



Warmer mid-day temperatures increase leaf intake by increasing forager speed and success in *Atta colombica* during the rainy season

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Abstract

Predicting the effects of climatic warming on social insects remains an important challenge. While warming is known to speed many rate processes, the acute effects of temperature on performance under field conditions remain poorly studied. The effects of temperature are usually nonlinear, and tropical animals have been predicted to be particularly likely to be negatively affected by global warming as they may have optimal temperatures that are close to current ambient temperatures. We observed three different *A. colombica* colonies three times per day (two times during daylight hours and one time at night) during June 2018 in Gamboa, Panama, measuring air temperature, ant traffic, intake of leaves per second, and ant walking speeds. We found that ant walking speed and intake of leaves increased at higher temperatures. Leaves carried per ant also increased with temperature, suggesting that warmer temperatures improve leaf-handling rates, at least over the thermal range studied here. However, there was also an independent effect of time of day, with higher foraging in the morning than the evening, despite similar air temperatures. Consistent with the positive effect of temperature on foraging rates, critical thermal maxima were well above ground temperatures. At least during the rainy season, our data suggest that moderate warming could enhance foraging success and herbivory of leafcutting ants in semi-deciduous moist forests throughout much of the day.

Keywords Running speed · Thermal tolerance · Leafcutter · Climate · Neotropics · Foraging

Introduction

Temperature varies dramatically with time of day, season, and is warming systematically in many parts of the world. Predicting the effects of climatic warming requires a detailed understanding of the relationships between temperature and biological processes, which can be complex (Diamond and Yilmaz 2018). Like all ectotherms, ant foraging is strongly and nonlinearly affected by temperature, with positive effects and then negative effects as temperature rises (Angilletta 2009; Huey and Stevenson 1979). Here we investigate the effect of hourly variation in air temperature on the foraging

success of the leafcutting ant, *Atta colombica*, in Gamboa, Panama.

In general, ectotherms exhibit thermal performance curves, with peak performance in an optimal temperature range (Angilletta 2009; Diamond and Yilmaz 2018; Huey and Stevenson 1979). How ectotherms respond to varying temperature on a daily, seasonal, and multi-year basis will depend on the position of the performance curve relative to absolute temperatures, and the plasticity of the performance curve (Huey et al. 2012). Organisms that are thermal specialists (narrower thermal performance curve) or with less ability to acclimate (a shift the thermal performance curve) will likely be affected more strongly by variation in temperature (Baudier et al. 2018; Deutsch et al. 2008; Huey et al. 2012). Insects at lower latitudes have been found to have narrower tolerance ranges than those at higher latitudes, leading to the suggestion that low-latitude, rain-forest insects may be particularly susceptible to climate change (Addo-Bediako et al. 2000; Deutsch et al. 2008). However, most thermal performance curves are measured in the lab, and there has been limited work linking temperature to metrics of insect

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performance in the field, in the context of realistic natural time scales on the colony level.

Temperature is known to be one of the most important factors influencing ant foraging and colony performance. Within a survivable temperature range, higher temperatures generally increase metabolic rates, walking speeds, and load sizes, and decrease developmental times for many ant species (Andrew et al. 2013; Bernstein 1979; Fowler and Robinson 1979; Gomides et al. 1997; Hurlbert et al. 2008; Jayatilaka et al. 2011; Penick et al. 2017; Rissing 1982). Clear thermal performance curves with positive and negative effects on foraging activity and success or colony growth and survival have been demonstrated for a few ant species (Andrew et al. 2013; Diamond et al. 2013; Hölldobler and Wilson 1990; Porter and Tschinkel 1987). Thus, the short-term effect of temperature on foraging success is expected to vary with season, at least in temperate regions, with positive effects in cooler seasons and negative effects in warmer seasons. Many ants, including leafcutters, shift their foraging times with season (Caldato et al. 2016; Fowler and Robinson 1979; Gamboa 1976; Hölldobler and Wilson 1990; Porter and Tschinkel 1987), likely to match their physiological optima to available temperature. While shifts in the timing of foraging can reduce thermal effects on foraging success across seasons, temperature changes during the day or associated with climatic variation still seems likely to influence ant foraging in either a positive or negative way, depending on how relationship between ambient and optimal temperatures for that ant species.

