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RESEARCH ARTICLE

Working in the rain? Why leaf-cutting ants stop foraging when it's raining

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Abstract

Understanding how environmental factors modulate foraging is key to recognizing the adaptive value of animal behavior, especially in ectothermic organisms such as ants. We experimentally analyzed the effect of rain on the foraging of leaf-cutting ants, a key ant group that is commonly found in rainy habitats. Specifically, we experimentally discriminate among direct and indirect effects of rain on laden ants and explore whether ants respond to rain predictors by incrementing their speed. Watered loads were frequently dropped although ants were not wet, and watered ants also dropped their loads although loads were not wet. Watered leaf fragments increased their weight by 143% and were dropped independently with regards to area or symmetry. Watering the trail did not affect the proportion of ants that dropped their loads. Ants increased their speed by 30% after experimental increments in relative humidity and the noise of raindrops on leaves near the trail. Our experimental results confirm earlier anecdotal evidence of the negative effect of rainfall on the foraging of leaf-cutting ants. We demonstrate that rain can strongly limit ant foraging through different mechanisms, affecting both the ant itself, and the maneuverability of laden ants, by increasing the weight of their loads. We also depict behavioral responses that may mitigate this negative effect on foraging: walking faster at signals of rainfall to reduce the portion of leaf fragments lost. Our results illustrate how environmental factors can directly and indirectly constrain ant foraging and highlight the relevance of behavioral responses to mitigate these effects.

Keywords *Atta cephalotes* · Ant behavior · Costa Rica · Foraging · Environmental restrictions

Introduction

Understanding how environmental factors modulate foraging is vital to recognizing the adaptive value of animal behavior. This is particularly relevant in ectothermic animals such as ants because their activity directly depends on climate (Hölldobler and Wilson 2011; Chown and Nicolson 2004). However, not all climatic variables that potentially restrict ant foraging have received similar consideration in research studies. For example, there is a lot of evidence of how temperatures affect ant foraging and how ants show physiological and behavioral adaptations to foraging at extreme thermal conditions (Whitford and Ettershank 1975; Lighton et al. 1987; Kaspari et al. 2015; Bujan et al. 2016; Esch et al. 2017; Spicer et al. 2017). There are fewer works that study the effect of wind on ant foraging and the adaptive ant behaviors that allow foraging under high windy conditions (Porter and Tschinkel 1987; Wolf and Wehner 2005; Alma et al. 2016). But the influence of rain on ant foraging, despite

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its relevance and potential negative effect, has been less studied and described only anecdotally. Here we experimentally analyze the effect of rain on the foraging of a key ant group: leaf-cutting ants.

Leaf-cutting ants (hereafter LCA) are ideal organisms for studying the behavior of ants under rainy conditions for several reasons. First, ant foragers are abundant, easy to find in nature and their manipulation is feasible in field experiments. Second, several LCA species inhabit rainy habitats (Hölldobler and Wilson 2011; Farji-Brener et al. 2016) and thus they often need to deal with rain. Third, rainfall may affect LCA directly and/or indirectly, allowing for the possibility to test several non-exclusive mechanisms of how rain affects ant foraging. Workers cut and collect plant fragments to use them as substrate to cultivate a mutualistic fungus, the source of food for the larvae (Hòlldobler and Wilson 2011). Typically, workers carry plant fragments that are several times larger than their bodies along cleared trails. Therefore, rain may: (a) disturb the ant itself, (b) increase the weight of carried loads affecting ant movement and stability (Röschard and Roces 2002; Moll et al. 2010; 2013) and/or may dilute the pheromone signals and muddy the trail hindering the walking of laden ants (Riley et al. 1974; Jaffe and Howse 1979). Finally, anecdotic evidence suggests that rain negatively affects LCA activity. For example, Hodgson (1955, p. 299) states that "[During heavy rain] the laden workers drop their leaves and run until they reach a position where the rain no longer strikes them. It is common to find them by the hundreds on the sheltered side of a tree buttress or root along the foraging trail". The key effect of rain, therefore, is the loss of an appreciable fraction of the day's foraging time (Weber 1972; Hart et al. 2002, AGFB personal observation). In sum, LCA are an ideal group to evaluate the effect of rain on ant foraging.

