




Day/night upper thermal limits differ within *Ectatomma ruidum* ant colonies

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Abstract In the tropics, daily temperature fluctuations can pose physiological challenges for ectothermic organisms, and upper thermal limits may affect foraging activity over the course of the day. Variation in upper thermal limits can occur among and within species, and for social insects such as ants, within colonies. Within colonies, upper thermal limits may differ among individuals or change for an individual throughout the day. Daytime foragers of the Neotropical ant *Ectatomma ruidum* have higher critical thermal maxima (CT_{max}) than nocturnal foragers, but whether these differences occur among or within colonies was not previously known. We investigated the potential mechanisms

accounting for day/night variation in CT_{max} of *E. ruidum* foragers by testing whether CT_{max} varied among or within colonies or due to individuals within colonies acclimating to changes in temperature over a short time scale (3 h). We found within- but not among-colony differences in CT_{max} on a diel cycle, and we found no evidence for among- or within-colony partitioning of foraging times by individual workers. Individuals did not acclimate to experimental manipulations of temperature, although additional experiments with more ecologically relevant temperature manipulations are needed to rule out this mechanism. In summary, we have shown that day/night differences in upper thermal limits can occur

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within ant colonies, but further investigation is needed to elucidate the mechanisms driving this variation.

Keywords Diel variation · Maximum critical temperature · Intra-colony variation · Acclimation

Introduction

Both long- and short-term temperature variation can pose physiological challenges for organisms (Gunderson and Stillman 2015; Oms et al. 2017). In the tropics, local temperatures vary relatively little seasonally but fluctuate relatively strongly throughout the day (Ghalambor et al. 2006; Esch et al. 2017). Throughout a day, maximum diurnal and minimum nocturnal temperatures frequently differ by more than 10 °C in tropical forests (da Rocha et al. 2004). Animals may respond to daily temperature fluctuations by foraging only during certain times of day, e.g., when temperatures are below a maximum threshold (Fraser et al. 1993; Cerdá et al. 1998; Kronfeld-Schor and Dayan 2003; Jayatilaka et al. 2011). For example, species with relatively low upper thermal limits often avoid foraging during the hottest times of day, which can affect their ecological interactions (e.g., Fitzpatrick et al. 2014) and responses to climate change. Alternatively, animals may forage across a large range of temperatures, e.g., by evolving a large range in thermal limits or by physiologically acclimating (Stillman 2003; Penick et al. 2017; Cahan et al. 2017; but see Gunderson and Stillman 2015). Plasticity in upper thermal limits (e.g., the ability to acclimate) is predicted to be limited in the tropics due to low thermal seasonality (Chown et al. 2004). However, plasticity is generally expected to evolve when environmental variation is greater within vs.

among generations (Via et al. 1995), such as where daily temperature fluctuations are strong. The effects of daily temperature fluctuations in the tropics on animal thermal physiology and the cascading effects on foraging behavior have previously received little attention (Esch et al. 2017).

Ants are a model system for investigating geographical and temporal patterns in thermal physiology and the resulting effects on foraging behavior. Ants are abundant, ecologically dominant (Wilson 1990), and amenable to assays for critical thermal limits on multiple scales, e.g., within and among colonies (Klotz 1984; Bestelmeyer 2000; Kaspari et al. 2015). Esch et al. (2017) examined day/night variation in the thermal physiology of the common Neotropical ant *Ectatomma ruidum* (Hymenoptera: Formicidae), finding that foragers collected during the day had significantly higher critical thermal maxima (CT_{max} , the upper temperature at which an organism loses muscle coordination; Huey and Stevenson 1979) than those collected at night. Species-level differences in thermal physiology have been documented in association with the partitioning of foraging on a daily cycle (Cerdá et al. 1997; Cerdá et al. 1998), but Esch et al. (2017) provided the first evidence that differences in thermal physiology occur throughout the day for ant foragers within a species.

