will adapt foraging time to maintain an optimal strategy (Norberg, 1977; Bernstein, 1979; Azevedo et al., 2014; Medeiros et al., 2014).

Herein, we characterized the foraging activity and the response to litter surface temperature by *D. lucida*. We expected that daily variation in air and litter surface temperatures to influence the foraging activity of *D. lucida*. Also, we expected more workers to forage during the optimal temperature range, due to physiological constraints and prey availability.

Materials and Methods

Study site

We carried out this study in the Vale Natural Reserve (VNR; 22,711 ha; 19° 09' 05" S, 40° 04' 15" W), Linhares, northern Espírito Santo state, south-eastern Brazil. VNR has flat relief and altitude between 28 to 65 m (Peixoto et al., 1995). VNR is an important remnant of the Tabuleiro Forest, which is a specific formation of the Atlantic Forest (Kierulff et al., 2014). VNR region has tropical and humid climate with two dry months (Alvares et al., 2014). The annual mean temperature is 24.3 °C and the annual mean rainfall is 1,214 mm (Kierulff et al., 2014).

Sampling

We conducted active visual survey in a 30 m × 30 m plot to locate *D. lucida* workers (19° 09' 14.5" S, 40° 04' 14.0" W) from September 29 to October 2, 2017. We used sardines as bait along the worker's route (Silvestre et al., 2015). We located three nests by following workers carrying the bait back to the nests.

We estimated height, width of the nest openings and canopy coverage over the nest openings with the aid of photos analyzed at ImageJ 1.52p software (Schindelin et al., 2012; Schneider et al., 2012). We neither disturbed the workers nor excavated the nests.

In the center of the sampling area, we measured air temperature (T_A) and relative humidity (RH) at 1.5 m high using a Kestrel portable weather device (model 3000); and litter surface temperature (T_S) using a Tekpower digital infrared thermometer (model DT-8380). T_A , RH and T_S were recorded every 30 min from 6 h to 18 h, which is the expected foraging period of *D. lucida* (Peixoto et al., 2010). It rained from 6 h to 9 h on the third day of sampling. Flow of workers ceased during the rain. The data affected by rain were not considered for the quantitative analyzes.

We observed foraging workers exiting the nests and searching for food in the surrounding litter. We recorded inflow and outflow of workers for 15 min in each nest per hour (Peixoto et al., 2010). We considered inflow (F_{IN}) as the number of workers entering the nest and outflow (F_{OUT}) as the number of workers exiting nests to forage. We considered

total flow (F_T) in the nest openings as the sum of flows of workers. Total flow is colinear with F_{IN} and F_{OUT} . Using the 15 min measured data, we estimated F_T per hour in each nest.

We used focal-animal sampling (Altmann, 1974) and followed the workers individually during foraging activities from the time workers exited until they returned to the nest. We remained at least 2 m away from the observed worker to avoid interference of behavior.

We recorded duration of foraging trip (t_f) as the time spent searching for food items from their exit to their return to the nests. We used t_f as a proxy to estimate foraging efficiency ($\eta \sim t_f^{-1}$). We considered a returning worker those that were observed collecting a food item (successful trip) or those that started moving toward the nest even without food item (unsuccessful trip). The efficiency rate of foraging was calculated as number of workers returning to the nest with food divided by total number of workers returning to the nest (Giannotti & Machado, 1991; Medeiros et al., 2014). We defined reached distance (D_r) as the maximum distance reached by a worker during a foraging trip, measured as a straight line from the nest opening to the returning point. We identified collected food items visually or from zoomed photos to the lowest possible taxonomic level.

Data analysis

First, we perform Pearson correlation analyzes between environment variables (T_S , T_A , and RH), $t_f - T_S$, and $t_f - D_r$. Because T_A is positively correlated with T_S , we used T_S for description of the behavioral patterns studied, since T_S represents the microclimate variable related to the microhabitat of *D. lucida* workers. We established the curves with the variation of the foraging activity (F_T) as function of T_S and time of day. A fourth-order polynomial fit was used in the nonlinear regression model to describe the bimodal pattern between F_T and time of day. We tested if there was a relationship between F_T and T_S applying a Pearson's Chi-squared test (χ^2) from a six-categories of T_S (from 19 to 31 °C, with regular intervals of 2 °C, as showed in Fig 2b) defining a contingency table. The relative frequencies of F_T (R_f) were calculated for each hour of the day and each T_S category as a proportion of F_T in each hour sampled or T_S range category divided by the total F_T of all hours or all T_S categories, as described by equation 1:

$$R_f(i) = F_T(i) / \sum_{i=1}^n F_T(i)$$

To calculate the relative frequencies of F_T , we calculated the means of F_T of all nests to represent the foraging activity in the sampling area. We applied linear regression analysis to describe the relationship between t_f and T_S . We used Student's t test to assess differences for each T_S category between successful and unsuccessful trips. We used Graphpad Prism 7.00 (GraphPad Software, 2017) to perform statistical analyses. A p-value ≤ 0.05 was considered significant. We presented the variables in terms of mean \pm standard error of the mean (SE).

Results

Characteristics of the sampling area and nest openings

The three monitored nests were beneath understory vegetation roots in a forested area (900 m²) with ground totally covered by leaf litter. The nest density was 33 nests/ha. The mean distance between nests was 11.3 ± 1.4 m, showing a triangular shaping on the ground (nest 1 to 2: 8.5 m, nest 1 to 3: 12.5 m and nest 2 to 3: 13.0 m). Mean canopy cover on the nest's openings was 79 ± 4 % (nest 1: 74%, nest 2: 86% and nest 3: 78%), which characterizes the sampling area as a mosaic of light and shade. The nests had an elliptical entrance with mean height of 20.4 ± 1.0 mm (nest 1: 18.5 mm, nest 2: 21.5 mm and nest 3: 21.3 mm) and mean width of 41.1 ± 1 mm (nest 1: 43.1 mm, nest 2: 39.7 mm and nest 3: 40.5 mm).

Environment variables

The T_A during the foraging activity was 27.2 ± 0.5 °C and T_S was 24.5 ± 0.6 °C (Table 1). T_A and T_S were positively correlated ($r = 0.89$, $p < 0.01$, $n = 26$). Highest temperatures were recorded in the middle of the day (Fig 1). The RH during the foraging activity was 82.6 ± 2.1 %, with lower RH in the same hours of higher temperatures (Fig 1). T_A and RH were negatively correlated ($r = -0.80$, $p < 0.01$, $n = 26$). T_S and RH were also negatively correlated ($r = -0.81$, $p < 0.01$, $n = 26$).

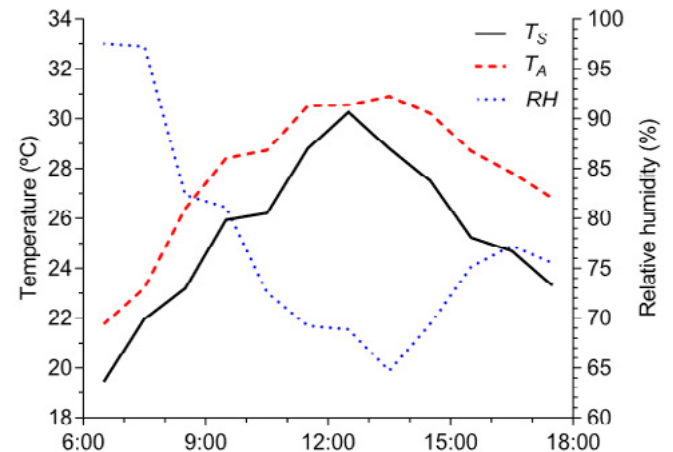


Fig 1. Mean air temperature (T_A , left y axis, red dotted line), litter surface temperature (T_S , left y axis, black solid line), and relative humidity (RH, right y axis, blue dotted line) at each hour of observation. Data sampled at Vale Natural Reserve, Linhares, state of Espírito Santo, Brazil.

Nest flow, foraging activity time, distance, and influence of temperature

Dinoponera lucida foraging activities were done between 7 h and 17 h. *Dinoponera lucida* exhibited a bimodal pattern of foraging activity ($r^2 = 0.26$, $p < 0.01$, $AICc = 209.6$, $df = 58$) (Fig 2a). The first F_T peak was between 8 h and 10 h. The second F_T peak was recorded between 14 h and 17 h.