Ant species differ substantially in their responses to thermal variation, and this variation can be correlated with foraging habitat and interspecific interactions. Tropical ant species differ strongly in the maximal and minimal temperatures for activity, with at least some of this variation being related to foraging habitat in canopy vs. in shaded understory (Kaspari et al. 2015). Cerda et al. (1998) found that the activity and foraging intake of eleven Mediterranean ant colonies varied with air temperature, with some species exhibiting positive relationships between foraging success and temperature, others a negative relationship, and some demonstrating a parabolic relationship. These varied relationships between temperature and foraging success were partly related to tendency to forage in the day vs. nighttime, with dominant species being more likely to forage under cooler or nocturnal conditions, and exhibiting negative relationships between temperature and foraging intake (Cerdá et al. 1998). Similarly, two species of Dolichoderine ants studied at a single location in Chile that compete for resources exhibited opposite foraging responses to temperature (Hunt 1974).

Leafcutter ants are very important foragers in the Neotropics (Hölldobler and Wilson 2011). In comparisons made across several months of the tropical leafcutter ant species,

Atta cephalotes, studied in the Trinidad during a portion of the season in which foraging was primarily nocturnal, foraging intake was positively correlated with temperature and light intensity (Lewis et al. 1974). However, it is not clear whether correlations between temperature and foraging rates and intake across months are caused by direct effects of temperature or indirect effects on plant growth or phenology. Prior studies in tropical regions have attributed within and across-day variation in foraging of leafcutters (*A. colombica*, *A. cephalotes*) primarily to variation in plant quality or the type of plant part harvested (Burd 1996; De Vasconcelos 1990; Rockwood 1976). Wirth et al. (1997) noted the importance of semi-deciduous forest rainfall events in determining within and across-day variation in foraging for *A. colombica*, with foraging being greatly reduced by rainfall events, as well as effects of competition with carpenter ants. Thus, it is as yet unclear whether variation in air temperature within or across days has positive, negative, or no effect on the foraging success of tropical leafcutter ants. While it is known that warmer temperatures increase ant walking speed within the range of normal ground (shaded) air temperatures in the neotropics, it is plausible that high temperatures in sunny areas of the canopy could inhibit foraging, breaking a positive correlation between shaded air temperatures and foraging success. Also, positive effects of temperature on walking speed could be over-ridden by variation in resource availability, temperature-independent leaf-handling times, or other factors.

Here we tested whether warmer shaded air temperatures occurring in the middle of the day enhance colony intake rates by facilitating walking speed or leaf cutting/handling (assayed indirectly by leaves carried per ant) for the leafcutter ant, *A. colombica*. This study occurred early in the rainy season when relatively cool air temperatures should maximize the likelihood that warming may enhance motor performance and foraging success.

Methods

Field observations were conducted during a two-week period in the rainy season (June) of 2018. We selected three partially-shaded *A. colombica* colonies with similar foraging rates and path widths located in the residential area of Gamboa, Panama. Each colony was assessed daily for 5 days within three different time windows: morning: 8:00–10:00 am, midday: 1:00–3:00 pm, and evening: 7:00–9:00 pm. These time windows were selected to compare daytime foraging at different temperatures (morning and midday) and daylight to dark foraging at similar temperatures (morning–night). Average high temperatures in Gamboa were approximately 31 °C and average lows were approximately 24 °C. The weather during measurements was

frequently sunny or cloudy, sometimes with light rain. In the event of heavy rain, measurements were postponed until the rain stopped. If the rain did not stop within the time window, the measurement for that day was skipped. Each time data were collected, the three colonies were tested in a haphazard order within the time window. For each colony, assessments were made at the same shaded location each time. We measured temperature just above the ground on the path with a mercury thermometer (accuracy: ± 0.1 °C) immediately before assessments of foraging. We counted the number of incoming, outgoing, and leaf-carrying ants that passed a set mark on the path within a 30 s window using a clicker counter and timer. Each count was replicated three times within a nest and observation time, then averaged. Number of leaves per ant was calculated by dividing number of ants per second by number of leaves per second.

We estimated the speed of leaf-carrying ants ($N=5$ ants for each sample period) and ants not carrying leaves ($N=5$ ants for each sample period) by timing how long it took an individual to move 25 cm along the path. If an ant on the path turned, stopped, or otherwise did not immediately walk down the path, the test was stopped, and a different ant was selected. The selected ants included small, medium, and large worker ants as ant size likely influences speed. Once the ant completed the 25 cm path, it was taken back to the lab, frozen, and weighed within 90 min of collection (A&D Mercury ER-182A electronic balance ± 0.0001 g).