We hypothesized several non-excluding causes of why LCA stop foraging and drop their loads during rainfall. Specifically, we proposed that rain can: (a) increase the weight of carried leaves, hindering the walking of laden ants, (b) disturb the ant itself, (c) muddy the ant trail making it difficult to transit by a laden ant. Additionally, we determined whether certain leaf characteristics increase the probability of it being dropped. We predicted that larger and/or asymmetric loads will be dropped more frequently than smaller and symmetric loads because of the potentially negative effect on ant stability and movement (Röschard and Roces 2002; Moll et al. 2010, 2013). Finally, we experimentally tested whether some rain predictors such as increments in relative humidity and the existence of raindrop noise increased the speed of laden ants. Since an appreciable amount of food is lost because of rain, it would be expected that laden ants increase their speed to arrive as soon as possible to their nest under environmental features that predict rainfall.

Methodology

Study site and species

Fieldwork was conducted during the dry season of 2017 (January–February) at La Selva Biological Station, a tropical wet forest reserve in the Caribbean lowlands of Costa Rica (10°N, 83°W). La Selva is a field station operated by the Organization for Tropical Studies (OTS) and has 4000 mm of rain annually. A complete description of this site is available in McDade et al. (1994). All sampling was performed using adult nests of *Atta cephalotes*, one of the most common LCA species in Central America (Hölldobler and Wilson 2011), on non-raining days. This species inhabits wet forests and builds conspicuous, long-lasting trail networks that are free of debris (Farji-Brener et al. 2015). Along these trails, workers cut and transport plant fragments of different sizes (Farji-Brener et al. 2011) which are often dropped when it rains (Hodgson 1955; Weber 1972; Hart et al. 2002, AGFB personal observation).

Methodology

Direct and indirect effects of rain on laden ants

To discriminate the effect of rain on the ant load, the ant itself and on the ant trail we performed the following three experiments. First, with a dropper, we carefully added 2 ml of water on the carried load of a randomly selected laden ant without wetting the ant. At the same time, we gently touched the carried load of a randomly selected nearby laden ant with an empty dropper as a control for dropper disturbance. We followed both, treated and control ants for 20 s and noted whether the load was dropped or not. Ants that were accidentally wet in the manipulation process were not considered in the analysis. We did this experiment on a total of 120 ants (60 per treatment) from 3 adult ant nests (40 per nest). Second, we did the same protocol but wetting the body of a randomly selected laden ant without wetting the carried load. We also gently touched the body of a nearby, randomly selected laden ant with an empty dropper, as a control for dropper disturbance. We followed both treated and control ants for 20 s and annotated whether the load was dropped or not. We did this second experiment on a total of 120 ants (60 per treatment) from 3 adult ant nests (40 per nest). In both experiments we compared the proportion of ants that dropped their loads in the treatments versus controls using a Chi-Square test. Third, to evaluate whether LCA drop their leaves because the rain muddies the trail, in a flat portion of 30 cm length of a main trail we counted the proportion of ants that dropped their loads 30 s before and after we added 500 ml of water on the trail. The water was carefully added to the trail at ground level without wetting the ant's body. We did this experiment in 16 trail sectors from 16 ant nests. The proportion of ants that dropped their loads before and after the addition of water was compared using a paired *t* test.

Comparison between abandoned and not-abandoned leaf fragments

To evaluate whether certain load characteristics make them more plausible to be dropped with rain, we collected all the carried leaf fragments from the treatments of the first two experiments. Loads were categorized according to whether they were dropped out or not (see above). The area of the carried leaf fragments was estimated in the laboratory using an area meter (LI-COR® model 3100C; Li-Cor Biosciences, Lincoln, Nebraska). We also measured the width of each ant head to estimate the load-carrying capacity of each ant as carried load area/ head width (larger values suggested relative higher carrying capacity). Load symmetry (aspect ratio) was estimated calculating the major axis/minor axis (in mm) of the carried leaf fragments via photos using the software ImageJ 1.50i®. Loads with values around 1 were considered symmetrical and loads larger 1.3 were considered asymmetrical because this value divides the distribution into two roughly equal halves.

We analyzed whether certain loads contained a higher predisposition to be dropped according to their area, symmetry and ant load-carrying capacity using logistic regressions. Finally, to estimate the increment in weight of loads due to rain, we collected 60 dry leaf fragments of different sizes carried by the control ants (i.e., loads that were not moistened in our field experiments). In the lab we compared the weight of each collected load before and after the addition of 2 ml of water using a paired *t* test.

