RESEARCH ARTICLE

Characterization of the thermal tolerances of forest ants of New England

E. W. Oberg · I. Del Toro · S. L. Pelini

Abstract Characterization of thermal tolerances of ants, which are both abundant and important in most terrestrial ecosystems, is needed since thermal constraints can inform how a species may respond to local climatic change. Here we identified the thermal tolerances of 16 common ant species of the Northeastern United States and determined relationships between body size, desiccation, and thermal tolerance among species. We hypothesized that maximum heat tolerances of these species would differ and be related to body size and capacity to resist desiccation. We identified four distinct groups of species belonging to one of three subfamilies, Dolichoderinae, Formicinae, or Myrmicinae, with different maximum thermal tolerances. Group "a" had a mean thermal tolerance of approximately 43°C (±1°C), group "b" had a mean thermal tolerance of 40°C (±1°C), group "c" had a mean thermal tolerance of 38°C (±0°C), and group "d" had a mean thermal tolerance of 36°C (±0°C). Groups "a" and "d" consisted of a single species (in the subfamilies Myrmicinae and Formicinae, respectively), while groups "b" and "c" were a mix of species in the subfamilies Myrmicinae, Formicinae, and Dolichoderinae. In the subfamily Formicinae, thermal tolerance increased with body size and critical water content, a metric of desiccation tolerance. In contrast, in the subfamily Myrmicinae, higher thermal tolerance was correlated with intermediate body size and lower critical water content. These findings suggest that the two dominant subfamilies in Northeastern deciduous forests have different relationships between body size, capacity to tolerate desiccation, and thermal tolerances across species. This variation in thermal tolerance suggests that climatic change may impact species differently.

Keywords Formicidae · Climate change · Thermal tolerance · Desiccation · Body size · Water balance

Introduction

Climate change, specifically the predicted warming by as much as 7°C (Meehl et al., 2007), is likely to influence nearly all species on earth. To evaluate the impact of regional climatic change on species and communities we must first understand the physiological responses of organisms to warming. One possible approach is to focus on the study of the physiological limits of species and taxa whose changes in abundance or behavior might have the greatest consequences on ecosystem processes and biodiversity. Ants are abundant, diverse, and play major roles in ecological processes, including seed dispersal and soil movement (Hölldobler and Wilson, 1990; Folgarait, 1998; Ness and Morin, 2008). Since ants can alter vegetation composition, soil structure, and nutrient availability, they are sometimes considered

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"ecosystem engineers" (Jones et al., 1994; Folgarait, 1998; Ness and Morin, 2008), although species can differ in their consequences, with some species playing disproportionate roles in particular processes such as seed dispersal (Fisher and Cover, 2007; Lengyel et al., 2009). Here, we study the maximum thermal limits of forest ants of New England (specifically in central Massachusetts, USA) with the aim of understanding the variation in thermal tolerance limits among species in two common subfamilies (Myrmicinae and Formicinae).

When exposed to higher temperatures, ants generally respond by increasing their activity (Hölldobler and Wilson, 1990). However, all ant species have thermal maxima beyond which they are unable to forage or survive (Hölldobler and Wilson, 1990; Cerda et al., 1998), and because of this limitation in other organisms, thermal tolerance has been used to predict species' extinction risk under climatic change (Deutsch et al., 2008; Hoffmann, 2010; Sinervo et al., 2010). More specifically, Wittman et al. (2010) demonstrated ant species' thermal tolerance maxima predicted response to changes in their environment and similarly, characterizing maximum and interspecific variation in thermal tolerance of common New England ant species may provide some insight into how ant community composition and ant-mediated processes may respond to regional climatic change. Furthermore, the recognition of traits related to thermal tolerance, such as microclimate preference, body size, and desiccation tolerance (Barker and Barker, 1980; Kaspari, 1993; Schilman et al., 2007; Clémencet et al., 2010), may help explain variation in thermal tolerance and be useful for predicting the impacts of climate change when thermal tolerance data cannot be collected.