To determine upper thermal tolerance, *A. colombica* were collected while foraging in mid-day from two source colonies in the San Luis reserve, Puntarenas, Costa Rica, during the rainy season (July) of 2014 ($N=14$ ants from each colony). Live ants were transported back to the lab, where they underwent upper thermal tolerance assays within two hours of collection. We used standard dynamic methods to measure critical thermal maxima (CT_{max}), using a ramping rate of 1 °C every ten minutes, with detailed methodology and equipment previously described by Baudier and O'Donnell (2019). After thermal tolerance assays were complete, all subjects were collected into ethanol, then photographed and measured for head width using ImageJ software (Schneider et al. 2012). A linear regression of log-transformed data tested for effects of body size (head width) on CT_{max} .

Statistical analyses

All analyses and plots were performed using RStudio version 3.5.1 (R Core Team 2018). We found no significant effect of colony on any of the variables, so ants from the different colonies were pooled for later analysis. We tested for significant linear and polynomial effects of temperature on ant speed, leaves per second, and leaves per ant using Z-transformed data. We present either the linear or polynomial fit with the best model chosen using a type II odds ratio

test. We also tested models using leaves per second into the colony as a linear function of ant speed and leaves per ant, again using Z-transformed data. For all analyses on ant speed and leaves per ant, we excluded the few data sets in which no ants were present. For all other analysis, we used the data set including the times there were no ants present.

ANOVA tests were run testing the significance of time of day on temperature, ant speed, leaves per second, leaves per ant, and z-transformed body mass. For the significant relationships, Tukey HSD post hoc tests used to determine which times of day were significantly different from each other. To test the effect of time of day and direction of travel on number of ants passing per second, we used a two-way ANOVA. To test if time of day had a significant impact independent of temperature, we use an ANOVA on both z-transformed data and on the residuals from the curvilinear models. We tested for linear effects of head width on CT_{max} by using both the raw data and the logarithms of the data.

Results

Ants of larger mass had faster travel speeds ($F_{1,258}=27.5$, $R^2=0.09$, $p<0.01$), but mass of foraging ants did not significantly differ across time of day (ANOVA: $F_{2,257}=1.1$, $p=0.35$), so we ignored ant mass in subsequent analyses. Ants carrying leaves ran faster as temperature increased in a curvilinear relationship ($F_{2,32}=36.9$, $R^2=0.68$, $p<0.01$; Fig. 1). This was also the case in ants without leaves ($F_{2,130}=63.4$, $R^2=0.49$, $p<0.01$). Additionally, leaves per second and leaves per ant increased with temperature in curvilinear relationships (Leaves per second: $F_{2,32}=35.6$, $R^2=0.65$, $p<0.01$; Leaves per ant: $F_{2,32}=24.0$, $R^2=0.58$, $p<0.01$; Fig. 1). Using the residuals of the curvilinear models and time of day, we found time of day had a significant effect on leaves per second and ant speed even when accounting for temperature (ANOVA: $p<0.05$). There was no significant interaction between temperature and time of day of these variables (leaves per second $p=0.50$; leaves per ant $p=0.10$; ant speed $p=0.56$). There was also a positive, linear, relationship between leaves per second and ant speed ($F_{1,33}=74.7$, $R^2=0.68$, $p<0.01$; Fig. 2) and between leaves per second and leaves per ant ($F_{1,33}=82.3$, $R^2=0.71$, $p<0.01$; Fig. 2).

Temperature varied with time of day (mean \pm 95% confidence limits, morning = 26.5 ± 0.5 °C, mid-day = 29.2 ± 0.8 °C, evening = 26.4 ± 0.3 °C; ANOVA, $F_{2,36}=29.7$, $p<0.01$). Morning and evening temperatures were not significantly different from each other (Tukey HSD $t=-0.24$ $p=0.97$). Time of day had a significant effect on the number of incoming ants per second (ANOVA: $F_{2,36}=33.4$, $p<0.05$), leaves per ant (ANOVA: $F_{2,36}=25.1$, $p<0.05$), leaves per second (ANOVA: $F_{2,36}=48.0$, $p<0.05$),