Flow of workers at nest openings was higher (74%) between 21.0 and 27.0 °C ($\chi^2 = 22.41$, $df = 5$, $p < 0.01$) (Fig 2b), and lower (26%) between 27.0 and 31.0 °C. We did not observe foraging activity under rainfall, even when T_S reached the values related to the highest F_T values. The mean F_T at nest openings was $3.8 \pm 0.6 \text{ h}^{-1}$ (Table 1). The mean D_F of foraging workers was $3.8 \pm 0.4 \text{ m}$. Some workers from nest 2 travelled 10.1 m away from the nest entrance, which was the maximum D_F observed. The mean t_f in foraging activity was $14.2 \pm 2.2 \text{ min}$. The t_f were independent of D_F ($r = 0.18$, $p = 0.15$, $n = 24$). The values of t_f were positively correlated to T_S values ($r = 0.76$, $p < 0.01$, $n = 24$), with linear regression model ($r^2 = 0.57$, $F_{1,22} = 29.60$, $p < 0.01$, $t_f = 3.614T_S - 75.227$) (Fig 3).

Table 1. Descriptive variables of the foraging activity of *Dinoponera lucida* and environmental conditions at Vale Natural Reserve, Linhares, state of Espírito Santo, Brazil. The values are presented for each sampling nest and values marked with T indicate a summary of all observations of each variable in the sampling area. SE: standard error of the mean, n: number of observations, D_F : distance reached during foraging activity, t_f : time spent in foraging trip, F_T , F_{IN} and F_{OUT} : total flow, inflow and outflow of workers in the nest openings, T_S : litter surface temperature, T_A : air temperature, and RH: relative humidity.

Variable	Nest	Minimum	Maximum	Mean	SE	N
D_F (m)	1	1.0	4.0	2.6	0.4	10
	2	1.0	10.1	4.5	0.6	19
	3	2.0	5.5	3.5	0.4	8
	T	1.0	10.1	3.8	0.4	37
t_f (min)	1	2.0	22.0	9.8	3.7	6
	2	2.0	20.0	11.8	1.7	12
	3	5.0	45.0	23.3	6.1	6
	T	2.0	45.0	14.2	2.2	24
F_T (h^{-1})	1	0.0	20.0	2.8	1.0	26
	2	0.0	28.0	5.7	1.0	33
	3	0.0	16.0	2.2	0.9	24
	T	0.0	28.0	3.8	0.6	83
F_{IN} (h^{-1})	1	0.0	8.0	1.7	0.5	26
	2	0.0	16.0	2.7	0.6	33
	3	0.0	12.0	1.0	0.6	24
	T	0.0	16.0	1.9	0.3	83
F_{OUT} (h^{-1})	1	0.0	12.0	1.1	0.5	26
	2	0.0	12.0	3.0	0.6	33
	3	0.0	8.0	1.2	0.5	24
	T	0.0	12.0	1.9	0.3	83
T_S (°C)	-	19.5	30.3	24.5	0.6	26
T_A (°C)	-	21.8	30.9	27.2	0.5	26
RH (%)	-	64.7	97.5	82.6	2.1	26