The objective of our study was to determine and compare the maximum thermal tolerances of 16 common ant species found in the Northeastern United States. We isolated ant individuals and tested each ant's maximum thermal tolerance. In addition to testing maximum thermal tolerances, we also examined physical characteristics of size and water balance to better understand heat tolerance. More specifically, we asked three questions: (1) What are the maximum thermal tolerances for ants commonly found in New England forests? (2) Do thermal tolerances differ among species? and (3) Is body size or percent water content in the body associated with a species' thermal tolerance? We hypothesized that ant species would display different thermal tolerances and that body size and percent water content would be correlated with thermal tolerance, suggesting that thermal tolerance may be dependent on the physical attributes of the species examined. This work on species' thermal tolerances is one piece of a larger puzzle we are putting together to understand ant community responses to warming.

Materials and methods

Study site and ant collection

We collected ants in June and July 2010 at the Harvard Forest, a 1,500-hectare Long Term Ecological Research site in Petersham, Massachusetts (42°31′48″N, 72°11′24″W, 300 m above sea level) located in the northern hardwood hemlock-white pine transition zone. During these 2 months, the average temperature at Harvard Forest was 20°C, and the average minimum and maximum temperatures were 15 and 26°C, respectively. We collected ants from a variety of forested and open habitats (Table 1). Upon finding each ant colony, we collected approximately 20 workers per species using an aspirator and immediately transported them back to the lab for identification and analysis. We assayed a total of 16 species in 10 genera and 3 subfamilies commonly collected in hardwood hemlock-white pine habitat (Aaron Ellison, pers. comm.): Dolichoderinae (1 genus/species), Myrmicinae (6 genera and 7 species), and Formicinae (3 genera and 8 species).

Data collection

We performed thermal tolerance assays on a minimum of eight individuals of each species within 4 h of field collection; this short time between collection and assay reduced the likelihood that individuals acclimated to laboratory temperatures. We prepared an individual for testing by placing it into a 1.5-ml microcentrifuge tube plugged with cotton. The plug limited ants from accessing the vial lid, which may have served as a thermal refuge and thus not exposed the individual to the intended experimental temperatures. Once ants were in the tubes, we randomly assigned each ant to a slot in an 8 × 6 Thermal-Lok Dry Heat Bath (USA Scientific, Orlando, Florida) pre-warmed to 38°C. We increased the temperature by 2°C every 10 min until 100% mortality was reached. At the end of each ten-minute interval, we checked the ants for survival and noted the temperature at which death or permanent muscle coordination loss occurred. Thermal tolerance was deemed the highest temperature at which an individual ant survived for the entire 10-min interval. We used a ninth tube with an ant as an unheated control.

We calculated water balance in later replicate trials. Using a Sartorius microbalance (model m2p, Sartorius AG, Goettingen, Germany) with accuracy of about 0.001 mg, we weighed ants prior to the heating treatments (hereafter "live mass"). Using the same thermal tolerance evaluation procedure described above, we then tested at least another eight individuals of each species. After the thermal tolerance protocol was replicated, we weighed the sacrificed individuals to measure moribund mass. We then dried the ants

Table 1 Ant species tested with heat tolerance, average length, number of individuals tested and traits

Species	Maximum thermal tolerance (°C)	Mean Weber's length	Standard deviation of Weber's length	Number of individuals tested	Habitat description	Characteristics/ecological function(s) (Aaron Ellison, pers. comm.)	Dominance (Fellers, 1987; Wittman et al., 2010)
Tapinoma sessile	40	0.89	0.048	16	Open field	Honeydew tender, seed disperser, carnivore	Behaviorally subordinate
Camponotus noveboracensis	40	2.48	0.452	16	Open field	Honeydew tender	Behaviorally dominant[a]
Camponotus pennsylvanicus	40	2.86	0.518	16	Forest	Honeydew tender	Behaviorally dominant[a]
Formica aserva	40	2.40	0.171	8	Open field	Slavemaker, temporary social parasite, honeydew tender, carnivore	Behaviorally dominant[a]
Formica neogagates	40	1.83	0.020	8	Open field	Honeydew tender	Behaviorally dominant[a]
Formica pergandei	40	2.17	0.126	8	Open field	Unknown	Behaviorally dominant[a]
Formica subsericea	40	2.36	0.139	32	Open field	Honeydew tender	Behaviorally dominant
Lasius alienus	36	0.91	0.103	16	Open field	Honeydew tender, seed disperser, carnivore	Behaviorally dominant
Lasius nearcticus	36	0.87	0.054	16	Forest	Honeydew tender	Behaviorally dominant[a]
Aphaenogaster rudis	38	1.60	0.082	24	Forest	Seed disperser, carnivore	Ecologically dominant (Pelini et al., 2011)
Crematogaster lineolata	44	0.96	0.117	16	Open field	Honeydew tender, carnivore	Behaviorally dominate[a]
Myrmica americana	38	1.58	0.063	8	Open field	Seed disperser	Behaviorally intermediate[a]
Myrmica punctiventris	38	1.44	0.083	8	Open field	Seed disperser	Behaviorally intermediate
Solenopsis molesta	40	0.42	0.000	16	Forest	Unknown	Behaviorally intermediate
Temnothorax longispinosus	40	0.73	0.048	8	Forest	Honeydew tender	Behaviorally subordinate[a]
Tetramorium caespitum	40	0.99	0.160	24	Open field	Unknown	Unknown