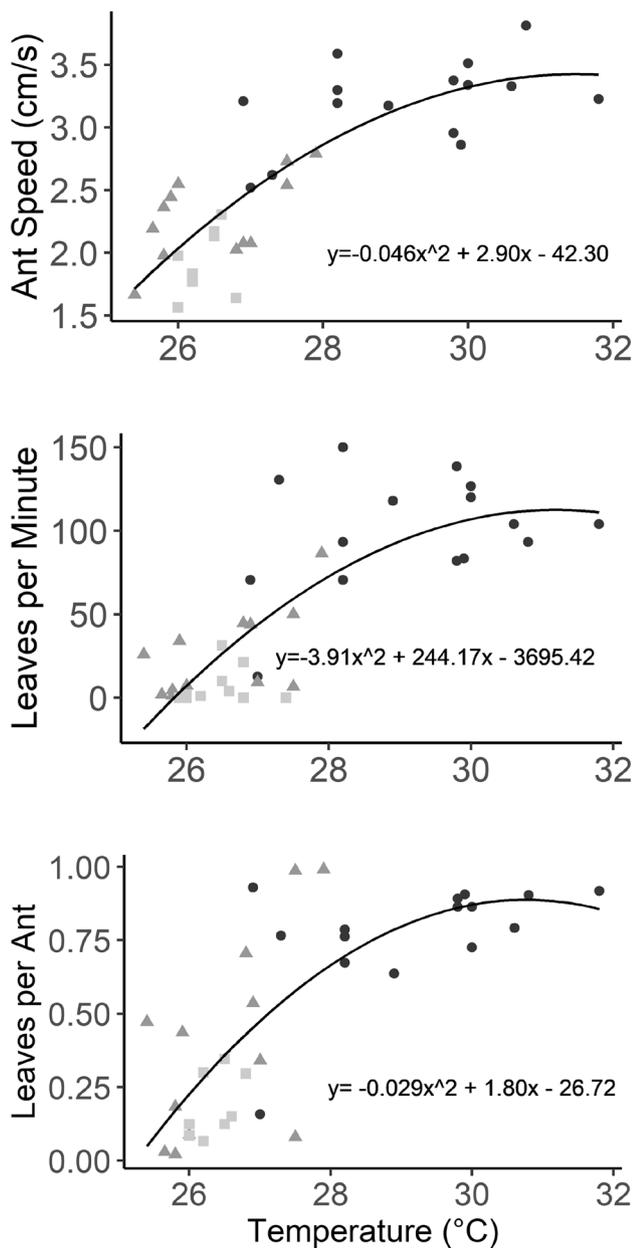


Fig. 1 Warmer temperatures were associated with faster leaf-carrying ant speeds, higher colonial intake rates of leaves, and the number of leaves carried per ant. Curvilinear relationships were determined to be a significantly better fit than linear relationships (ANOVA: $p < 0.05$). Equations present best-fit models of the data. Triangles represent morning measurements, circles midday, and squares evening

leaf-carrying ant speed (ANOVA: $F_{2,32} = 47.9$, $p < 0.05$), and outgoing ants per second (ANOVA: $F_{2,36} = 64.2$, $p < 0.05$; Fig. 3). Incoming ant speed and leaf flow were significantly higher at midday than during the morning or evening but did not differ between morning and night (Fig. 3), consistent with the temperature variation across these times. However, leaves per ant, incoming ants per minute, and outgoing ants per minutes were significantly different all times per day