Testing predictors of rain events: relative humidity and raindrop noise

To test whether rainfall predictors such as increments of relative humidity and raindrop noise affected the speed of laden ants, we performed the following two experiments. First, we made a humidity chamber of transparent plastic. This rectangular chamber (approximately 50 × 30 × 20 cm; length, width and height, respectively), moistened with wet cottons, was located on a trunk trail 5 m away from the nest entrance. Preliminary measures showed that inside the chamber the relative humidity increased between around 13% depending on the external environmental humidity (higher increments at lower external humidity). The chamber covered the entire width of the trail and had a wide entrance and exit holes where the laden ants could enter and exit easily. We measured the ant speed (expressed in m/min) in trail sections 30 cm before the chamber, 30 cm inside the humidity chamber, and 30 cm coming out of the chamber (Fig. 1a). Each ant was considered its own

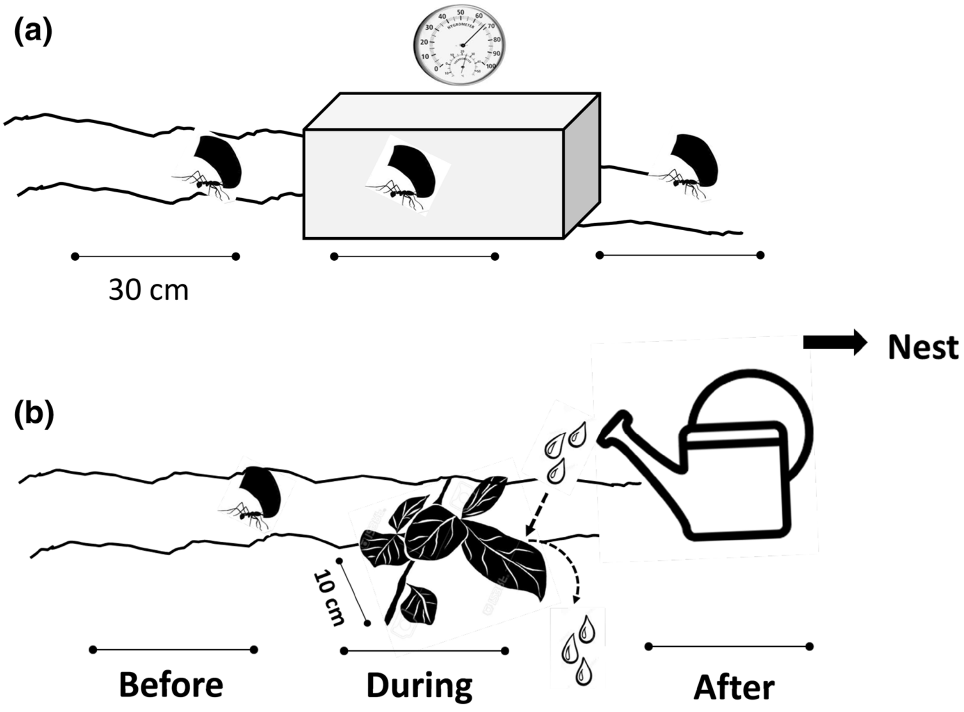

Fig. 1 Experimental design to test the effects of increments in relative humidity (above) and the noise of raindrops on a leaf surface (below) on the speed of leaf-cutting ants. Increments in relative humidity were generated by a field-humidity chamber located on the ant trail. Raindrops noise was generated by throwing water with a watering can to a buried *Calathea* sp. leaf located besides the trail (see text for details). We measured the speed of ants before, during and after the treatments. Each ant was considered as its own control

control. We choose this procedure instead of using a control box where the cottons were left without water because ant speed may vary with ant size and carried load. We measured 60 laden ants from 4 trails of 2 nests. In the second experiment, we located a big leaf (60 × 30 cm, length and width respectively) of *Calathea* sp. ~ 5 cm apart from a trunk trail side. The leaf was buried in the ground with its stem. LCA sensed vibrations only as substrate-borne signals, since LCA are unable to perceive airborne sound (Roces and Tautz 2001). Thus, we speculate that the vibrations of rain drops on the leaf surface were transmitted through the leaf stem and soil ground to the surface of the ant trail. We generated noise of raindrops throwing water with a watering can onto our experimental leaf. The leaf was oriented with its tip facing away from the trail so that drops never touched the ant trail nor the ants. We measured ant speed (expressed in m/min) in trail sections of 30-cm length before, "during" and after the location of the experimental leaf. The experimental leaf was located at the center of the 30-cm length "during" trail section and was watered only when the measured ant walked in that sector (Fig. 1b). Each ant was considered its own control. We measured a total of 20 laden ants from 3 nests. In both experiments, the data was analyzed with a Friedman test, a non-parametric alternative to the one-way ANOVA with repeated measures (or blocks). Treatments (before, during and after) were considered as fixed factors and each ant was considered a block (random).