Although diurnally foraging *E. ruidum* had a significantly greater CT_{max} than nocturnal foragers (Esch et al. 2017), the underlying sources of this variation are unclear. Day/night intraspecific variation in ant upper thermal limits can occur along two axes: among colonies (i.e., entire colonies forage at different temperatures) or within a colony (i.e., individuals forage at different temperatures due to fixed physiological differences or acclimate to changing thermal conditions). Since Esch et al. (2017) sampled diurnally vs. nocturnally foraging *E. ruidum* along different transects and did not resample colonies, they were unable to determine whether CT_{max} varied among or within colonies. CT_{max} could differ among colonies due to genetic or physiological differences or if colonies acclimate to different temperature conditions, e.g., as the result of nesting in different microenvironments (Jumbam et al. 2008). Within a colony, day/night differences in CT_{max} could occur if workers have alleles adapted to different temperature conditions and as a result forage during different times (Wiernasz et al. 2008) or if individuals acclimate to changes in temperature throughout the day. While differences in upper thermal limits among colonies may be adaptive by allowing colonies to partition the environment, differences within colonies may be adaptive by allowing colonies to forage across a wider range of environmental conditions. Thus, understanding the causes of day/night differences in *E. ruidum* CT_{max} is necessary to determine the potential ecological effects and adaptive significance of this variation.

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In this study, we investigated the patterns of day/night differences in upper thermal limits of *E. ruidum* in Costa Rica. We extended the methods from Esch et al. (2017) by sampling nest-mate workers at multiple timepoints from several known colonies, to assess whether colonies partitioned foraging activity across the daily cycle. We first tested whether the pattern of higher CT_{max} for diurnal foraging workers held. We then asked whether day/night CT_{max} differences were associated with: (1) among-colony differences in foraging activity time or (2) within-colony differences, either due to workers partitioning foraging times or acclimating to changes in temperature. To test among these possibilities, we marked workers from ten colonies to determine whether individuals partitioned foraging on a diel cycle and also measured CT_{max} of workers collected from the same colonies both during the day and at night. In addition, we tested whether workers acclimated to short-term extreme experimental temperature manipulations (for 3 h), predicting that ants exposed to high and low temperatures would exhibit higher and lower upper thermal limits, respectively, compared to those held at ambient air temperature. By investigating the patterns of intraspecific variation in upper thermal limits, we provide novel evidence that CT_{max} can differ on a day/night cycle within ant colonies.

Materials and methods

Natural history

This work was conducted at the La Selva Biological Station (N10°25.53', W84°0.10') in northeastern Costa Rica in March 2017. At La Selva, the mean daily temperature is 25.0 °C, with mean daily maximum and minimum temperatures of 31.2 and 21.7 °C, respectively, and a mean annual rainfall of 4360 mm (La Selva station automated weather data collection: <http://www.ots.ac.cr/meteoro/default.php?pestacion=2>; accessed 16 Apr 2017). *Ectatomma ruidum* is a common Neotropical ant that nests in secondary forests, attaining densities up to 1 colony m⁻² at La Selva (McGlynn et al. 2010). Colonies consist of a single queen and occupy a single nest (i.e., are monogynous and monodomous), with one 3–4 mm wide entrance dug into the ground (Guénard and McGlynn 2013).

Experimental design

To evaluate whether ants within colonies forage during different times of day, we located and marked ten *E. ruidum* nest entrances with surveyor flags on March 13 in the Holdridge Arboretum at La Selva (N10°25.76946', W84°0.56676'). We baited foraging workers within 1 m of each colony entrance with small piles of crumbled sweetened

breakfast cereal, and we confirmed the nest entrance destination of each forager. Foragers were marked from the colonies with different colors of model paint in the morning (930 h; “marked morning foragers”) and afternoon (1330 h; “marked afternoon foragers”) (Fig. 1). We revisited the same colonies on March 14 and collected samples of foragers both nocturnally (20.7 °C; 400–430 h; $n=44$ total ants) and diurnally (30.3 °C; 1400–1430 h; $n=86$ total ants) (Fig. 1), recording paint color if the ants had been previously marked. We collected 0–18 ants per colony per sampling period (workers from two colonies were active diurnally but not nocturnally).