[a] Denotes inference made based on what is known about the genus and observations made of other species in the genus

for 12 h at 65°C and subsequently weighed them a final time to determine dry mass. We calculated the percentage of weight that was total water content (TWC) by subtracting dry mass from live mass, dividing by live mass, and then multiplying by 100 (Schilman et al., 2007). We found critical water content (CWC), the metric used to compare tolerance of desiccation, by subtracting dry mass from moribund mass, dividing by live mass, and then multiplying by 100 (Schilman et al., 2007).

We mounted each individual ant using standard curatorial procedure and vouchered the samples at Harvard's Museum of Comparative Zoology in Cambridge, Massachusetts. For every mounted ant, we measured Weber's length—the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum (Weber, 1938; Brown, 1953)—using a dissecting microscope at 12× magnification with 25× eyepieces and an ocular micrometer. Weber's length is known to be correlated with various other morphometric traits and so is a good variable to use when evaluating body size of ants (Nipperess and Beattie, 2004; Weiser and Kaspari, 2006).

Data analysis

We used ANOVA followed by post hoc Tukey tests for interspecific comparisons of thermal tolerance. We also used ANOVA to determine differences at the subfamily level in thermal tolerance, Weber's length, and CWC. We regressed body size and CWC values against thermal tolerance values using non-linear regression (quadratic, exponential, and logistic models); R^2 and P values are reported. In all cases we considered $P < 0.05$ as statistically significant. We used backward model selection on multiple linear regression models that included Weber's length, CWC, TWC, subfamily, and habitat type (open field or forest) as predictor variables of thermal tolerance. We tested for interactions between the predictor variables and included them in our multiple linear regression analysis. We also present AIC values to identify the best models (i.e., the lower the AIC value, the better the model fit). All analyses were completed using R software version 2.11.1 (R Development Core Team, 2007).

Results

We identified four groups of species with statistically different thermal tolerances (Fig. 1). Group "a" consisted of the Myrmicinae species *Crematogaster lineolata*, which had a mean thermal tolerance of 43.2°C and ranged from 40.0 to 44.0°C. Group "b," which had a mean thermal tolerance of 40.1°C, was the most diverse and consisted of six Formicinae species, three Myrmicinae species, and a single Dolichoderinae species (*Tapinoma sessile*). Group
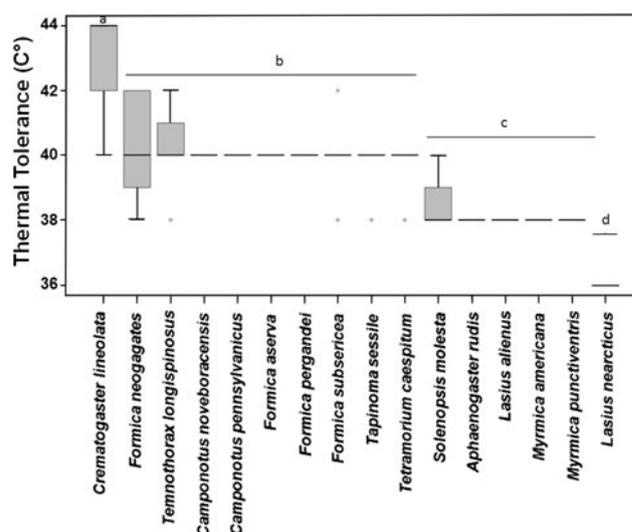

Fig. 1 Distribution of species' maximum thermal tolerances. *Boxes* indicate 75 and 25% of the distribution of the data. *Lines* with a *dash* indicate the distance between the inner quartiles and the maximum and minimum. The *bold line* in the middle indicates the median of the data. Any outliers are identified as *circles* or *dots*. Groups a, b, c, and d are significantly different ($P < 0.05$) from each other as indicated by Tukey test

"c" consisted of four species: three Myrmicinae species and a single Formicinae species that shared a thermal tolerance of 38°C. Group "d" consisted of the Formicinae species *Lasius nearcticus*, which had a thermal tolerance of 36°C, with no variation among individuals. Due to observed differences among subfamilies, subsequent analysis examined variation of species traits at the subfamily level.