Results

Direct and indirect effects of rain on laden ants

Wet loads were more frequently dropped than loads that were not moistened. While workers never dropped their leaf fragments that were touched by an empty dropper, experimentally wet leaf fragments were dropped in 67% of the cases ($X^2 = 60$, $P < 0.01$, Fig. 2a). Wet loads were heavier to carry. The addition of only 2 ml of water increased the load's weight by 143% (0.035 ± 0.04 versus 0.085 ± 0.03 g, mean ± SD, $t_p = 7.6$, $df = 58$, $P < 0.01$). This increment in weight not only delays laden ants; wet loads often fell and got stuck to the ground. After a few failed attempts to pick-up the fallen leaf fragment, workers abandoned their loads on the trail and returned unladed to the nest. Wet ants also dropped their loads more frequently than ants that were only touched by an empty dropper. While control ants never dropped their loads, ants that were experimentally wet (but not their loads) dropped their carried leaf fragments 54% of the time ($X^2 = 38$, $P < 0.01$, Fig. 2b).

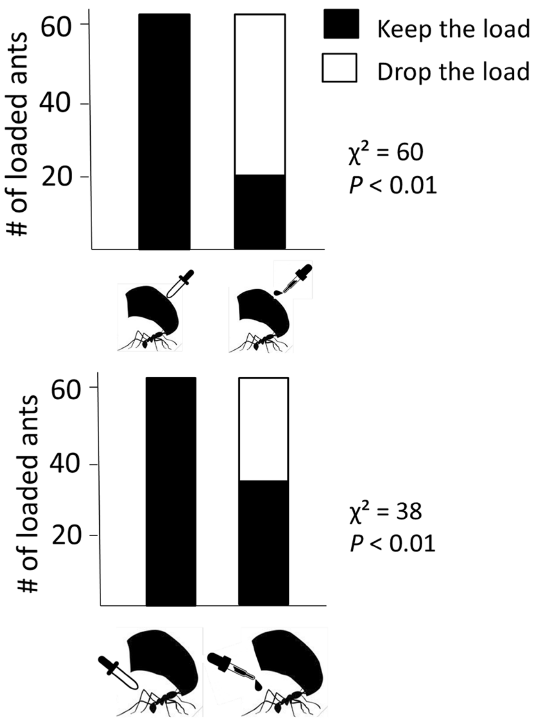

Fig. 2 Number of laden ants that keep or dropped their loads after adding 2 ml of water with a dropped to the load (but not to the ant, above), and to the ant (but not to the load, below) regarding a control (loads and ants that were kindly touched with an empty dropper, respectively). See text for more details

Comparison between abandoned and not-abandoned leaf fragments

The probability of dropping a leaf fragment was not related with load area, symmetry (aspect ratio) or the ant carrying capacity (logistic regressions, all $P > 0.23$). Finally, the proportion of ants that dropped their loads was very low and similar before and after the addition of water on the trail (0 ± 0 versus 0.02 ± 0.04, respectively, mean ± SE, $t_p = 1$, $df = 16$, $P = 0.33$).

Testing predictors of rain events: relative humidity and raindrop noise

The two rain predictors measured, relative humidity and the noise of raindrops on a leaf surface, increased the speed of laden ants. First, ants significantly accelerated their speed after experimental increments in relative humidity (Friedman Anova = 7.65, $df = 2$, $N = 60$, $P = 0.02$). The ant speed before and inside the chamber were similar (1.28 ± 0.07 and 1.29 ± 0.06, respectively, mean ± SE) but lower than their speed when coming out the humidity chamber (1.43 ± 0.06 m/min, Fig. 3) Second, ants significantly accelerated their speed after the trail section where we generated