We measured CT_{max} in the lab following the protocol of Esch et al. (2017). We placed each nocturnally foraging ant ($n=44$) and a subset of the diurnally foraging ants collected from each colony ($n=46$) in 1.5 mL plastic Eppendorf tubes capped with cotton in a digital heat block [Thermo Scientific Compact Digital Dry Bath/Block Heater, double block capacity, model 88871002, temperature control accuracy and uniformity at 37 °C $\leq \pm 0.5$ °C; the heat block unit was the same device used to measure CT_{max} by Esch et al. (2017)]. CT_{max} assays were initiated within 60 min of collection to minimize opportunities for thermal acclimation during handling. The block temperature started at 33 °C and increased by 1 °C every 5 min, following the protocol used by Esch et al. (2017). Before raising the temperature, we lightly tapped each tube to determine whether the ants were able to move in response. The highest temperature at which ants responded when we tapped the tube was recorded as the CT_{max} .

To evaluate whether foraging workers acclimate to changes in temperature, we experimentally exposed workers to different controlled temperatures and subsequently

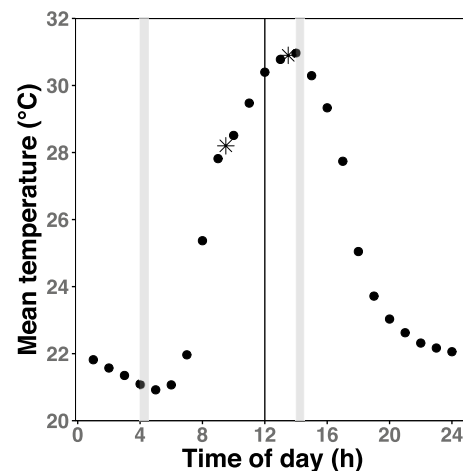


Fig. 1 Mean hourly temperatures at the La Selva Biological Station from March 12–18, 2017. Black asterisks indicate when ant foragers were initially marked with paint, and gray vertical bars indicate when ants were recollected for CT_{max} measurements. The black vertical line indicates when ants were collected for the acclimation test

measured their CT_{max} . In the afternoon on March 17 (1200 h, after temperatures had risen since 5 a.m.) (Fig. 1), we collected workers from six *E. ruidum* colonies by placing finely crushed crackers as bait approximately 10 cm from each colony entrance. We collected all workers carrying crackers back to the nest after 30 min (2–12 per colony; $n=45$ total). For 3 h, we exposed ants from each colony to one of the three temperature treatments: low (3 °C; $n=15$), ambient (25 °C; $n=14$), or high temperature (33 °C; $n=16$). We then measured their CT_{max} following the same protocol described above. In separate trials, we exposed ants to the three temperature treatments for 6 and 12 h, which are likely more biologically relevant acclimation periods, but in both cases, the ants at 33 °C were visibly heat stressed (the ants appeared moribund prior to the start of the assays; data from these trials were not analyzed). All data are available from the Dryad Digital Repository (Nelson et al. 2017).

