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Seasonal plasticity of thermal tolerance in ants

JELENA BUJAN ^{1,2,5} KARL A. ROEDER ^{2,3} STEPHEN P. YANOVIK ^{1,4} AND MICHAEL KASPARI ²

¹*Department of Biology, University of Louisville, Louisville, Kentucky 40292 USA*

²*Geographical Ecology Group, Department of Biology, University of Oklahoma, Norman, Oklahoma 73019 USA*

³*Department of Entomology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801 USA*

⁴*Smithsonian Tropical Research Institute, Apartado 0843, Balboa, Republic of Panama*

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Abstract. Analyses of heat tolerance in insects often suggest that this trait is relatively invariant, leading to the use of fixed thermal maxima in models predicting future distribution of species in a warming world. Seasonal environments expose populations to a wide annual temperature variation. To evaluate the simplifying assumption of invariant thermal maxima, we quantified heat tolerance of 26 ant species across three seasons that vary two-fold in mean temperature. Our ultimate goal was to test the hypothesis that heat tolerance tracks monthly temperature. Ant foragers tested at the end of the summer, in September, had higher average critical thermal maximum (CT_{max}) compared to those in March and December. Four out of five seasonal generalists, species actively foraging in all three focal months, had, on average, 6°C higher CT_{max} in September. The invasive fire ant, *Solenopsis invicta*, was among the thermally plastic species, but the native thermal specialists still maintained higher CT_{max} than *S. invicta*. Our study shows that heat tolerance can be plastic, and this should be considered when examining species-level adaptations. Moreover, the plasticity of thermal traits, while potentially costly, may also generate a competitive advantage over species with fixed traits and promote resilience to climate change.

Key words: acclimation; CT_{max} ; heat tolerance; *Solenopsis invicta*; thermal limits; thermal plasticity.

INTRODUCTION

Ectotherms are particularly vulnerable to climatic change (Angilletta 2009, Buckley et al. 2013), with current warming potentially contributing to recent declines in arthropod numbers (Bale et al. 2002, Wilson and Maclean 2011). Understanding the extent that ectotherms can acclimate to higher temperatures will be crucial for predicting their future diversity, abundance, and distribution patterns (Deutsch et al. 2008, Sunday et al. 2012, García-Robledo et al. 2016). Intraspecific variation in thermal tolerance is often considered fixed, an artifact that results from inadequate replication over time (Addo-Bediako et al. 2000, Calosi et al. 2008, Deutsch et al. 2008, Hoffmann et al. 2013, Sheldon and Tewksbury 2014, Kaspari et al. 2015, García-Robledo et al. 2016). But for ectotherms living in seasonal environments (and migratory or invasive species that

disperse easily to environments with varying climates) the ability to track changes in temperature via hardening and acclimation (Sgrò et al. 2016) could be particularly advantageous.

Here, we test for the existence and range of thermal plasticity in an ant community from a highly seasonal savanna-woodland. Ants are widely distributed ectotherms and their foraging behavior tracks environmental temperature (Cerdá et al. 1998, Roeder et al. 2018). Heat tolerance in ants varies widely (Diamond and Chick 2018), often tracking mean habitat temperatures (Gehring and Wehner 1995, Kaspari et al. 2015, Boulay et al. 2017, Baudier et al. 2018). However, recent studies show that ant heat tolerance can be invariant across elevational thermal gradients at regional scales (Bishop et al. 2017, Nowrouzi et al. 2018). Heat tolerance in these species might not be a fixed trait, but instead acclimatized to the specific microhabitat (Baudier et al. 2018) or the sampling season (Kay and Whitford 1978), which is why it fails to follow annual means.

Among ant populations of the same species, thermal maxima can be higher for individuals living in warmer

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⁵E-mail: jelena.bujan@gmail.com

urban environments compared to their rural counterparts (Angilletta et al. 2007, Diamond et al. 2017), and ants can acclimate to warmer conditions in the lab (Jumbam et al. 2008). Because ants are globally distributed, show acclimation ability, and occupy all climates except the ice caps, they are a model taxon to test how changes in environmental temperatures affect the plasticity of thermal tolerance.