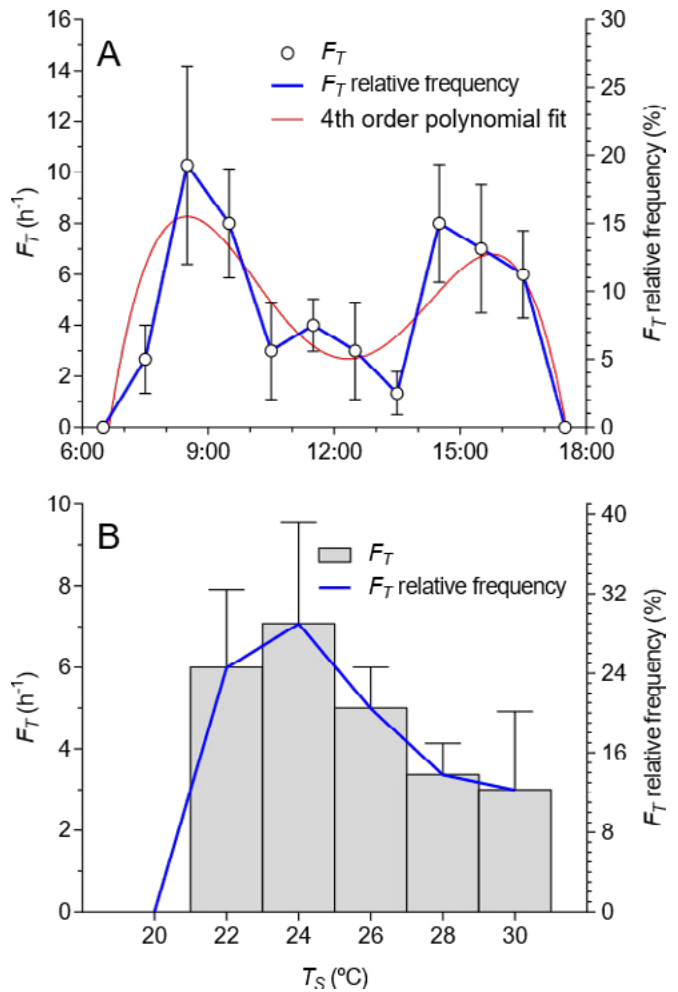


Fig 2. Flow of workers at openings of *Dinoponera lucida* nests. (a) Total flow of workers (F_T , left y axis, black circles), fourth-order polynomial fit used in the nonlinear regression model of F_T as a function of the time of day (left y axis, red solid line), and relative frequency of F_T at different time of day (right y axis, blue solid line). (b) Total flow of workers (F_T , left y axis, grey bars), and relative frequency of F_T (right y axis, blue solid line) at each litter surface temperature category. Data sampled at Vale Natural Reserve, Linhares, state of Espírito Santo, Brazil. Error bars represent standard errors.

We recorded 17 successful trips ($T_S = 24.6 \pm 0.4 \text{ }^\circ\text{C}$) and seven unsuccessful trips ($T_S = 26.8 \pm 0.8 \text{ }^\circ\text{C}$). The T_S was lower during successful trips ($t = 2.62$, $p = 0.01$). We recorded 37 returns to the nests (29 with food) resulting in an efficiency rate of foraging of 0.78 ± 0.06 (nest 1: 0.70, nest 2: 0.78, nest 3: 0.89).

Collected food items

We recorded 48 food items collected by *D. lucida* workers, of which, 94% were animals and 6% vegetation items (Table 2). All food items were solid. We observed workers capturing macroinvertebrates with high mobility (such as spiders, grasshoppers, 78%), low mobility (insect larvae and gastropods, 13%), and no mobility (insect pupae, 9%). These percentages about mobility of macroinvertebrates consider only identified animal food items.

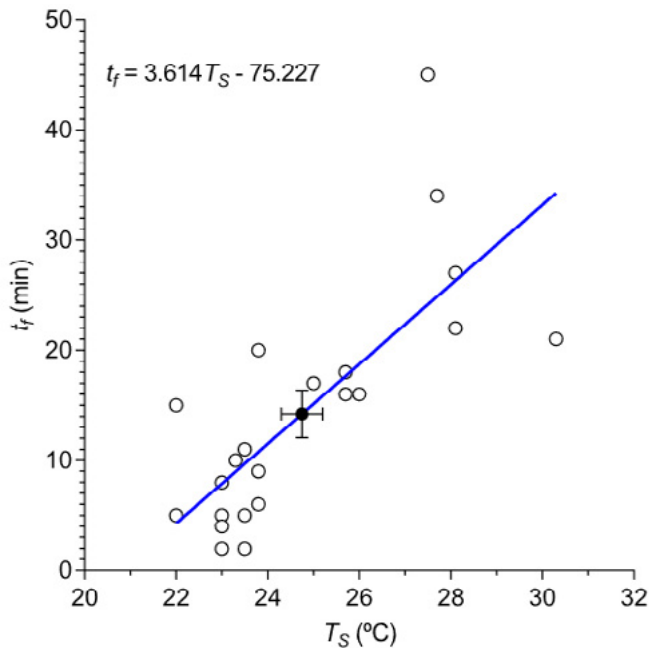


Fig 3. Scatterplot and linear regression line (blue solid line) of the time spent in foraging trip (t_f) of *Dinoponera lucida* workers as a function of the litter surface temperature (T_s) at Vale Natural Reserve, Linhares, state of Espírito Santo, Brazil. The filled circle with the error bars represents the bivariate means and standard errors.