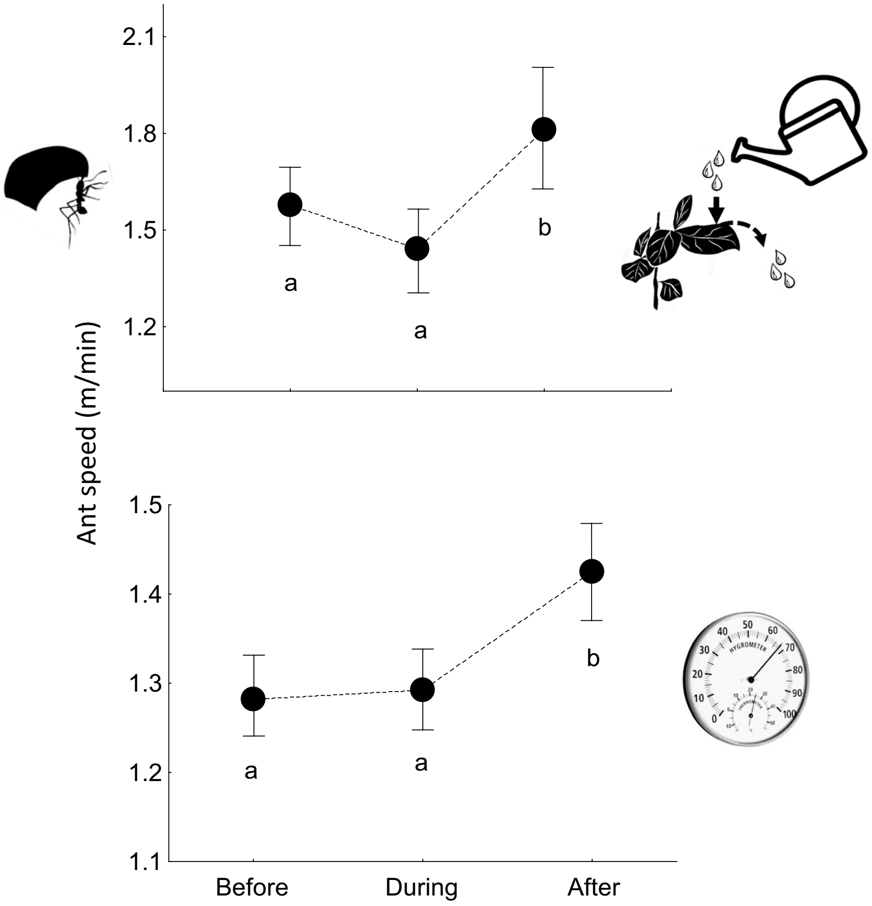

Fig. 3 Speed of ants (m/min) before, during and after treatments that predict the beginning of a rainfall, noise of raindrops on a leaf surface (above) and experimental increments on relative humidity (above). Methodological details are in Fig. 1. Different letters denoted statistical significant statistical differences ($P < 0.05$, Friedman anova an post hoc comparisons)

raindrop noise (Friedman Anova = 7.55, $df = 2$, $N = 20$, $P = 0.02$). Ant speed before and during the noise treatment were similar (1.58 ± 0.12 and 1.45 ± 0.12, respectively, mean ± SE), but lower than their speed after the treatment section (1.81 ± m/min, Fig. 3).

Discussion

The way organisms acquire food is of utmost importance in relation to reproductive success and population demography. Therefore, it is expected that animals show behaviors that reduce the impact of abiotic constraints on foraging (Krebs et al. 1993). Here, we experimentally confirm the anecdotic evidence of the negative impact of rainfall on LCA, depict some mechanisms through which rainfall may stimulate the dropping of leaf fragments, and illustrate certain adaptive behavior to reduce the impact of the rain.