Ant workers are exposed to multiple challenges when foraging, including large differences in temperature over the course of a day and across seasons (Kay and Whitford 1978, Bestelmeyer 2000, Baudier et al. 2018, Prather et al. 2018). Here we test the hypothesis that workers of ant colonies in seasonal environments exhibit annual variation in thermal tolerance. Specifically, we predicted that foragers will have higher heat tolerances in warmer months vs. cooler months. Furthermore, we predict that species active across different seasons will be more likely to show thermal plasticity, as their workers experience a broader range of temperatures during an annual cycle. To test for thermal plasticity, we used an ant community in southern Oklahoma that experiences strong temperature variation during an annual cycle.

MATERIALS AND METHODS

We sampled ants and conducted thermal assays in the summer (3–7 September 2015), winter (2–4 December 2015) and spring (14–17 March 2016) at the University of Oklahoma Biological Station (Oklahoma, USA, 33.88° N, 96.80° W). Average monthly air temperatures spanned 23.0°C across the year at this location with our sampled months maintaining relatively consistent averages of 6.6°C in December, 12.2°C in March, and 24.3°C in September over the past 20 yr (monthly averages compiled from 1996–2015 from the Oklahoma Climatological Survey). The studied ant community was invaded by the red imported fire ant, *Solenopsis invicta*, so our sampling included both native and invasive ant species.

Thermal tolerance assays

During each sampling period, we aimed to locate at least three nests of the most common ant species. We collected approximately 30 workers per colony in the vicinity of their nest, but not all of them were tested. We usually tested three colonies per species and five workers per colony in each month of sampling. However, for less abundant species, the number of workers tested was dependent on the number of active foragers found (Appendix S1: Table S1). Within two hours from the initial field collection, we measured the critical thermal maximum (CT_{max}), the temperature at which voluntary muscle movement stops (Lutterschmidt and Hutchison 1997, Kaspari et al. 2015), of five workers from each colony. We put each of the five individual workers into separate 1.5-mL microcentrifuge tubes. We filled the inside of the lid of each tube with modeling clay to remove a

potential thermal refuge (as in Bujan et al. [2016]). We then placed tubes into a digital dry bath (USA Scientific Thermal-Lok two-position dry heat bath, advertised accuracy $\pm 0.2^\circ\text{C}$; Ocala, Florida, USA) set at 36°C, and used an established dynamic ramping protocol to quantify CT_{max} (Kaspari et al. 2015). Every 10 minutes, each tube was inspected and rotated to determine if the ant had lost muscle control, i.e., loss of a righting response (as in Diamond et al. 2012). The dry bath was then increased in temperature by 2°C and the process was repeated until all ants had reached their upper thermal limit. The temperature at which each worker lost movement ability was recorded as its CT_{max}.

Statistical analyses

We performed all analyses in R version 3.3.2 (R Core Team 2018) using CT_{max} of each worker. We used a Kruskal-Wallis test to compare differences in community-level CT_{max} across 26 species and three sampling months. To determine which months were statistically different from each other we used Dunn's test with adjusted *P* values for multiple comparisons with the Holm method (Holm 1979). We used the same analyses to test the effect of seasons on community-level CT_{max} in species active across two and three months. To test the effect of sampling months on CT_{max} of different species, we fit generalized linear models (GLMs) using the month of sampling, species, and their interactions as predictor variables. We then used the Akaike Information Criterion (AIC) to select the optimal model and explored the significance of model terms via pairwise comparisons using the R package *emmeans* (Lenth 2019). Because of the large number of pairwise comparisons we separately analyzed species active in two seasons and three seasons (Appendix S1: Tables S2, S3).