In Myrmicinae, we found a quadratic relationship between Weber's length and thermal tolerance (Fig. 2a). Myrmicinae species of intermediate sizes (e.g., *C. lineolata*) were the most heat tolerant, whereas both larger and smaller ants were less heat tolerant (Fig. 2a). In these Myrmicines there was no clear relationship between Weber's length and CWC (Fig. 2c) but a relationship between CWC and thermal tolerance was observed. This trend indicated that Myrmicine ants that have higher CWC levels may have lower thermal tolerances (Fig. 2e).

In Formicinae, we observed a logarithmic relationship between thermal tolerance and Weber's length, indicating that larger ants were more heat tolerant than smaller ants (Fig. 2b). Larger Formicinae had larger CWC values (Fig. 2d). Finally, we observed a positive relationship between thermal tolerance and CWC (Fig. 2f). The finding of different relationships between physical traits (e.g., Weber's length, TWC, and CWC) and thermal tolerance levels suggests that there exists a strong interaction between the traits and the two main subfamilies considered in this study. Thus we explored these interactions further using the multiple regression models (Table 2).
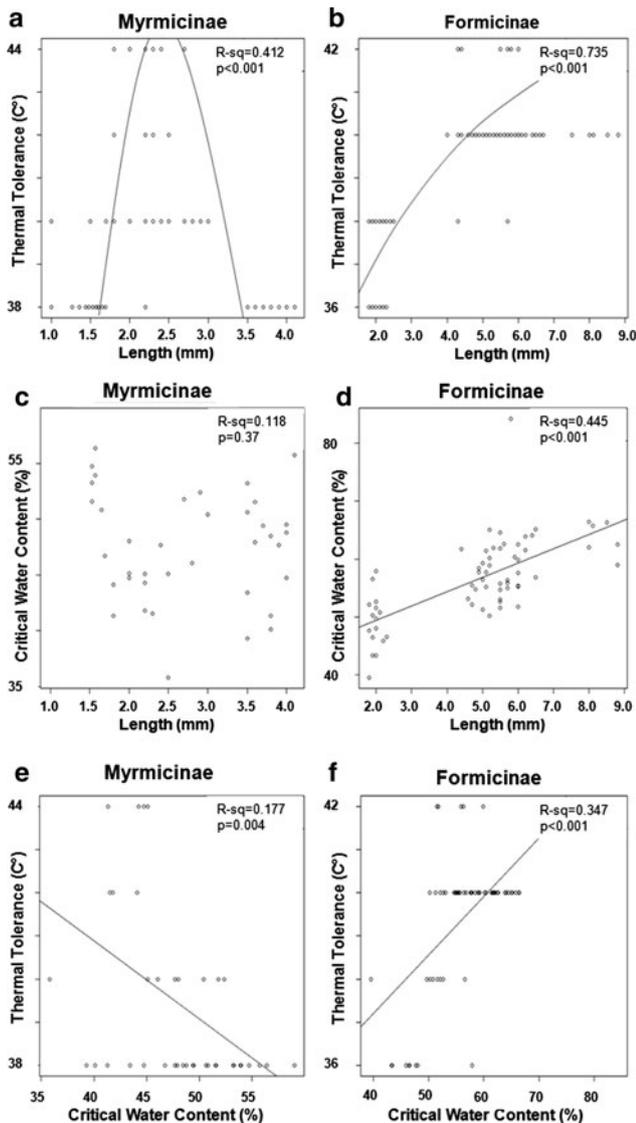
Fig. 2 Nonlinear regressions for two subfamilies Myrmicinae and Formicinae. **a** Weber's length (mm) versus thermal tolerance in Myrmicinae $F = 31.1$, $df = 84$. **b** Weber's length (mm) versus thermal tolerance (°C) in Formicinae $F = 166.4$, $df = 117$. **c** Weber's length (mm) versus critical water content (CWC) in Myrmicinae $F = 1.0$, $df = 37$. **d** Weber's length (mm) versus critical water content (CWC) in Formicinae $F = 51.6$, $df = 62$. **e** Critical water content (CWC) versus thermal tolerance (°C) in Myrmicinae $F = 9.4$, $df = 38$. **f** Critical water content (CWC) versus thermal tolerance (°C) in Formicinae $F = 34.4$, $df = 62$

