Out on a limb: Thermal microenvironments in the tropical forest canopy and their relevance to ants

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ABSTRACT

Small, cursorial ectotherms like ants often are immersed in the superheated air layers that develop millimeters above exposed, insolated surfaces (i.e., the thermal boundary layer). We quantified the thermal microenvironments around tree branches in the tropical rainforest canopy, and explored the effects of substrate color on the internal body temperature and species composition of arboreal ants. Branch temperatures during the day (09:00–16:00) were hottest (often > 50 °C) and most variable on the upper surface, while the lowest and least variable temperatures occurred on the underside. Temperatures on black substrates declined with increasing distance above the surface in both the field and the laboratory. By contrast, a micro-scale temperature inversion occurred above white substrates. Wind events (ca. 2 m s^{-1}) eliminated these patterns. Internal temperatures of bodies of *Cephalotes atratus* workers experimentally heated in the laboratory were 6 °C warmer on white vs. black substrates, and 6 °C cooler than ambient in windy conditions. The composition of ant species foraging at baits differed between black-painted and unpainted tree branches, with a tendency for smaller ants to avoid the significantly hotter black surfaces. Collectively, these outcomes show that ants traversing canopy branches experience very heterogeneous thermal microenvironments that are partly influenced in predictable ways by branch surface coloration and breezy conditions.

1. Introduction

Thermal environments fundamentally influence the physiology, performance, behavior, and ecology of organisms (Huey, 1991). In particular, ectothermic animals are physiologically bound to a range of thermal conditions that can change quickly and unpredictably, often exceeding their thermal tolerance limits (Stevenson, 1985; Sunday et al., 2014). However, small cursorial ectotherms often are constrained to microhabitats that are susceptible to thermal extremes (Kaspari et al., 2015). For example, unlike lizards and other relatively large ectotherms, many small ectotherms like insects cannot fully lift the bulk of their body mass above superheated surfaces and air layers (Bakken, 1989). Consequently, some insects (e.g., ants) have developed morphological and behavioral mechanisms to manage physiological constraints in extreme thermal environments such as deserts (Sommer and Wehner, 2012; Cerdá and Retana, 2000).

Air near the surface of a hot substrate superheats, creating a thermal boundary layer (TBL), similar to fluid boundary layers (Ferro and Southwick, 1984; Vogel, 1994). The thickness of the TBL varies with factors like wind speed and vertical location within a forest (i.e., ground vs. canopy; Bakken, 1989; Nobel, 1974; Oke, 2002), and interacts directly with an organism's body size. Specifically, very small species are continuously immersed in superheated air, potentially limiting their ability to maintain activity as temperature increases (Kaspari et al., 2015). However, as body size increases, conductive heating from the surface and boundary layer should decline while radiative heating from the sun increases (Kaspari et al., 2015). Thus, the interaction of body size, surface temperature, and TBL thickness are particularly relevant for small ectotherms (Bakken, 1992; Bell, 1980; Stevenson, 1985).

Ant workers, by virtue of their small size and wingless condition, presumably are immersed in TBLs when foraging on hot, exposed surfaces (Kaspari et al., 2015). Perhaps as a consequence of this frequent exposure to intense heat, ants exhibit higher thermal tolerance than other well-studied ectotherms (Kaspari et al., 2015, 2016; Spicer et al., 2017; Wehner et al., 1992). Moreover, ant species can span nearly four orders of magnitude in mass (Kaspari and Weiser, 1999), differ interspecifically in thermal and desiccation tolerance (Bujan et al., 2016; Kaspari et al., 2015), and are key ecological components of most terrestrial habitats (Hölldobler and Wilson, 1990). Thus, ants are a particularly good focal taxon for studies of the biological relevance of TBLs.

Although tropical forest canopy ants do not exhibit the extreme thermal tolerance of desert-dwelling species (Kaspari et al., 2015; Shi et al., 2015; Spicer et al., 2017; Willot et al., 2016), they routinely traverse surfaces that are relatively hot. For example, under dry and clear conditions, tropical tree branches can heat to 55 °C, which is up to 20 °C warmer than ambient air temperature (Kaspari et al., 2015). However, unlike the open sand of desert environments, surface temperatures in tree crowns are likely to be extremely variable over relatively small spatial and temporal scales.