Statistical analysis

Analyses were conducted in R v. 3.3.2 (R Core Team 2016). To determine whether diurnally foraging ants (“diurnal foragers”) had a higher CT_{max} than those foraging nocturnally (“nocturnal foragers”) and whether there were differences among colonies, we used a generalized linear model (GLM) with ant foraging time, source colony, and their interaction as fixed effects (excluding one colony, where only two ants were collected). Because the time \times source colony interaction was not significant, it was removed from the model to evaluate the significance of the main effects. We used the ‘glm()’ function with a quasi-poisson distribution (because the data were underdispersed) in the ‘stats’ package (R Core Team 2016). To evaluate the patterns of day/night differences in CT_{max} , we tested for day/night partitioning of foraging among and within colonies. To evaluate among-colony foraging partitioning, we used a linear model to test whether the numbers of nocturnal and diurnal foragers collected per colony were negatively correlated using the ‘lm()’ function in the ‘stats’ package. To test for within-colony foraging partitioning, we evaluated whether marked afternoon foragers were more likely to be recollected diurnally (vs. nocturnally) and whether marked morning foragers were more likely to be recollected nocturnally (vs. diurnally). For this analysis, we conducted Fisher’s exact tests (separately for marked afternoon and morning foragers) using the ‘fisher.test()’ function in the ‘stats’ package, including the number of colonies where the marked foragers were recollected diurnally and nocturnally in the model. Finally, to determine whether ants acclimated to short-term changes in temperature, we evaluated whether the CT_{max} of workers depended on the experimental temperature treatment, ant source colony, and their interaction using a generalized

linear model with a quasi-poisson distribution. Because the temperature treatment \times source colony interaction was not significant, it was removed from the model to evaluate the significance of the main effects.

Results

The CT_{max} of diurnal foragers was 1.1 °C greater than that of nocturnal foragers (GLM $F_{1,78}=71.0$, $P<0.001$; $n=88$) (Fig. 2), but there was no significant ant source colony \times foraging time interaction (GLM $F_{7,71}=1.544$, $P=0.167$; $n=88$) and no significant main effect of source colony (GLM $F_{8,78}=1.10$, $P=0.371$; $n=88$). Colonies did not partition the day/night foraging cycle: there was no significant relationship between the number of diurnal and nocturnal foragers collected per colony (linear model $F_{1,8}=0.677$, $P=0.434$; $n=10$) (Fig. 3). Furthermore, workers within colonies did not partition the day/night foraging cycle: there was no effect of sampling time (diurnal vs. nocturnal) on the number of colonies from which marked afternoon foragers (Fisher’s exact test $P=1$; $n=20$) or marked morning foragers (Fisher’s exact test $P=1$; $n=20$) were recollected (Fig. 4). There was also no evidence for thermal acclimation to controlled temperatures: the CT_{max} of workers exposed to temperature manipulations (3 h at low, ambient, and high temperatures) did not depend on temperature treatment (GLM $F_{2,37}=1.592$, $P=0.217$; $n=45$) (Fig. 5), ant source colony (GLM $F_{5,37}=1.331$, $P=0.273$; $n=45$), or the temperature treatment \times source colony interaction (GLM $F_{9,28}=0.589$, $P=0.795$).

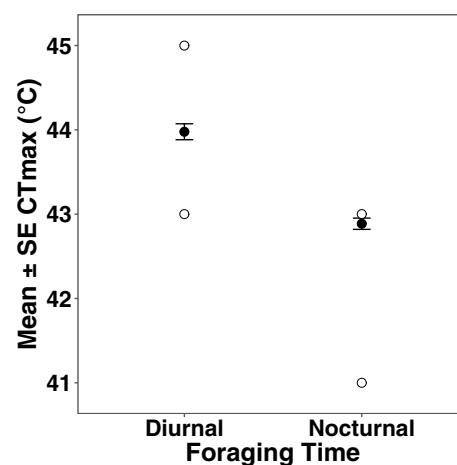


Fig. 2 CT_{max} (means \pm SE; white circles indicate minimum and maximum values) of *E. ruidum* workers collected from ten colonies diurnally (30.3 °C, 1400–1430 h; $n=44$) and nocturnally (20.7 °C, 400–430 h; $n=44$) (GLM $F_{1,78}=71.0$, $P<0.001$)