To inspect for phylogenetic signal, we calculated genus-level averages of CT_{max} and used Pagel's λ (Pagel 1999). We performed phylogenetic analysis using the R packages *ape* (Paradis et al. 2004) and *phylosignal* (Keck et al. 2016). As not all genera were active across our focal months, we separately inspected the effect of phylogeny on CT_{max} in each month. We did not find any phylogenetic signal in CT_{max} of six genera active in December ($\lambda = 0.22$, $P = 0.92$), 17 genera active in March ($\lambda = 0.89$; $P = 0.29$), or 13 genera that were active in September ($\lambda = 0.80$; $P = 0.27$), presumably reflecting the small number of closely related genera sampled in the community.

RESULTS

Seasonal plasticity of CT_{max} in a community

In total, we measured the CT_{max} of 635 foragers from 117 ant colonies. These ants represented 26 species in 18 genera and 5 subfamilies. We recorded the highest number of active species during spring (March) when we

collected and tested all 26 species, fewer species were active during the summer (September; $n = 17$), and only six species were foraging in the winter (December). At the community level, the species CT_{max} was the highest in September ($\chi^2 = 50.4$, $df = 2$, $P < 0.001$; median = 50°C ; interquartile range = $48\text{--}54^\circ\text{C}$), then March (50°C ; $46\text{--}52^\circ\text{C}$) and lowest in December (48°C ; $44\text{--}50^\circ\text{C}$).

Seasonal plasticity of CT_{max} in conspecifics

Five ant species actively foraged across all three seasons: *Crematogaster laeviuscula*, *Dorymyrmex flavus*, *Forelius pruinosus*, *Pheidole bicarinata*, and the invasive *Solenopsis invicta*. Sampling month and species identity, together with their interactions, were best predictors of their CT_{max} . These species showed a wide degree of thermal plasticity ranging from 0.5° to 7.7°C difference in mean CT_{max} between summer and winter months. *Dorymyrmex flavus* was the only species in which CT_{max} remained unaltered across all seasons (Fig. 1). At the other end of the spectrum, the thermophile *F. pruinosus* had CT_{max} 7.7°C higher in September compared to March and December (Fig. 1; Table S2). Intermediate in their range of CT_{max} differences between September and December were the three species of myrmecine ants: *S. invicta* ($\Delta CT_{max} = +3.4^\circ\text{C}$), *C. laeviuscula* ($\Delta CT_{max} = +3.6^\circ\text{C}$), and *P. bicarinata* ($\Delta CT_{max} = +4.8^\circ\text{C}$, Fig. 1; Appendix S1: Table S2). The critical thermal maxima of these five seasonal generalists showed the same pattern observed at the community level: CT_{max} was the lowest during December (Fig. 2; median = 50°C), higher in March (median = 52°C) and the highest in September (median = 54°C , $\chi^2 = 48.5$, $df = 2$, $P < 0.001$). Compared to the species active across only two seasons, seasonal generalists had higher average CT_{max} in December and September (Fig. 2).

The only species active in winter and spring, *Prenolepis imparis*, also increased its CT_{max} by 2°C during the warmer month (Appendix S1: Fig. S1, Table S3). There were 11 species foraging only in March and September, and not found foraging in the winter, and these species overall had seasonally invariant CT_{max} (Fig. 2). However, two of these species (*Pheidole dentata* and *Monomorium minimum*) had higher CT_{max} in September compared to March (Appendix S1: Fig. S1, Table S3). The remaining nine species were predominantly active in March when their average CT_{max} ranged from 42° to 52.4°C (Appendix S1: Fig. S2).

DISCUSSION

Although models of range expansion often assume fixed thermal traits (Lancaster 2016), we found that ant heat tolerance was plastic over the year, likely acclimating to mean monthly temperatures. As predicted, the tested species in this temperate ant community had, on average, lower CT_{max} in cooler months. Most of the species driving this pattern were seasonal generalists with