Two characteristics of tree substrates fundamentally affect their associated thermal microenvironments. First, cylindrical surfaces offer diverse amounts of exposure to insolation (Woods et al., 2015). Consequently, an insect crawling on an especially hot surface can find refuge from the heat by scurrying several centimeters in almost any direction. Second, tropical tree branches and trunks are highly variable in terms of color and reflectance. For instance, crown branches of many tropical trees have light colored surfaces due to abundant lichen cover (Yanoviak and Dudley, 2006). Although highly reflective, these surfaces become quite hot when directly exposed to solar radiation (Bakken, 1989; Gauslaa and Solhaug, 2001), whereas shaded areas of the same trees are considerably cooler (Kaspari et al., 2015). Canopy surfaces are also less sheltered from wind, which generally cools surfaces, reduces TBL thickness (Bell, 1980; Nobel, 1974), and increases thermal energy loss by the organism (Bakken, 1992; Barlett and Gates, 1967).

The principal goal of this project was to characterize the thermal microenvironments experienced by arboreal ants, both temporally and spatially, and to investigate how these conditions affect ant body temperature and foraging behavior. Specifically, we focused on three questions: 1) How do daytime surface temperatures vary around the circumference of a canopy branch?; 2) How does the shape of the TBL profile change with substrate color and in the presence of wind?; and 3) Do the thermal microenvironments of canopy branches influence internal body temperature and species composition while foraging? We addressed these questions by describing the thermal microenvironment available to small cursorial ectotherms traversing exposed branches in the canopy of a lowland tropical forest.

2. Materials and methods

Field and laboratory research was conducted on Barro Colorado Island (BCI), Panama (9.15°N, 79.85°W) during the 2014–2015 dry season (December–February). BCI is a seasonally moist tropical forest that receives ca. 3000 mm of rainfall per year. Field work was conducted in the dry season because average monthly solar radiation is higher between December-May (17.9 Mj/m^2) than June-November (13.9 Mj/m^2; Paton, 2016). Conversely, maximum monthly temperature varies by only a few degrees on BCI throughout the year (i.e., 29.2–31.7 °C from 1984 to 2015). More information about BCI is available elsewhere (Croat, 1978; Leigh et al., 1996).

Field work was conducted exclusively in the crowns of six *Pseudobombax septenatum* (Jacq.) Dugand trees on BCI. We used the single-rope technique (Perry, 1978) to access each tree crown. We chose *P. septenatum* because adults are large, often emergent (Clark and Clark, 1992), canopy trees that also are deciduous, dropping their leaves during the dry season (Croat, 1978). All of the trees used in this study were at least 30 m apart, liana-free, and leafless at the time of data collection. This ensured that the ant assemblages in each tree were independent (Adams et al., 2016), and that canopy branches received full sun.

2.1. Daytime temperatures on a canopy branch

To characterize temporal and spatial variation in the thermal microenvironment around the circumference of individual tree branches, we secured a four-channel data logger (RDXL4SD, Omega Engineering; Stamford, CT USA) and T-type wire thermocouples (HYP-1; Omega
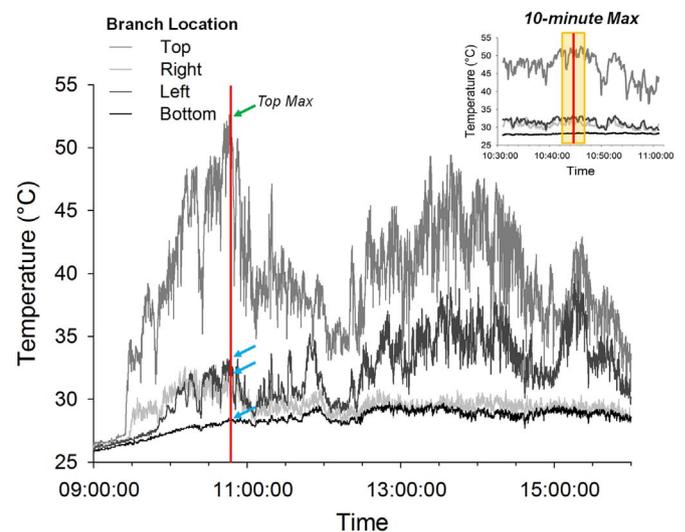

Fig. 1. Example of the variation in surface temperature on the top, bottom, and right and left sides of a canopy branch during the normal activity period of diurnal arboreal ants (09:00–16:00) on a clear day. Arrows indicate the maximum top surface temperature recorded during the activity period (*Top Max*; green arrow), and simultaneous right, left, and bottom branch surface temperatures (blue arrows). Inset: The variable *10-min Max* (yellow shading) was defined as the range of temperatures recorded during the five minutes before and the five minutes after *Top Max*. The red line is a visual aid, centered on *Top Max*, which bisects temperature readings on the right, left, and bottom of the focal branch at that time point. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Engineering) to the top, bottom, and sides of a focal branch on five *P. septenatum* trees (SI Fig. 1). Focal branches were chosen based on accessibility, ability to support the equipment, and angle (as parallel to the ground as possible). The logger was set to record temperature at 2 s intervals and allowed to run for 2–4 days to ensure recording at least one very sunny day.