Table 2 Results of backward multiple linear regression model selection, with thermal tolerance as the dependent variable, showing AIC, R^2 and P values for all models evaluated

	AIC	R^2	P
All ants			
Length + subfamily + habitat type	160.6	0.336	<0.001
Length + habitat type	192.6	0.227	<0.001
Length + subfamily	209.3	0.171	<0.001
Habitat type + subfamily	219.0	0.137	<0.001
Length: subfamily + habitat type	145.1	0.386	<0.001
Length: habitat type + subfamily	161.5	0.336	<0.001
Length + subfamily: habitat type	153.4	0.360	<0.001
Length	239.4	0.071	<0.001
Subfamily	160.5	0.001	0.345
Habitat type	160.9	0.139	<0.001
Myrmicinae only			
Length + habitat type	110	0.167	<0.001
Length: habitat type	81.2	0.409	<0.001
CWC + habitat type	37.6	0.472	<0.001
CWC: habitat type	27.6	0.598	<0.001
TWC + habitat type	38.6	0.458	<0.001
TWC: habitat type	29.0	0.584	<0.001
Length	108	0.0165	0.122
CWC	47.9	0.177	0.004
TWC	62.3	0.0224	0.356
Habitat type	47.9	0.181	<0.001
Formicinae only			
Length + habitat type	17.7	0.661	<0.001
Length: habitat type	12.1	0.679	<0.001
CWC + habitat type	34.4	0.351	<0.001
CWC: habitat type	30.7	0.415	<0.001
TWC + habitat type	57.7	0.0945	0.0181
TWC: habitat type	56.8	0.120	0.01348
Length	13.9	0.575	<0.001
CWC	35.9	0.347	<0.001
TWC	59.4	0.0611	0.02742
Habitat type	59.1	0.0961	<0.001

Results are divided into models for all ants regardless of what subfamily they belong to and models segregated by subfamily (Myrmicinae and Formicinae)

To avoid collinearity among predictors, since length, CWC, and TWC are all significantly correlated, we included only one of these variables in the regression model

Here we present the best fit predictor for each model

From the multiple regression models (Table 2), we determined that, for all ants, the best model was one that included the interaction term between Weber's length and subfamily and the additive variable of habitat type where the species was collected (AIC = 145, $R^2 = 0.39$, $P < 0.001$). Subsequent models treated each subfamily independently. In these models we included only one physical trait per model, since Weber's length, CWC, and TWC are all significantly correlated (Weber's length × TWC: $r = 0.425$, $P < 0.001$; Weber's length × CWC: $r = 0.593$, $P < 0.001$; TWC × CWC: $r = 0.631$, $P < 0.001$), to avoid collinearity among predictors. For Myrmicines, we show that the best multiple regression model was one that included only the interaction term between CWC and habitat type (AIC = 27.61; $R^2 = 0.598$; $P < 0.001$). The additive models and single variable models did not perform as well

(Table 2). For Formicines, the best multiple regression model was one that included only the interaction term between length and habitat type (AIC = 12.1; $R^2 = 0.679$; $P < 0.001$).

Discussion

We found that common ant species of the Northeastern United States differed in their maximum thermal tolerances. Variation across species in thermal tolerance suggests that climatic change will impact species differently. Deutsch et al. (2008) used the difference between maximum thermal tolerance and current temperature as a metric to understand impacts of climatic change on ectotherms around the globe and suggested that the most severely affected would be those with the smallest difference between thermal tolerance and current temperature. Similarly, Wittman et al. (2010) demonstrated that, within a community of ants, those with the lowest thermal tolerances were most sensitive to changes in abiotic conditions. Applying this concept to ants in our region, rising temperatures will be closest to the maximum thermal tolerances for the least thermally tolerant ants (e.g., groups "c" and "d" in Fig. 1), and therefore may have negative consequences for these groups. While average regional temperatures may remain below these ants' thermal tolerances, it is very likely that heat waves will increase in frequency, intensity, and duration and ants will experience temperature extremes that meet or surpass their thermal tolerance more often (Meehl et al., 2007). Ultimately, because ants are responsive to temperature, we are likely to observe changes in species distributions or local extinctions of populations. Conversely, ensuing alterations of ecological dominance patterns may benefit the more thermal tolerant species (e.g., groups "a" and "b"); for example, Pelini et al. (2011) observed an increase of *C. lineolata*, an abundant ant in Northeastern United States forests, but decreases in species evenness with their in situ minichamber warming experiment. Such changes can result in new species interactions, community reassembly, and changes in ant-mediated ecosystem processes such as nutrient cycling and productivity (Barry et al., 1995; Parmesan and Matthews, 2005).