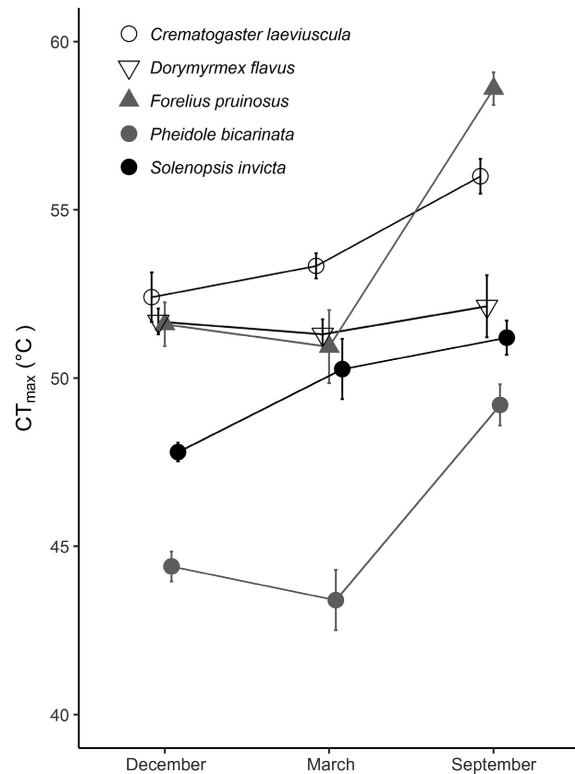


FIG. 1. Species-level changes in mean critical thermal maximum (CT_{max}) across five species captured in all three seasons. Different shapes represent two subfamilies, Dolichoderinae (triangles) and Myrmicinae (circles), and the error bars denote \pm SE.

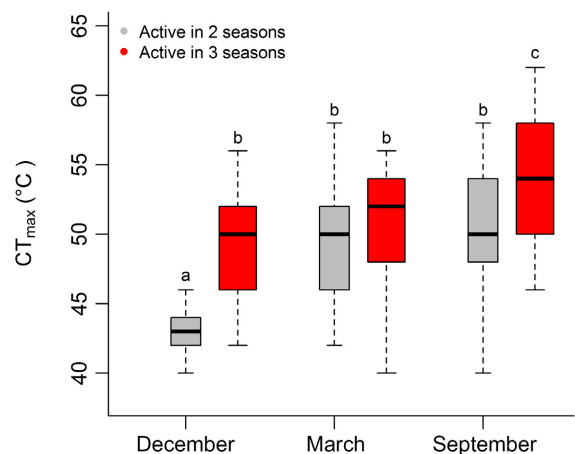


FIG. 2. Seasonal differences in CT_{max} across five species that were active in all sampled seasons (red) and 12 species active in only two seasons (gray), mostly in March and September. Groups that are significantly different are marked with different letters ($\alpha = 0.05$). Box and whisker plots show CT_{max} medians across seasons (mid line), upper and lower quartiles (box edges), as well as the maximum and minimum values (whiskers).

pronounced thermal plasticity across the months of December, March, and September. Generalist species had higher CT_{max} and greater thermal plasticity

compared to bi-seasonally active species (Fig. 2), which suggests that thermophilic ants could more easily acclimate to temperature increase, similar to aquatic beetles (Calosi et al. 2008). The invasive red imported fire ant was among the thermally plastic species, suggesting that acclimation ability is yet another trait (Bertelsmeier et al. 2017) that can contribute to the success of invasive ant species. However, native ants showed thermal plasticity comparable to that of *S. invicta* or even higher. Native ants in this community forage at temperatures unfavorable for *S. invicta* (Roeder et al. 2018) and here we show that acclimation of their CT_{max} likely allows them to maintain that advantage year-around.

In terrestrial ectotherms, CT_{max} is less plastic than CT_{min} (Hoffmann et al. 2013) and, in ants, it can be invariant along gradients of temperature (Bishop et al. 2017, Nowrouzi et al. 2018). In our study, we found both a wide range of average CT_{max} across species and seasonal plasticity within species, particularly in those active across all three seasons. The highest acclimation range was from the community's most heat tolerant species *F. pruinosus*.