We recorded the median and range of surface temperatures logged over 09:00–16:00 (the normal activity period of diurnal arboreal ants) from the warmest, clearest day during the measurement period for each tree. The hottest surface temperature recorded on the top of each focal branch during the 7 h range (hereafter, *Top Max*) was the basis for comparison with surface temperatures on the bottom and sides of the same branch at the same time (Fig. 1). We also measured the range and median temperature during an extreme heating window (10 min) centered around *Top Max* (hereafter, *10-min Max*). Specifically, *10-min Max* consisted of all surface temperature readings 5 min before and 5 min after *Top Max* on each focal branch (Fig. 1 inset). This heating window is biologically relevant to an arboreal ant that is actively foraging in a sun fleck or on an exposed branch.

2.2. Thermal boundary layer profile on colored and wind-exposed substrates

We measured the TBL profile on the focal branches described above with a series of mini-hypodermic thermocouple probes (HYP-0, Omega Engineering). The probes were secured to the upper surface of a focal branch in an offset vertical array at 0.1, 0.5, 1.0, and 2.0 mm orthogonal to the surface. The lowest probe (at 0.1 mm) had partial contact with the branch surface (SI Fig. 2). We collected temperature data from the array every 2 s during 1 min of continuous direct sunlight exposure. The 1-min recording period was preceded by an acclimation period of at least one minute of full sun exposure. Airspeed near the array was measured with a portable anemometer (Extech Instruments, Nashua, NH, USA). Winds up to 3 m s^{-1} occasionally occurred near the surface of canopy branches, but we only measured temperatures when the anemometer recorded zero wind speed for one minute.

We investigated the effect of substrate color on TBL thickness in the

field by painting two additional branches in each focal tree either black or white and repeating the procedure described above. Exterior latex paint was applied to the upper surface of the branches in a continuous patch ca. 15 cm wide and 30 cm long. We measured the reflectance of painted and unpainted branches with a portable spectroradiometer (Eye-One, GretagMacbeth; Grandville, MI USA).

We also recorded TBL temperatures (as described above) on black and white smooth ceramic tiles in the laboratory. We positioned a mercury-vapor heat lamp (125 W, Solar Glo, ExoTerra, Mansfield, MA, USA) 9 cm above the tile and illuminated the surface for 1 min. We used the microthermocouple array described above to record temperatures at 0.1, 0.5, 1.0, and 2.0 mm above the surface. The procedure was repeated five times on the black tile and six times on the white tile.

To measure the effect of wind on TBL thickness, we repeated the laboratory procedure above while exposing the tiles to air current. Specifically, after 1 min of heating, the outflow of a tabletop electric fan (~30 cm diameter) was positioned to produce a steady air current across each tile surface at speeds similar to those we observed in the field (2.0–2.5 m s^{-1}). We recorded the TBL temperature profile under the artificial wind regime six times for each tile color.

To quantitatively characterize the TBL in the field, we identified the distance above the surface (i.e., 0.1, 0.5, 1.0, and 2.0 mm) where the highest and lowest temperature readings occurred on each branch (hereafter, *Branch TBL$_{max}$* and *Branch TBL$_{min}$*). This approach allowed for variable starting temperatures among the different branches. Similarly, in the laboratory, we identified the highest and lowest temperature readings (hereafter, *Tile TBL$_{max}$* and *Tile TBL$_{min}$*) on each tile color and wind condition.

2.3. Arboreal ant body temperature and species composition

We used the heat lamp and tile apparatus described above to determine the interactive effects of substrate color and wind on ant body temperatures in the laboratory. We collected workers of a common Neotropical arboreal species, *Cephalotes atratus* (Linnaeus 1758), and killed them by freezing at −20 °C for 1 h. This species is continuously polymorphic and the workers we used ranged in mass between 12.8 and 71.4 mg. The dead ants were thawed, weighed, and then decapitated so that microthermocouple probes could be inserted directly into their thorax via the cervical opening (Spicer et al., 2017). We placed three ants separated by 1 cm directly under the lamp on black or white tiles, and measured local air temperature with a fourth microthermocouple probe positioned under the lamp ca. 2 mm above the tile surface (i.e., at the same height as the probes inserted into the ants). We turned on the lamp following a 2 min equilibration period (determined by relatively constant and similar temperatures of all four probes) and recorded internal temperature of the ant bodies after 1 min of heating. To determine the effects of wind and substrate color on ant body temperature, we repeated the procedure while applying the outflow from a fan as described above (wind speed = ca. 2 m s^{-1}). At least 30 *C. atratus* were tested on each substrate color (black or white) under each wind condition (present or absent). Ants were collected from multiple colonies and each ant was used only once (i.e., n > 120).