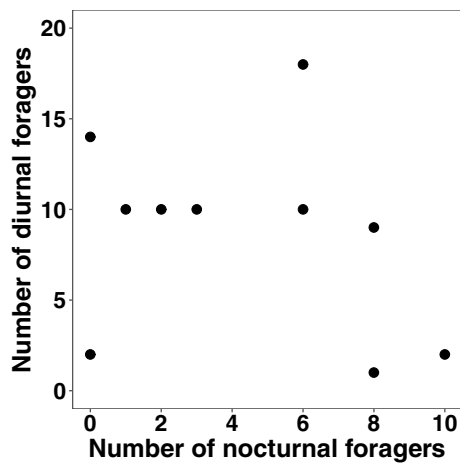


Fig. 3 Relationship between the number of *E. ruidum* workers collected per colony ($n=10$) diurnally (30.3 °C, 1400–1430 h) vs. nocturnally (20.7 °C, 400–430 h) (linear model $F_{1,8}=0.677$, $P=0.434$)

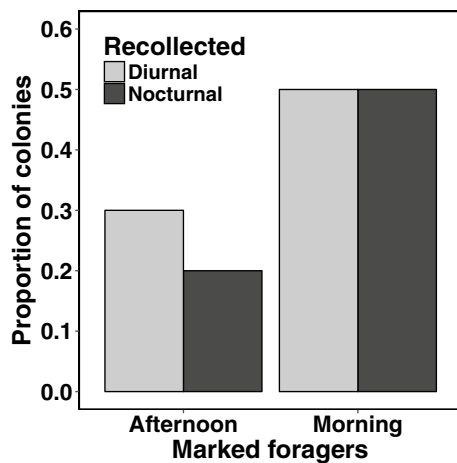


Fig. 4 Proportion of *E. ruidum* colonies ($n=10$), where workers that had previously been marked in the morning (“marked morning foragers”) or afternoon (“marked afternoon foragers”) were recollected the following day, either diurnally (30.3 °C; 1400–1430 h) or nocturnally (20.7 °C; 400–430 h) (Fisher’s exact tests $P=1$)

Discussion

Diurnal *E. ruidum* foragers had a 1.1 °C higher CT_{max} than nocturnal foragers, which is the same difference in CT_{max} measured between diurnal and nocturnal *E. ruidum* foragers in a Costa Rican dry forest in June 2016 by Esch et al. (2017). The mean CT_{max} values that we found for diurnal and nocturnal foragers (42.9 and 44.0 °C, respectively) are also the same as those found by Esch et al. (2017). Because we collected ants from the same colonies both diurnally and nocturnally, we have established that day/night differences in CT_{max} occur within colonies. We found no evidence that colonies or workers within colonies partition their foraging

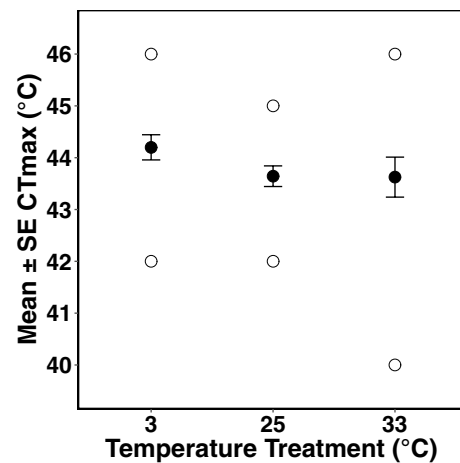


Fig. 5 CT_{max} (means \pm SE; white circles indicate minimum and maximum values) of *E. ruidum* workers exposed to low (3 °C; $n=15$), ambient (25 °C; $n=14$), and high (33 °C; $n=16$) experimental temperature manipulations for 3 h. There were no significant effects of temperature treatment (GLM $F_{2,37}=1.592$, $P=0.217$; $n=45$), ant source colony (GLM $F_{5,37}=1.331$, $P=0.273$; $n=45$), or the temperature treatment \times source colony interaction (GLM $F_{9,28}=0.589$, $P=0.795$)

on a day/night cycle, suggesting that day/night differences in *E. ruidum* forager CT_{max} are caused by plasticity in upper thermal limit at the individual level. However, the CT_{max} of foragers did not change with experimental exposure to extreme high or low temperatures across 3 h. Thus, while we have documented intra-colonial variation in CT_{max} as a mechanism for day/night foraging specialization, the mechanisms responsible for this variation in upper thermal limits remain unknown.