Discussion

Dinoponera lucida presented bimodal cycle on daily foraging activity with a higher peak in the morning. The foraging activity was higher in a range of litter surface temperature between 21.0 and 27.0 °C, and successful foraging trips were mostly during lower litter surface temperatures (24.6 ± 0.4 °C) in comparison to unsuccessful trips (26.8 ± 0.8 °C). Similar patterns were found for *D. lucida* and *Dinoponera quadriceps* Kempf, 1971, both showing bimodal foraging cycles and higher peak in the morning than in the afternoon (Peixoto et al., 2010; Medeiros et al., 2014). In contrast, *Dinoponera longipes* Emery, 1901 seems to be mainly nocturnal, but workers are also active during the day (Morgan, 1993). In addition, *Dinoponera gigantea* (Perty, 1833) also has a bimodal pattern of foraging activity, but with higher peaks at dawn and dusk (Fourcassié & Oliveira, 2002). Finally, *D. lucida* likely reduces foraging in response to temperature cues to minimize foraging activity during times of low prey availability (Norberg, 1977; Bernstein, 1979).

Dinoponera lucida prey mainly on macroinvertebrates which are also influenced by litter temperature (Bernstein, 1979; May, 1979; Willmer, 1982; Colinet et al., 2015; Pincebourde & Suppo, 2016; Welch et al., 2020). Several epigeic ectotherm taxa, which are potential preys for *D. lucida*, tend to migrate to deeper layers of litter to forage or for refuge (Willmer, 1982; Colinet et al., 2015; Pincebourde & Suppo, 2016). The foraging activity of *D. quadriceps* also is positively related to availability of potential prey (Medeiros et al., 2014).

Table 2. Food items collected by *Dinoponera lucida* workers in foraging activity at Vale Natural Reserve, Linhares, state of Espírito Santo, Brazil. N: number of records. Percentages presented in parentheses are relative to the total of items.

Kingdom	Taxon	Item	N (%)
	Arachnida: Araneae	spider	5 (10.4)
	Arachnida: Scorpiones	scorpion	1 (2.1)
	Blattodea	cockroach	1 (2.1)
	Coleoptera	beetle	1 (2.1)
	Hemiptera: Pentatomidae	shield bug	1 (2.1)
	Hymenoptera: Apoidea	bee	1 (2.1)
Animalia	Insecta	insect larva, likely Lepidoptera	2 (4.2)
	Insecta	insect pupa	2 (4.2)
	Blattodea: Isoptera	termite	4 (8.3)
	Mollusca: Gastropoda	gastropod	1 (2.1)
	Orthoptera: Caelifera	grasshopper	4 (8.3)
	Squamata: Serpentes	snake scale	1 (2.1)
	Vertebrata	fecal pellet	1 (2.1)
	Unidentified	macroinvertebrate	20 (41.7)
	<i>Swartzia myrtifolia</i> var. <i>elegans</i> (Schott) R.S.Cowan	seed	1 (2.1)
Plantae	<i>Cordia magnoliifolia</i> Cham.	fruit	1 (2.1)
	Angiospermae	tree bark	1 (2.1)

Our data suggest that *D. lucida* limits foraging according to the activity pattern of prey, suggesting an optimization strategy driven by prey availability (Emlen, 1966; MacArthur & Pianka, 1966; Norberg, 1977; Perry & Pianka, 1997), with litter temperature serving as a proxy for successful foraging likelihood rather than being a direct influence on *D. lucida* foraging behavior.

Foraging attempts had no relationship with time spent or distance reached, suggesting that the foraging success depends on choosing the appropriate time. It seems that these ants optimize their foraging behavior by relying on the chances to find a food resource instead of covering large areas or traveled distance during the foraging trip. Our data on patterns of flow of workers of *D. lucida* in foraging was similar to other populations (Peixoto et al., 2010). The increase of time spent in foraging trip could be related to search and capture efficiency, supporting the hypothesis of optimal food searching (Emlen, 1966; MacArthur & Pianka, 1966; Norberg, 1977; Perry & Pianka, 1997). The positive correlation between time spent in foraging trip and litter surface temperature suggests the existence of an optimal

temperature range for the foraging activity. However, it is not clear that the workers use temperature as a proxy. It seems that temperature is an effective proxy for prey availability. In addition, as temperature is highly correlated with time of day, it may be that they simply use time of day as a proxy for prey availability. It also seems possibly that foraging activity is directly related to prey availability, with ants foraging more when preys are abundant and less as prey availability decreases. As *D. lucida* is an eusocial species, some decisions about the time to forage could be related to communication between the nestmates (Leonhardt et al., 2016). Further studies could assess these questions assertively with prey density data combined with the other sampled data.