To determine the effect of the thermal microenvironment on ant species composition while foraging in the field, we placed baits (a tuna-honey mixture) on the upper surfaces of the painted (black and white) and unpainted branches in the six *P. septenatum* trees. Baits were placed > 24 h after painting. All three focal branches in a tree (black, white, and unpainted) were baited at the same time, and a wire thermocouple (HYP-1) was positioned near the bait. The logger recorded temperature every 2 s. The bait on each branch was photographed (Canon PowerShot ELPH 150) every minute for 15 min, and then every 5 min for one hour. We used the photographs to compare species composition across the three branch treatments. Surface temperature was recorded at the time of each photograph, and data were collected only when branches were in consistent full sun. Subsamples of ants

were collected to verify species identity. Body length, measured as the distance from the apex of the clypeus to the apex of the gaster, was measured for five mid-sized workers per species. Voucher specimens were deposited at the University of Louisville; the United States National Museum, Washington DC; the Smithsonian Tropical Research Institute, Panama; and the Fairchild Museum at the University of Panama.

2.4. Statistical analysis

We characterized the thermal microenvironment around the circumference of canopy branches in the field based on the average median and range of surface temperatures recorded for the entire 7 h period. To describe the available thermal microenvironments at the moment when the top of the branch was hottest, we calculated the average surface temperature at all four branch locations (top, bottom, left and right sides) when *Top Max* occurred. Finally, to characterize the thermal microenvironment during the warmest window of time during the day (*10-min Max*), we report the median and range of surface temperatures at all four locations on the branch.

We used analysis of variance (ANOVA) to determine how *Branch TBL$_{max}$* and *Branch TBL$_{min}$* differed by branch color. We similarly used two-way ANOVAs to investigate how *Tile TBL$_{max}$* and *Tile TBL$_{min}$* differed by tile color and the presence or absence of wind. Finally, we used an ANOVA to determine how the thickness of the boundary layer (the absolute value of the difference between *TBL$_{max}$* and *TBL$_{min}$*) differed among treatments for branches and tiles.

To explore the effects of the thermal microenvironment on ants, we used analysis of covariance (ANCOVA) to determine the role of wind and substrate color on internal temperature of *C. atratus* bodies, with ant mass as the covariate. Internal ant temperature was subtracted from the temperature of the bare microthermocouple (i.e., local air temperature) to control for minor differences in initial conditions among replicate trials. To determine the effects of substrate color on ant species composition while foraging in the field, we characterized the median and range of surface temperatures during which ants were present over the one-hour observation period on each of the branch treatments. We used PERMANOVA (Anderson et al., 2008) to determine if ant species composition at baits during this time differed between branch treatments (black, white and unpainted). We treated species composition as the product of branch treatment with tree identity as a random grouping factor. We chose a Jaccard index to calculate the similarity matrix from presence/absence species composition data. We used 9999 permutations for analyses and a post-hoc pairwise PERMANOVA analysis to determine how composition varied among the three treatments. We used indicator species analyses to determine which ant species were responsible for differences among the three treatments (de Cáceres and Legendre, 2009; de Cáceres et al., 2010). Post hoc Tukey HSD tests were used to compare treatment groups when differences were detected by ANOVA. Data were transformed as needed to fit model assumptions. Statistical analyses were performed in JMP 10 (SAS Institute Inc, 2012) or R version 3.2.3 (R Core Team, 2016). All means are reported ± 1 standard error (SE).