Some insects exhibit plasticity of heat tolerance (Hoffmann et al. 2002, Klok and Chown 2003, Calosi et al. 2008, Slatyer et al. 2016), but these acclimation responses can vary even in closely related species. For example, a temperate Dolichoderinae ant species does not acclimate to higher temperatures (Andrew et al. 2013), unlike the invasive Argentine ant, from the same subfamily (Jumbam et al. 2008). We recorded the same pattern for the two Dolichoderinae species from our community: while CT_{max} of *D. flavus* stayed constant across the seasons, CT_{max} of *F. pruinosus* significantly increased during the summer. Within the desert specialist ant genus *Myrmecocystus*, only some species show plasticity of their lethal limits (Kay and Whitford 1978). Combined, these data suggest plasticity itself is a labile trait, and that the assumption of fixed CT_{max} , common in global studies (Sunday et al. 2012, Lancaster 2016, Diamond and Chick 2018), may underestimate the resilience of these populations to global warming.

Our working hypothesis is that seasonality in a colony's CT_{max} arises primarily after its workers are foraging, and not during the larval and pupal development. We assume workers are the ones acclimating and not the brood for a couple of reasons. First, at the end of the growing season most temperate zone ants prepare for hibernation (Kipyatkov 1993), so the December foragers likely belong to the same set of brood as the September foragers and should share the same physiological traits. Second, one of the thermally plastic ants we sampled, the winter specialist *Prenolepis imparis*, produces only a single batch of brood per year (Tschinkel 1987). If brood acclimation results in thermal plasticity, then the CT_{max} of this species would not vary seasonally, as observed in this study (Appendix S1: Fig. S1). Finally, a seasonal effect of temperature on brood development should be

carried over from the previous season, as in most cases it takes several months for brood development in temperate zone species (Kipyatkov 1995). If this were the case then summer workers should have lower CT_{max} as they were developing during the spring, which we did not observe. In some ants, however, species with higher CT_{max} require higher temperatures for brood development (Penick et al. 2017) and there is some evidence from the lab, that rearing brood at higher temperatures can produce workers with higher lethal temperatures (Oms et al. 2017). We therefore cannot rule out that our different sampling periods may have included foragers from different cohorts acclimated to available rearing temperatures.

Another explanation for the observed seasonal differences in CT_{max} could be resource availability. Many ants in our community rely on honeydew provided by sap-sucking trophobionts, whose abundance varies greatly across seasons (Price et al. 2011). The plentiful carbohydrates in honeydew not only fuel worker activity but also may increase the thermal tolerance of ants. For example, sucrose solution, acting as a proxy for honeydew, was shown to increase CT_{max} of ants in a Panamanian rainforest enabling them to forage at warmer temperatures (Bujan and Kaspari 2017). As such, we posit that an ant's peak CT_{max} should coincide with peak honeydew production (i.e., aphid abundance), but this question remains to be further tested.

Among the thermally plastic species was the invasive *S. invicta*, which shows a wide range of CT_{max} in North America when averaged across seasons and lab acclimation treatments (Verble-Pearson et al. 2015). Other invasive ant species like the Argentine ant, *Linepithema humile*, also show a certain CT_{max} acclimation to high temperatures (Jumbam et al. 2008). However, low desiccation resistance limits the spread of *L. humile* to arid and hot environments (Schilman et al. 2005, Menke et al. 2007). Thus, physiological traits like thermal tolerance (Holway et al. 2002) and desiccation resistance (Schilman et al. 2007), when combined with thermal plasticity, could be important for the global success of nonnative ants in novel climates.

The results of this study suggest that plasticity of heat tolerance in ants is caused by seasonal changes in temperatures; however, the mechanisms behind it remain unexplored. Are the recorded changes caused by the acclimation of brood or adult workers? Is resource availability in the environment mediating these physiological changes? Future studies exploring the consequences of thermal ecology, and particularly thermal acclimation, on community structure and population distribution would thus benefit from combining temporally distributed replicates of thermal tolerance with the information on foraging behavior and diet. Thermal plasticity could be a trait that offers ants, including invasive species, a competitive advantage in a warming environment. Greater attention to thermal plasticity will

doubtless yield benefits in our ability to predict population and community structure in a warming world.

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