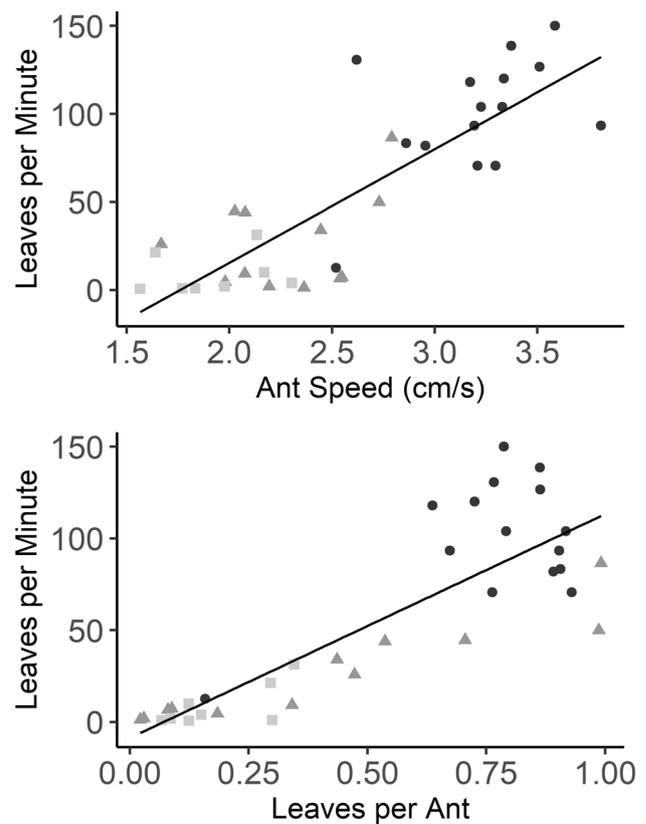


Fig. 2 Leaves per minute was linearly related to both ant walking speed ($F_{1,33} = 74.7$, $R^2 = 0.68$, $p < 0.01$) and leaves carried per ant ($F_{1,33} = 82.3$, $R^2 = 0.71$, $p < 0.01$). Triangles represent morning measurements, circles midday, and squares evening

(Fig. 3). There was a significant interaction between time of day and whether ants were incoming or outgoing ($F_{2,36} = 4.3$, $p < 0.05$; Fig. 4). During morning measurements, there were more outgoing than incoming ants, while the reverse was true at night (Fig. 4).

Mean CT_{max} of *A. colombica* \pm standard deviation was 40.4 ± 2.6 °C. CT_{max} also increased linearly with body size ($F = 4.8$, $df = 26$, $p < 0.05$; Fig. 5), with a minimum recorded CT_{max} of 33 °C observed in a minim worker and a maximum CT_{max} of 43 °C observed for several media workers.

Discussion

Our data support the hypothesis that, at least during the rainy season, higher temperatures allow *A. colombica* to bring in leaves at a higher rate, due to higher walking speeds and greater proportion of ants carrying leaves. Temperatures and weather conditions during the sampling period were similar to Gamboa averages for June. The increase in the number of leaves carried per ant at higher temperatures suggests that higher temperatures may increase cutting or leaf-handling

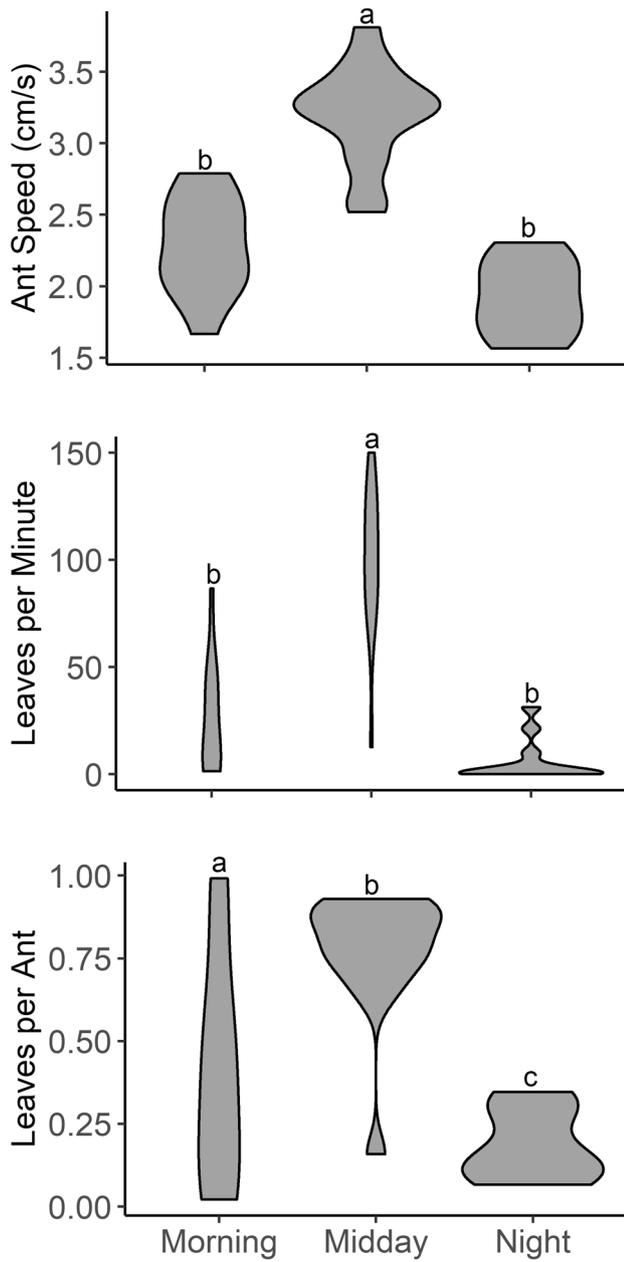


Fig. 3 Leaf-carrying ant speed, leaf intake rate, and leaves carried per ant in the morning (8:00–10:00 am), midday (1:00–3:00 pm), and evening (7:00–9:00 pm). Three colonies were tested at the three times per day across a six-day period. Groups with the same letters did not differ ($p > 0.05$ Tukey HSD). Graphs show violin plots describing the probability density of data at different values