3. Results

3.1. Daytime temperatures on a canopy branch

Surface temperatures recorded on the top of exposed canopy branches ranged from 25.8 to 52.6 °C (average median = 34.9 ± 1.57 °C) over the 7 h period during the warmest, clearest day recorded for each focal branch. The daily average median surface temperature was consistently higher than ambient temperature measured in canopy trees (ca. 28 °C, n=10, SY personal observation). Average *Top Max* of exposed canopy branches during the 7 h period was ca. 17 °C higher than temperatures on the underside (top: 47.2 ± 2.07 °C; bottom:
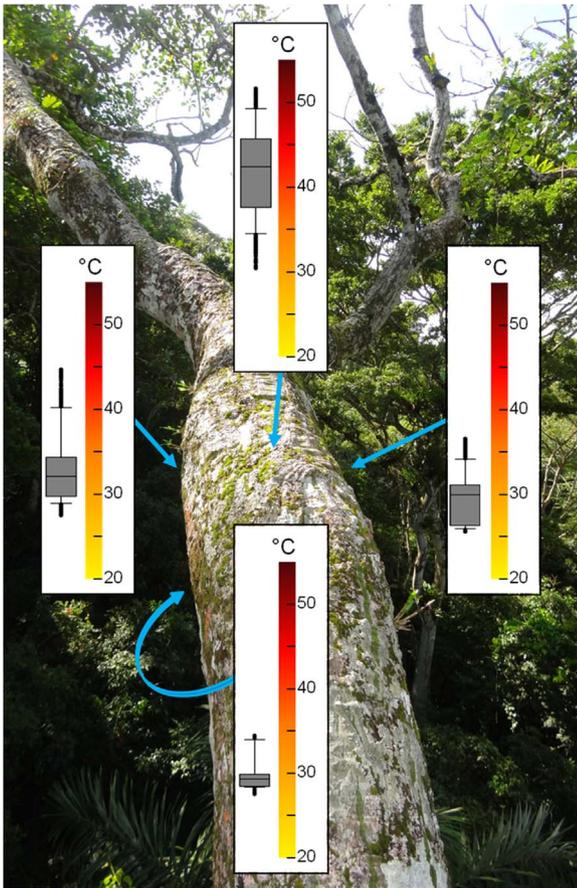
Fig. 2. Range of surface temperature (°C) during the maximum heating window (*10-min Max*) on top, bottom, left and right sides of canopy branches (n = 5) during a clear day. Median, 25th, and 75th percentiles are shown in the box plots. Error bars indicate the 10th and 90th percentiles. Outliers are plotted as solid black dots.

30.3 ± 0.95 °C), and ca. 14 °C higher than temperatures measured at that same time point on left and right sides (left: 35.1 ± 2.75 °C; right: 30.4 ± 1.90 °C). The *10-min Max* surface temperature on the top, underside, and sides of focal branches differed by as much as ca. 14 °C (Fig. 2). The top and sides were more variable than the underside, which was related to their orientation relative to the sun (i.e., the top and east side of a northward pointing branch heated quickly in the morning, and in the afternoon, the west side and top were warmer; Fig. 1).

3.2. Thermal boundary layer profile on colored and wind-exposed substrates

White painted branches were more reflective than the unpainted and black branches over the wavelength range 350–750 nm (SI Fig. 3). The average height of the hottest and coolest air within 2 mm of a branch surface (*Branch TBL_max* and *Branch TBL_min*) differed by branch color (*Branch TBL_max*: $F_{2,11}$ = 8.87, p = 0.0051; *Branch TBL_min*: $F_{2,11}$ = 75.91, p < 0.0001; Fig. 3). Specifically, on black and unpainted branches *Branch TBL_max* occurred near the surface, whereas on white painted branches *Branch TBL_max* was farther away (Fig. 3). Similarly, on black and unpainted branches *Branch TBL_min* was further away from the surface than on white painted branches (Fig. 3). Although the thickness of the TBL was similar among branch colors (1.2 ± 0.65 mm; $F_{2,11}$ = 2.45, p = 0.13), the shape of the thermal profile differed among them. Specifically, on black and unpainted branches air cooled as distance from the surface increased, whereas a micro-scale temperature inversion occurred over the white branches (SI Fig. 4). The mean temperature difference between *Branch TBL_max* and *Branch TBL_min* on each
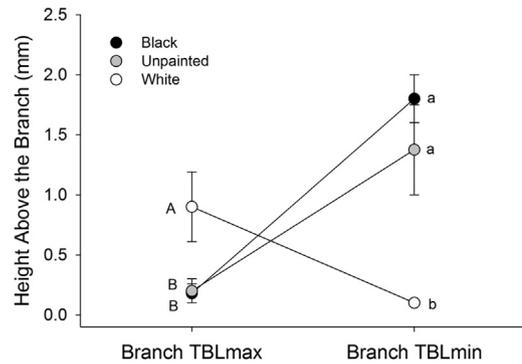

Fig. 3. Average (± 1 SE) height (mm) in the thermal boundary layer (TBL) above the branch surface of the highest (*Branch TBL_max*) and lowest (*Branch TBL_min*) recorded temperatures on black, unpainted and white branches in the field. Means denoted with the same letter are not statistically different.

branch (black, unpainted, white) was 2–3 °C; however, the range of temperatures experienced by ants differed by as much as 17 °C (black painted branches; Fig. 4). Although we did not record data during breezy conditions, observationally, differences between *Branch TBL_max* and *Branch TBL_min* were conspicuously reduced or eliminated during wind gusts.