Chown et al. (2009) demonstrated that the rate of temperature change used to determine thermal tolerance maxima affects the magnitude of the results, but this does not affect our interspecies comparison since all of the species in our study were tested using the same methodology. However, the low intraspecific variation observed in eight of the species tested may be similar to the pattern detected by Chown et al. (2009) with *Linepithema humile*. Chown et al. (2009) suggested that methods that use high rates of temperature change

may result in low variances in the thermal tolerances in the species evaluated, which can explain some of the patterns we observe with our data.

The finding of different relationships between physical traits (e.g., Weber's length and CWC, Fig. 2a, b, e, f) and thermal tolerances suggests that there exists a strong interaction between the traits and the two main subfamilies considered in this study. In our multiple regression model that considered all of the ant species in our study, the resulting R^2 value was relatively low ($R^2 = 0.386$, $P < 0.001$, Table 2), but nonetheless the model demonstrates that the thermal tolerances in both subfamilies were best predicted by including Weber's length as a predictor variable. In addition, the results from our multiple linear regression model show that, at least for the ants species in our study, ant species' thermal tolerances are correlated with habitat type as expected (Table 2) (Hölldobler and Wilson, 1990). This relationship was more obvious when we treated each subfamily independently and habitat type was interacting with either CWC (in Myrmicines) or length (in Formicines).

We believe the different trends in CWC further demonstrate that the two subfamilies use two different mechanisms to maximize thermal tolerance. The more thermally tolerant Formicinae individuals reduced desiccation stress by retaining a higher percentage of internal fluids. Conversely, the more thermally tolerant Myrmicinae individuals tolerated desiccation stress by surviving with lower percentage of water content. Schilman et al. (2007) observed both of these strategies in xeric ants of Southern California.

Our analysis suggests that for Myrmicinae, water balance and size vary with thermal tolerance, but there are likely to be other important factors involved that require further investigation (e.g., habitat type). These factors may explain how *C. lineolata* (which in our region is found in open, high temperature habitat) demonstrates an ability to tolerate fluid loss and also have a high thermal tolerance. Behavioral mechanisms (e.g., heat avoidance) not quantified in this study may also be responsible for explaining the Myrmicinae's ability to tolerate high temperatures regardless of body size.

Thermal tolerance findings help to highlight species that may be more susceptible to the negative impacts of regional climatic change and could help predict which species may become more dominant under future climate scenarios. Variation in traits, CWC being the important trait for Myrmicinae and size the important trait for Formicinae, is an important consideration for future studies analyzing ant community changes with warming; it may explain differences in species viability observed among species with similar thermal tolerance. It is important that future studies evaluate how species with relatively low thermal tolerances (e.g., Groups "c" and "d" in Fig. 1) will respond to regional

warming. Some of the species of interest may be *L. nearcticus*, *Aphaenogaster rudis*, and *M. punctiventris*, which are ecologically dominant and/or abundant species in the eastern United States (Ellison et al., 2007) but have a relatively low thermal tolerances (36 and 38°C). These species also play important roles in processes like seed dispersal, decomposition of organic matter, and soil movement, so any negative influence due to climate change on these species (e.g., changes in distributions and abundances) could potentially have cascading effects on other components of the forest ecosystem of the Northeastern United States (Lyford, 1963; Culver and Beattie, 1978; Handel et al., 1981; Zelikova et al., 2008). Additionally, future analysis should examine relationships between ants and other organisms in the forest (e.g., ant-aphid mutualism) as well as consider thermal tolerances of paired organisms. This research is necessary to obtain a more complete assessment of the overall impact of climatic change on ants and the Northeastern United States forest ecosystem and provides novel insight into the thermal tolerances of the common ants of our study region.

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