speeds. However, temperature was not the only factor affecting leaf intake; colony leaf intake was higher in the morning than the evening despite similar temperatures. More ants were returning to the nest in the evening, consistent with a general suppression of night-time foraging during this time of year (Fig. 4). As leafcutter ants can forage nocturnally (Rockwood 1975; Wirth et al. 1997), it is not clear why they

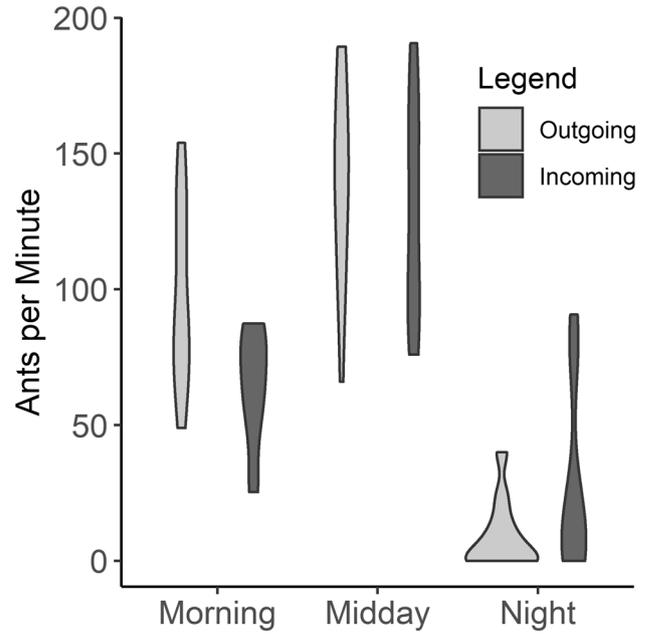


Fig. 4 Rates of outgoing and incoming ants during the morning (8:00–10:00 am), midday (1:00–3:00 pm), and evening (7:00–9:00 pm). Violin plots describe the probability density of data at different values

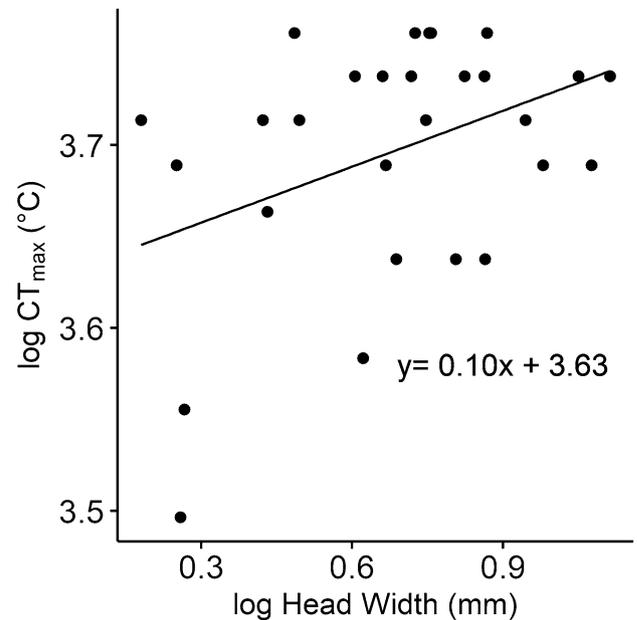


Fig. 5 Log-transformed maximum critical temperature (CT_{max}) was linearly related to log-transformed head width in *Atta colombica* ($F = 4.8$, $df = 26$, $p < 0.05$)

so strongly suppress night-time foraging in the rainy season even when temperatures are suitable. Foraging may be quicker and/or more efficient in the daytime due to warmer temperatures and/or the ability to use visual cues. Predator

avoidance may also play a role in determining foraging times (Orr 1992). Additionally, rains mostly occurred at night during this period, and rains have been demonstrated to induce foragers to drop their leaves, potentially due to the increase in weight (Farji-Brener et al. 2018). While our data supports the hypothesis that higher midday temperatures increase ant speeds and handling times, it is also possible that lower foraging rates during morning measurements may be caused, in part, by daily foraging rhythms. If nighttime foraging is suppressed and then begins again during daylight hours, measurements taken in the morning may inadvertently exclude the ants that have yet to leave the nest. Additionally, outgoing foragers outnumbered incoming foragers during morning measurements, a pattern that may signify the start of foraging (Fig. 4).