After 1 min of heating under the lamp in the laboratory, the distance above the surface where *Tile TBL_max* and *Tile TBL_min* occurred differed by substrate color and the presence or absence of wind (for both tests, $F_{3,19}$ > 16.62, p < 0.0001; Fig. 5). Specifically, in still air, *Tile TBL_max* on the black tile occurred near the surface, whereas *Tile TBL_max* on the white tile was farther away (Fig. 5a), similar to air above the white painted branches in the field (Fig. 3). Wind removed the difference in *Tile TBL_max* on black and white tiles, and shifted average *Tile TBL_max* closer to the surface for both tile colors (Fig. 5a). *Tile TBL_min* also varied by color and the presence of wind. Specifically, *Tile TBL_min* was closer to the surface on white tiles vs. black tiles, and was farther from the surface in the presence of wind (Fig. 5b). The interaction of tile color and wind contributed to differences in the thickness of the TBL ($F_{3,19}$ = 5.46, p = 0.0071), where the TBL of black tiles was 1.6 ± 0.17 mm thick regardless of wind treatment, and white tiles in windy conditions had a thinner TBL than those in still air (1.0 ± 0.20 mm and 1.7 ± 0.17 mm, respectively).

3.3. Arboreal ant body temperature and species composition

In the laboratory, the difference in internal body temperature of *C. atratus* from ambient was reduced by ca. 6 °C in windy conditions (2.0–2.5 m s^{-1}), and was ca. 6 °C warmer on the white tile than on the black tile ($F_{4,116}$ = 13.75, p < 0.0001; Fig. 6). Temperatures of the different colored branches during the ant foraging study ranged from 29.0 to 57.6 °C. The black and white paint extended branch surface temperature ranges beyond those recorded on unpainted branches, with black paint having the more pronounced effect (white: 29.0–45.7 °C; black: 34.6–57.6 °C; unpainted: 29.6–44.0 °C). Ants foraged at the extremes of this range (29.0–55.1 °C). In total, 10 ant species were recorded at baits during the experiments (SI Table 1). Ant species composition differed among the three branch treatments (Pseudo-$F_{2,17}$ = 1.94, p = 0.04), and this result was driven entirely by differences between the black and unpainted treatments (t = 1.58, p = 0.04). Species composition was similar between black and white treatments (t = 1.38, p = 0.09) and between white and unpainted treatments (t = 1.22, p = 0.20). The indicator species analysis lacked sufficient power to determine whether compositional differences were associated with certain species; however, the two smallest ant species recorded (*Azteca instabilis* and *Pseudomyrmex oculatus*) rarely occurred on black branches, whereas the largest species recorded, *Neoponera villosa,* routinely foraged on black branches (SI Table 1). To explore this pattern further, we
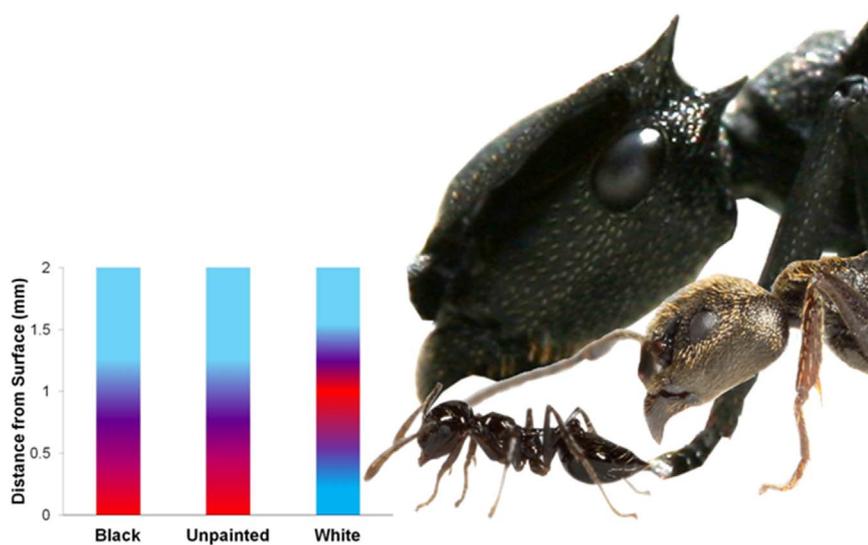
Fig. 4. Schematic of the thermal boundary layer (0.1–2 mm) above the surface of black, unpainted, and white canopy branches with three common arboreal ant representatives shown for comparison. The thorax of the large black *Cephalotes atratus* remains relatively cool on all substrates. The thorax of the mid-sized brown ant (*Dolichoderus bispinosus*) remains relatively cool on dark substrates (i.e., black and unpainted canopy branches), but is warmer on the white substrate due to the inverse boundary layer. In contrast, the thorax of the small *Crematogaster brasiliensis* heats in the thermal boundary layer of dark surfaces and remains cool on the white painted branch. Actual temperature ranges among black, unpainted, and white thermal boundary layers (TBLs) differed, such that the extremes represented by blue and red shading are 33.7–51.1, 32.0–36.9, 28.7–34.9 °C, respectively. Ants are shown approximately to scale. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