According to our data *D. lucida* was predominantly carnivorous and might be categorized as a hunting and collecting species (Almeida & Queiroz, 2015). We did not observe predation of other ant species, even when they were abundant near a worker in the foraging activity. Similarly, ants were not in the diet of *D. quadriceps* (Araújo & Rodrigues, 2006). Ants, however, have been observed in low frequency in the diet of other species of *Dinoponera* (Fourcassié & Oliveira, 2002; Peixoto et al., 2010). Considering the number of prey items, ants comprise 2% of *D. lucida* diet (Peixoto et al., 2010) and 4% of *D. gigantea* diet (Fourcassié & Oliveira, 2002). The capture of animals with high mobility (78% of the total macroinvertebrate items) indicates that *D. lucida* performs active hunting besides collection of food items. This performance was also observed in other species of *Dinoponera*, including capture of relative larger prey such as small lizards (Sousa & Freire, 2010; Ribeiro et al., 2011; Carvalho et al., 2012). *Dinoponera lucida* seems to have a more diverse diet than we recorded, which may be related to our short sampling period. Specifically, we identified a relatively low frequency of plant items (6%) when compared to 16% from other population of *D. lucida* (Peixoto et al., 2010), 22% from *D. gigantea* (Fourcassié & Oliveira, 2002) and 30% from *D. quadriceps* (Araújo & Rodrigues, 2006). Workers of *D. quadriceps* (Araújo & Rodrigues, 2006) and *D. gigantea* (Fourcassié & Oliveira, 2002) collect mainly animal food items, mostly arthropods, as we observed for *D. lucida*. It is possible that the diet of *D. lucida* and others *Dinoponera* vary seasonally according to the availability of food resources in their territories. Therefore, additional studies on the diet composition of *D. lucida* may be useful to better describe its ecological role in the Atlantic Forest.

Dinoponera lucida and congeners use underground nests in closed-canopy forest (Paiva & Brandão, 1995; Peixoto et al., 2010). *Dinoponera* as well as the other Ponerinae ants avoid foraging with high insolation (Willmer & Corbet, 1981; Willmer, 1982). It is likely underground and closed-canopy nests prevent water loss (Chown et al., 2011) and regulate nests temperatures (Willmer, 1982; Jones & Oldroyd, 2006).

Our results were only focused on three nests. We recommend further study to assess populations level responses to microclimatic factors across the species range. The density

recorded herein, however, was similar to the reported by Peixoto et al. (2010), but far from describing a continuous and homogeneous distribution of *D. lucida* nests in the forest. Nests of *D. lucida* occur in an aggregate distribution (Peixoto et al., 2010), a consequence of its reproduction mode by colony fission (Mariano et al., 2008; Campiolo et al., 2015). During the active search for nests, we found vast areas within the Atlantic Forest in VNR without the presence of *D. lucida* workers. This is aligned to the endangered conservation status of the species by Brazilian Red List (Ministério do Meio Ambiente, 2014; Instituto Chico Mendes de Conservação da Biodiversidade & Ministério do Meio Ambiente, 2018), which does not seem to be particularly abundant, even where adequate conditions and resources exist.

Our data support the hypothesis of optimal foraging regulated by habitat temperature. It would be a direct response by prey species and an indirect response by *D. lucida* as they may respond more directly to prey availability. Time spent in foraging trip and litter temperature were positively correlated. Flow of workers was higher in an optimal litter surface temperature range, with more successful foraging trips and more food items (mainly macroinvertebrates) collected in the same temperature range. The better understanding about *D. lucida* activity patterns can assist in the planning of study activities, such as monitoring and inventory of this endangered and endemic species.

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Author Contributions

FC: conceptualization, methodology, investigation, formal analysis and writing

CZ: conceptualization, methodology, investigation and writing

RBF: conceptualization, methodology and writing

ACSA: conceptualization, methodology and writing

TGS: formal analysis and writing

CW: formal analysis and writing

Declarations

Conflict of interest

The authors declare that they have no conflict of interest to disclose.

Compliance and ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed.

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