Average CT_{max} for *A. colombica* (40.4 °C) was well above ambient temperature measured near the ground in these experiments (Fig. 5). However, the most sensitive small foragers with CT_{max} of as low as 33 °C would be thermally challenged by ground temperatures not much greater than those observed at mid-day in this study. Furthermore, exposed and sunny canopy leaf temperatures at mid-day likely far exceed ground temperatures (Kaspri et al. 2015), suggesting that high thermal stress may provide some limits on exposed canopy foragers of *A. colombica*. High temperatures on foraging trails cause *A. colombica* to stop foraging (Spicer et al. 2017) and reduce performance in repeated heat exposure (Ribeiro et al. 2012). However, our data suggest that at least within our sampling period, higher temperatures were associated with a curvilinearly increasing foraging success. Our models show that as temperatures warm from approximately 24 °C in the morning toward mid-day peaks temperatures of about 31 °C, and then cool again, that foraging success is generally positively associated with warmer temperatures, excepting a plateau above 30 °C. While we found no direct evidence for suppression of foraging by high temperatures, based on results from other ectotherms, this likely occurs, though apparently above the highest shaded air temperatures we measured in this study (32 °C).

Although much work has suggested that tropical species may suffer from climatic warming (Deutsch et al. 2008; Tewksbury et al. 2008), the actual effects of climate change on insects will be complex, and much remains to be learned. High temperatures likely already limit leafcutter ant foraging in sun-exposed areas, especially in the dry season, and warming could increase the fraction of the day this occurs. However, over cooler, rainy parts of the year, and at higher elevation, our data suggest that warmer temperatures, up to a point, may cause improvements in leafcutter foraging, increasing herbivory. Climate-change effects on foraging success will also depend on the rain-free times available with acceptable temperatures, the effect of warming on plant growth rate and quality, and

effects of predators and parasites. Finally, changing soil temperatures have the potential to impact within-nest performance, though again, behavioral thermoregulatory strategies may ameliorate these effects. In summary, predicting climatic effects on the fitness of leafcutter ants remains an important challenge, but our data suggest that moderate warming could increase the foraging success and the herbivorous impact of leafcutter ants throughout much of the day during rainy seasons in semi-deciduous moist forests.

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Data availability Data sets used in this study are archived at the Dryad Digital Repository (see Electronic supplementary material).

References

- Addo-Bediako A, Chown SL, Gaston KJ (2000) Thermal tolerance, climatic variability and latitude. *Proc R Soc Lond B Biol Sci* 267(1445):739–745
- Andrew NR, Hart RA, Jung M-P, Hemmings Z, Terblanche JS (2013) Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, *Iridomyrmex purpureus* (Formicidae), with potential climate change. *J Insect Physiol* 59:870–880
- Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, New York
- Baudier KM, D'Amelio CL, Malhotra R, O'Connor MP, O'Donnell S (2018) Extreme insolation: the importance of climatic variability to the evolution of thermal tolerance limits. *Am Nat* 192(3):347–359
- Baudier KM, O'Donnell S (2019) Rain shadow effects predict population differences in thermal tolerance of leaf-cutting ant workers (*Atta cephalotes*). In press, *Biotropica*
- Bernstein RA (1979) Schedules of foraging activity in species of ants. *J Animal Ecol* 1979:921–930
- Burd M (1996) Foraging performance by *Atta colombica*, a leaf-cutting ant. *Am Nat* 148(4):597–612
- Caldato N, Forti LC, Bouchebti S, Lopes JFS, Fourcassié V (2016) Foraging activity pattern and herbivory rates of the grass-cutting ant *Atta capiguara*. *Insectes Soc* 63(3):421–428
- Cerdá X, Retana J, Cros S (1998) Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. *Funct Ecol* 12(1):45–55
- De Vasconcelos HL (1990) Foraging activity of two species of leaf-cutting ants (*Atta*) in a primary forest of the central Amazon. *Insectes Soc* 37(2):131–145
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci* 105(18):6668–6672
- Diamond SE, Yilmaz AR (2018) The role of tolerance variation in vulnerability forecasting of insects. *Curr Opin Insect Sci* 29:85–92