separated the two smallest ant species (*A. instabilis* and *P. oculatus*; n = 84) and the three largest ant species (*Camponotus sericeiventris*, *Cephalotes atratus*, and *N. villosa*; n = 33) into size categories (small and large, respectively). We found that small-sized workers visit bait on cooler surfaces (35.7 ± 0.38 °C) than large-sized workers (37.0 ± 0.5 °C; Wilcoxon Z = 1.66, p = 0.098), although this was marginally significant. Up to three species visited a single bait during the foraging trials. When multiple species co-occurred at a bait, most foragers were of a single species (> 66% of total abundance).

4. Discussion

Thermal microenvironments affect the physiology, performance, and behavior of small ectotherms like ants; however, the effects of temperature on the ecology of these organisms (i.e., local distribution and habitat use) remains poorly understood (Woods et al., 2015). Here, we show that ants and other small cursorial organisms face especially challenging thermal conditions in the relatively unpredictable spatial and temporal environments that characterize the rainforest canopy. The results of this study also suggest that such conditions affect arboreal ant species composition during active foraging bouts.

The branch temperature profiles we measured, along with the tendency for exposed leaf surfaces to be warmer than ambient air (Kaspari et al., 2015; Woods et al., 2015), suggest that small, cursorial, arboreal ectotherms like ants have relatively limited access to thermal retreats. Because thermal microenvironments on branch surfaces differ by as much as 17 °C over relatively short temporal and spatial scales, ants and other ectotherms must make rapid behavioral decisions to prevent overheating (Bakken, 1989; Huey, 1991; Kearney et al., 2009; Martin
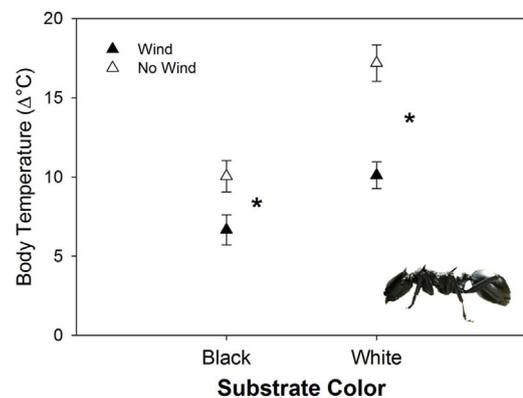

Fig. 6. Average (± 1 SE) difference between the internal body temperature of *Cephalotes atratus* workers and ambient temperature on black and white tiles, with and without wind (2.0–2.5 m s⁻¹). Asterisks indicate means within a color that differ from each other.

and Huey, 2008; Sunday et al., 2014). The results of this study show that the least variable and coolest location available for foragers on a canopy branch is on the underside. However, access to this retreat requires both speed and the ability to remain securely attached to the surface, both of which vary with temperature in ants (Federle et al., 2004; Hurlbert et al., 2008). Our field observations indicate that few ants actually use the undersides of branches as foraging pathways, perhaps due to the tendency for dense epiphytic lichens, bryophytes, and mosses to also occupy this shaded space (Yanoviak et al., 2017).

The results of this study corroborate similar patterns of model temperature readings obtained from black and white painted metal
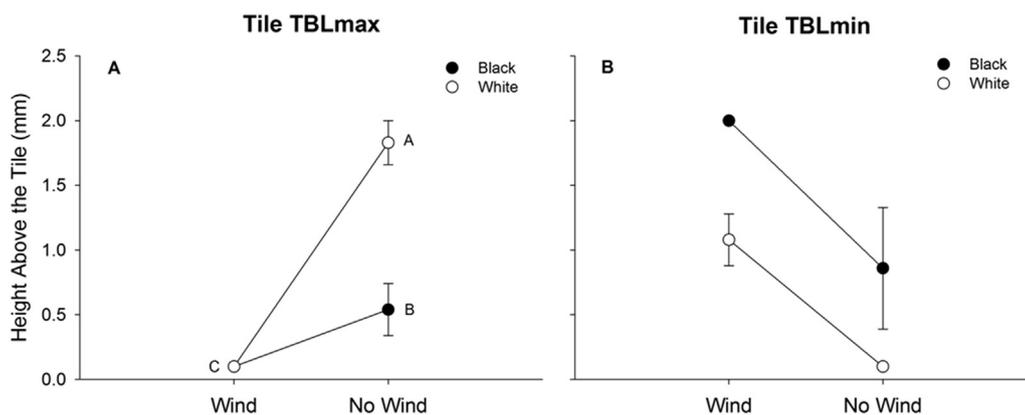