Previous work on other ant species has shown that the CT_{max} of foragers collected throughout the day from the same colony can be constant (Ribeiro et al. 2012). However, CT_{max} has been shown to shift on daily cycles for other animals (Willhite and Cupp 1982; Sørensen and Loeschcke 2002). Daily differences in CT_{max} could be adaptive for ants if they allow colonies to forage across a wider range of temperatures throughout the day, either if workers with different upper thermal limits forage during different times or if workers acclimate to daily changes in temperature.

We found no evidence for day/night partitioning of foraging among or within colonies. There was no relationship between the number of diurnal and nocturnal foragers collected per colony, indicating that there is no among-colony foraging partitioning on a daily cycle (Fig. 3). However, several colonies were only active during one sampling period (e.g., from one colony, we collected 14 and 0 workers at 1400 and 400 h, respectively; Fig. 3), indicating that some colonies may partition foraging on daily cycles. More rigorous surveys of *E. ruidum* colony activity on a daily cycle are needed to determine whether colony-level differences

in foraging activity occur (Jumbam et al. 2008). Furthermore, the likelihood of recollecting marked afternoon and morning foragers from a colony diurnally or nocturnally did not differ, indicating that workers within colonies do not partition foraging on a daily cycle (Fig. 4). Thus, day/night differences in upper thermal limits were not explained by partitioning of foraging among or within colonies.

Workers did not acclimate to changes in temperature on a short timescale, although additional tests are needed to eliminate acclimation as a potential mechanism driving day/night differences in upper thermal limits. Experimentally exposing ants collected during the afternoon (1200 h) (Fig. 1) to low (3 °C), ambient (25 °C), and high temperatures (33 °C) for 3 h did not alter their CT_{max} (Fig. 5). However, when we exposed ants to these temperatures for longer, more biologically relevant time periods (6 and 12 h), workers were heat stressed at the high temperature. It is possible that we would have found a different pattern if we had exposed ants to a narrower range of temperatures (e.g., temperatures that foragers are more likely to experience on a daily cycle) for longer time periods while controlling humidity to prevent desiccation. However, ants exposed to the low and ambient temperatures for 6 and 12 h did not differ in CT_{max} , indicating that acclimation may not be a likely mechanism. Previous work finding evidence for ant thermal acclimation has typically been conducted over longer acclimation periods (e.g., 7 days; Jumbam et al. 2008; Chown et al. 2009). Moreover, plasticity in critical thermal limits is predicted to be low in the tropics due to low seasonal variation in temperature (Chown et al. 2004), and in general, plasticity in ectotherm critical thermal limits is low (Gundersen and Stillman 2015). However, for other animals such as amphibians and reptiles, CT_{max} is known to change following daily patterns (Willhite and Cupp 1982). Since day/night differences in ant activity may be driven by light (Narendra et al. 2010) or circadian cycles (Jayatilaka et al. 2011), it is possible that rather than temperature, one of these factors triggers daily changes in *E. ruidum* CT_{max} . Additional experiments are needed to rule out acclimation as a mechanism driving day/night differences in CT_{max} .

In summary, the upper thermal limit of *E. ruidum* workers varies within colonies on a daily cycle, although the mechanisms driving this variation are still unknown. Importantly, day/night variation in CT_{max} within colonies could be adaptive, allowing colonies to forage across a wide range of thermal niches throughout the day. Since critical thermal limits can affect the ability of animals to locate and utilize resources, these limits may thus drive species abundances and distributions (Bishop et al. 2017). The ability to tolerate and respond to temperature variation during foraging, both on short-term (e.g., throughout the day) and longer term scales (e.g., across seasons or years), could ultimately influence how species respond to climate change. If ant colonies

are able to forage in the tropics throughout the day despite relatively large fluctuations in temperature, they may also be more likely to tolerate longer term changes in climate.

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