Our experiments demonstrated that rain directly and indirectly disturbed laden ants. On one hand, watered ants frequently dropped their load even though the leaf fragments that they were carrying were dry. This suggests that raindrops may physically disturb the ant itself by their impact and/or by reducing their ability of location/communication. For example, a cuticle covered with water might hinder the reception and the emission of pheromones by exocrine glands (Hòlldobler and Wilson 2011), including trail pheromones (Riley et al. 1974; Jaffé and Howse 1979; Califano and Chaves-Campos 2011). On the other hand, wet loads were frequently dropped although ant bodies remained dry. This suggests that rain also negatively affect foraging indirectly, increasing load weight and disrupting the stability of laden ants. Only 2 ml of water increased loads weight in 143%, making them difficult to hold and carry. As discussed before, this increment in weight often generated the fall of the loads and their adhesion to the ground. It is known that LCA carry leaf fragments several times larger and heavier than their own bodies, which may increase the risk of falling over (Ròschard and Roces 2002; Moll et al. 2010, 2013). Our results indicate that the load's effect on maneuverability during transport is critical, suggesting that LCA often carry fragments that are near the limit of their maneuvering ability (Moll et al. 2010, 2013). This may also help to understand why LCA transport loads below their predicted optimum by the theory of central place foraging (Burd and Howard 2005). Moreover, considering the economics of transporting wet fragments, carrying the extra weight requires an increased expenditure of energy, but offers no additional energetic gain to the colony. Therefore, it is possibly that ants should abandon wet fragments at some point of wetness, even if they are capable to transporting them in terms of stability and maneuverability.

It has been proposed that transporting small leaf fragments may (a) increase information transfer and allow workers a higher recruitment rate (Bollazzi and Roces 2011), (b) increase walking speed along trails avoiding the bottlenecks generated by slow conspecifics carrying larger loads (Farji-Brener et al. 2011), (c) reduce the handling time on fungal gardens and facilitate their transfer among fungal chambers (Burd and Howard 2005), and (d) reduce the effect of wind delaying laden foragers (Alma et al. 2016). Here we demonstrate another reason why ants avoid carrying larger and heavier leaf fragments: water deeply affects their maneuverability during transport, increasing the cost of transport without additional benefits. Finally, the addition of water to the trail does not stimulate the drop of the carried leaf fragments. The amount of water used together with the fact that we performed the experiment in the dry season—when the soil absorbed water faster than during wet season—may help to explain this result. Despite of this, our results suggest that the indirect effect of rain increasing the weight of loads is relatively more important than the indirect effect of muddying the trail, at least at low rainfall levels and during the period of high an activity (dry season). Although rainfall in nature obviously affects ants, carried loads and the trail simultaneously, our manipulation approach allowed the discrimination of different mechanisms that can generate the same pattern: the dropping of carried leaf fragments. The experimental results suggest that rainfall destabilizes laden ants because it increases the weight of leaf fragments, physically disturbs the ant itself, and—at higher rainfall levels—muddies the ant trail, in this order of importance.

It has been proposed that temperature limits the geographical distribution of LCA (Farji-Brener and Ruggiero 1994). Extreme high and low temperatures affect ant physiology directly (Lighton and Feener 1989) and their fungi-culture capacity (Mueller et al. 2011; Branstetter et al. 2017). But extreme temperatures also indirectly limit ant distribution reducing vegetation richness and abundance. Rainfall may have contrasting effects on LCA. In one way, as discussed earlier and demonstrated here, rain generates the loss of a considerable portion of harvested material, decreasing the input of food into the nest and potentially reducing colony growth. Wet habitats also increase the risk of contamination of the ant fungus culture (Farji-Brener et al. 2016). But increments in rainfall levels, especially in tropical and subtropical regions, are often associated with an enhanced vegetation richness and abundance, the key food source of LCA. Given that several leaf-cutting ant species live in habitats with relatively high rainfall levels (Farji-Brener and Ruggiero 1994; Farji-Brener et al. 2016), the high plant richness and vegetation abundance typical of tropical and subtropical wet forests may offset the higher risk of fungal infection and the foraging restriction imposed by rain in rainy habitats. Here we describe a behavior that may help to maintain this positive balance: a speed increase with environmental signals that predict rain. LCA walked up to 30% faster after being exposed to two typical rain predictors: an increment in relative humidity and the noise of raindrops on the surface of leaves. These support previous studies confirming that LCA are able to sense differences in relative humidity (Roces and Kleineidam 2000). LCA thus might detect small environmental changes that predict rain and respond to them in adaptive terms, incrementing their speed and thus reducing the portion of leaf fragments that could have been lost. Behavioral responses like this may help LCA colonize wet habitats despite the negative effects of rain. In sum, we demonstrated that rain can strongly limit LCA foraging through different mechanisms, and depicted behavioral responses that may mitigate this negative effect on foraging. Our results illustrate how environmental factors can directly and indirectly constrain ant foraging and highlight the relevance of behavioral responses to mitigate these effects.

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