Fig. 5. Average (± 1 SE) height (mm) in the thermal boundary layer (TBL) above the tile surface of the highest (*Tile TBL_max*; A) and lowest (*Tile TBL_min*; B) recorded temperatures on black and white tiles in still air, and with wind from a fan applied in the laboratory (2.0–2.5 m s⁻¹). Means denoted with the same letter are not statistically different.

pipes exposed to sunlight in still air (i.e., dark surfaces are hotter than light; Bakken, 1989). As anticipated, a distinct TBL developed both on canopy branches in the field and on tiles in the laboratory. However, the temperature inversion that developed over white substrates in the field and laboratory was not expected (SI Fig. 4). We suspect that this inversion was due to the higher reflectivity of the white surface relative to darker surfaces. This effect can occur if re-radiation of heat from the surface is relatively low, causing the air directly above the surface to heat. Although more detailed measurements are needed to fully understand this result, similar idiosyncratic thermal conditions were recorded for silver painted lizard models (Pearson, 1977).

Consistent with the results of other studies, the TBL was greatly reduced when wind speed was 2–3 m s^{-1} (Bell, 1980; Nobel, 1974). Consequently, the breezy conditions that often occur in the canopy offer a temporary reprieve from thermal extremes for small cursorial organisms that suddenly find themselves in a superheated circumstance (e.g., when a sunfleck passes over a branch surface). However, organisms very near the surface still experience higher temperatures under breezy conditions than organisms just 2 mm taller, regardless of surface color. This effect likely results from the stillness of surface-level air in the boundary layer (Vogel, 1994), which increases local thermal convection. Thus, small insects < 2 mm tall on dark substrates, and < 1 mm tall on light substrates, inadvertently avoid the cooling effects of wind as a consequence of their low stature (Willmer and Unwin, 1981).

Like lizards and other larger organisms (Bakken, 1989), some large ants likely escape TBLs via their height. For example, very small tropical arboreal ants (body length < 2 mm; *Tapinoma* spp., *Brachymyrex* spp., and *Solenopsis* spp.) are completely immersed in the first 0.5 mm of the TBL, whereas workers of larger species (body length > 10 mm; *Atta* spp., *Neoponera* spp., and *Paraponera clavata*) likely stand above it (Kaspari et al., 2015). The internal body temperatures of *C. atratus* resting on ceramic tiles in the laboratory are consistent with this expectation. Specifically, the results suggest that *C. atratus* workers and ants of similar (or larger) size likely experience superheated surfaces and TBLs mainly with their tarsi, and perhaps occasionally with the ventral surface of the gaster (e.g., when depositing pheromones). However, the results also suggest that these ants experience very high temperatures near their core body height above light colored surfaces due to temperature inversions occurring at ca. 1 mm (Fig. 4). Our field observations suggest that species partition their use of hot branch surfaces based on body size, with small species generally avoiding hot, black-painted branches. However, more data are needed to confirm this result. Likewise, more detailed studies are needed to determine the strength of the species distribution trends we observed, and their relationship with morphological features such as exoskeleton color (Bishop et al., 2016a, 2016b; Spicer et al., 2017). Regardless, predictions concerning ant foraging behavior based on the interaction between body size and surface temperature must also account for surface reflectance properties and the presence or absence of wind (Spicer et al., 2017; Willmer and Unwin, 1981).

Whereas thermal microenvironments of tree surfaces in the tropical forest canopy are spatially and temporally heterogeneous, the effects of such variability on the local distribution and behavior of ants and similar arboreal organisms deserves further study. In particular, the results of this work raised three potentially fruitful questions for further research. First, do factors such as leaf size, tree identity, substrate diameter, humidity, conductivity, and surface roughness also affect surface temperature and micro-TBL profile as described in macro-TBL studies (Bakken, 1989; Leuzinger and Körner, 2007; Leuzinger et al., 2010; Pearson, 1977; Shuttleworth, 1989)? Second, does variation in body size positioning allow certain species of tropical arboreal ant to tolerate elevated TBL temperatures? Finally, what other ant traits (apart from variation in critical thermal maximum and desiccation rate; Bujan et al., 2016; Kaspari et al., 2015) affect their ability to forage on superheated branch surfaces? Ultimately, answering these questions will improve our understanding of how small cursorial ectotherms negotiate heterogeneous thermal microenvironments.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtherbio.2017.06.002.

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