- Diamond SE, Penick CA, Pelini SL, Ellison AM, Gotelli NJ, Sanders NJ, Dunn RR (2013) Using physiology to predict the responses of ants to climatic warming. *Integr Comp Biol* 53(6):965–974
- Farji-Brener AG, Dalton MC, Balza U, Courtis A, Lemus-Domínguez I, Fernández-Hilario R, Cáceres-Levi D (2018) Working in the rain? Why leaf-cutting ants stop foraging when it's raining. *Insectes Soc* 65(2):233–239
- Fowler HG, Robinson SW (1979) Foraging by *Atta sexdens* (Formicidae: Attini): seasonal patterns, caste and efficiency. *Ecol Entomol* 4(3):239–247
- Gamboa GJ (1976) Effects of temperature on the surface activity of the desert leaf-cutter ant, *Acromyrmex versicolor versicolor* (Per-gande) (Hymenoptera: Formicidae). *Am Midl Nat* 1976:485–491
- Gomides CHF, Della Lucia TMC, Araujo FS, Moreira DDO (1997) Foraging speed and transported leaf area in the ant *Acromyrmex subterraneus* (Hymenoptera: Formicidae). *Rev Biol Trop* 45(4):1663–1667
- Hölldobler B, Wilson EO (1990) *The ants*. Harvard University Press, Cambridge
- Hölldobler B, Wilson EO (2011) *The leafcutter ants: civilization by instinct*. W.W. Norton & Company Inc, New York
- Huey RB, Kearney MR, Krockenberger A, Holtum JA, Jess M, Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Phil Trans R Soc B* 367(1596):1665–1679
- Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am Zool* 19(1):357–366
- Hunt JH (1974) Temporal activity patterns in two competing ant species (Hymenoptera: Formicidae). *Psyche J Entomol* 81(2):237–242
- Hurlbert AH, Ballantyne F, Powell S (2008) Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. *Ecol Entomol* 33(1):144–154
- Jayatilaka P, Narendra A, Reid S, Cooper P, Zeil J (2011) Different effects of temperature on foraging activity schedules in sympatric Myrmecia ants. *J Exp Biol* 214:2738
- Kaspari M, Clay NA, Lucas J, Yanoviak SP, Kay A (2015) Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. *Glob Change Biol* 21(3):1092–1102
- Lewis T, Pollard GV, Dibley GC (1974) Micro-environmental factors affecting diel patterns of foraging in the leaf-cutting ant *Atta cephalotes* (L.) (Formicidae: Attini). *J Animal Ecol* 43(1):143–153
- Orr MR (1992) Parasitic flies (Diptera: Phoridae) influence foraging rhythms and caste division of labor in the leaf-cutter ant, *Atta cephalotes* (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 30(6):395–402
- Penick CA, Diamond SE, Sanders NJ, Dunn RR (2017) Beyond thermal limits: comprehensive metrics of performance identify key axes of thermal adaptation in ants. *Funct Ecol* 31:1091–1100
- Porter SD, Tschinkel WR (1987) Foraging in *Solenopsis invicta* (Hymenoptera: Formicidae): effects of weather and season. *Environ Entomol* 16(3):802–808
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria. <https://www.R-project.org>
- Ribeiro PL, Camacho A, Navas CA (2012) Considerations for assessing maximum critical temperatures in small ectothermic animals: insights from leaf-cutting ants. *PLoS ONE* 7(2):e32083
- Rissing SW (1982) Foraging velocity of seed-harvester ants, *Veromessor pergandei* (Hymenoptera: Formicidae). *Environ Entomol* 11(4):905–907
- Rockwood LL (1975) The effects of seasonality on foraging in two species of leaf-cutting ants (*Atta*) in Guanacaste Province, Costa Rica. *Biotropica* 1975:176–193
- Rockwood LL (1976) Plant selection and foraging patterns in two species of leaf-cutting ants (*Atta*). *Ecology* 57(1):48–61
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9:671
- Spicer ME, Stark AY, Adams BJ, Kneale R, Kaspari M, Yanoviak SP (2017) Thermal constraints on foraging of tropical canopy ants. *Oecologia* 183(4):1007–1017
- Tewksbury JJ, Huey RB, Deutsch CA (2008) Putting the heat on tropical animals. *Science* 320(5881):1296–1297
- Wirth R, Beyschlag W, Ryel RJ, Hölldobler B (1997) Annual foraging of the leaf-cutting ant *Atta colombica* in a semideciduous rain forest in Panama. *J Trop Ecol* 13(5):741–757