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Complex body size differences in thermal tolerance among army ant workers (*Eciton burchellii parvispinum*)

Kaitlin Baudier^a, Sean O'Donnell^{b,*}^a School of Life Sciences, Arizona State University, USA^b Biodiversity Earth & Environmental Science and Biology, Drexel University, USA

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ABSTRACT

In social insects, group members can differ in thermal physiology, and these differences may affect colony function. Upper thermal tolerance limits (CTmax) generally increase with body size among and within ant species, but size effects on lower thermal tolerances (CTmin) are poorly known. To test whether CTmin covariation with body size matched patterns for CTmax, we measured CTmax and CTmin in workers of four size-based worker subcastes in the army ant *Eciton burchellii parvispinum*. CTmax increased with worker body size as expected. CTmin showed a more complex relationship with size: the two intermediate-size subcastes (media and porters) tolerated lower temperatures than the smallest (minims) and the largest (soldiers) worker subcastes. Body-size effects on CTmax were not predictive of body-size effects on CTmin. These patterns held for colonies collected across elevations that spanned approximately 8 °C in mean annual temperature, even though high-elevation colonies had significantly lower CTmin overall. We predict *Eciton* army ant subcastes will be differentially affected by directional changes in high and low temperature extremes. Worker subcastes perform distinct but complementary roles in colony function, and differential temperature effects among subcastes could impair colony performance and negatively impact colony fitness.

1. Introduction

Species-mean thermal physiology traits, such as thermal tolerance limits, covary with local temperature conditions across continental, geographic (e.g., elevational), and even micro-habitat scales within sites (Gaston and Chown, 1999; Sunday et al., 2011; Kaspari et al., 2015; Baudier et al., 2018). However, the species-mean measures of thermal physiology and temperature sensitivities that are often used in macro-scale analyses can mask repeatable individual differences in thermal biology (Sinclair et al., 2016). For example, in eusocial insects, temperature extremes that do not exceed the species-mean thermal tolerance can still negatively impact colony fitness. Social insect workers are often differentiated into specialized subcastes that perform distinct but complementary roles in colony function (Wills et al., 2018). The weak-link hypothesis posits that if some colony members (e.g., a subcaste) differ in their vulnerability to extreme temperatures, the thermal sensitivity of the most vulnerable subcaste can constrain colony performance (Modlmeier et al., 2012; Baudier and O'Donnell, 2017). Within-colony thermal physiology variation may be an important component of climate effects on colony fitness.

Weak-link effects may occur in species of ants that have size-

differentiated polymorphic workers. Morphological subcastes can differ in thermal physiology: larger-bodied ant workers generally have higher maximum thermal tolerances (CTmax) than their smaller nest mates (Cerdá and Retana, 1997; Ribeiro et al., 2012; Verble-Pearson et al., 2015). When smaller-bodied workers are more sensitive to extreme high temperatures, colony-level selection may differentially affect the evolution of worker thermal physiology based on worker body size (Baudier et al., 2015).

Lower thermal limits, as indicated by minimum critical temperatures (CTmin), can also constrain workers' individual performance (Modlmeier et al., 2012). Little is known about the relationship of CTmin with body size. This is an important consideration because CTmax and CTmin can vary independently within and among species (Hoffmann et al., 2013; Bishop et al., 2016): the patterns of body size-effects on CTmax may not predict body size-effects on CTmin within a species. Individual nestmate differences in both CTmin and CTmax could be relevant to ant colony function (Baudier and O'Donnell, 2017). Furthermore, directional climate change appears to be driving faster and stronger shifts in low temperatures (e.g., night time temperatures) than in high temperatures, particularly at tropical sites (Frich et al., 2002; Clark et al., 2003). Developing an understanding of body size

* Corresponding author.

E-mail address: so356@drexel.edu (S. O'Donnell).<https://doi.org/10.1016/j.jtherbio.2018.10.011>

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effects on CT_{min} is important to making accurate predictions of climate change effects on ant behavior and ecology.

We asked whether upper and lower thermal physiology limits showed similar patterns of covariation with body size. To address this question, we measured CT_{max} and CT_{min} in differently-sized workers of the highly polymorphic army ant *Eciton burchellii parvispinum*. *Eciton b. parvispinum* is widely distributed in Costa Rica, mainly ranging on the Pacific slope and spanning elevations from sea level to 1650 masl (O'Donnell et al., 2011; Winston et al., 2017). The *E. b. parvispinum* worker force is divided into four morphologically and behaviorally distinct worker subcastes, from smallest to largest: minims, media, porters, and soldiers (Powell and Franks, 2005, 2006; Jaffé et al., 2007). Subcastes perform distinct tasks for their colonies. Porters are specialized for transporting large prey items, and soldiers specialize on colony defense (Powell and Franks, 2005, 2006).

We measured CT_{max} and CT_{min} from each *E. b. parvispinum* subcaste, replicated across colonies collected over the species' elevation range in Costa Rica. Because CT measures in army ants can vary among elevations (Baudier et al., 2018), we accounted for elevation effects in our analyses. We asked whether the four subcastes differed in CT_{max} and CT_{min}, and in thermal tolerance breadth (CT_{max} – CT_{min}). We assessed whether subcaste variation in CT_{max} could be used as a reliable proxy for subcaste variation in CT_{min}.

2. Materials and methods

2.1. Field collections

Thermal tolerance data were collected on *E. b. parvispinum* workers in Costa Rica. Low and high elevation forest sites were sampled both in dry-wet season transition (March–May) and in wet season (July–August) months. Collections were made at the following locations and dates: *Low elevation sites* total n = 15 colonies (275–660 masl)- Santa Rosa National Park 10.85°N, 85.64°W, 6–30 May 2016, n = 8 colonies; Maritza Biological Station 10.96°N, 85.50°W, 16–18 May 2016, n = 5 colonies; San Luis Valley Reserve, 10.26°N, 84.83°W, 3 August 2014, n = 2 colonies. *High elevation sites* total n = 22 colonies (1185–1640 masl)- Monteverde 10.31°N, 84.31°W; 9–15 July 2014, 30 March - 28 April 2016; n = 14 colonies; San Gerardo Biological Station 10.36°N, 84.78°W; 24–25 July 2014, 22–23 March 2015, 21 April–18 May 2016; n = 8 colonies. Mean annual temperatures range from approximately 19.0 °C (Monteverde) to 26.9 °C (Santa Rosa) across the elevations we sampled; however, at any given elevation, mean monthly temperature varies relatively little over the course of the year (difference between warmest and coolest month: Santa Rosa 3.1 °C, Monteverde 1.2 °C). The average daily temperature range is higher than this seasonal variation (Average monthly daytime high minus average monthly nighttime low temperature: Santa Rosa 9.7 °C, Monteverde 6.8 °C). The Santa Rosa – Monteverde site difference in average monthly high temperature (9.4 °C) was greater than the site difference in average monthly low temperature (6.4 °C) (Fig. S1).

To obtain subject ant workers, we used trail-walk encounter methods to locate *E. b. parvispinum* foraging raids (O'Donnell et al., 2007; Kumar and O'Donnell, 2009). When possible, we tracked worker ants carrying prey back to the bivouac (nest) site and we tracked colony emigrations across days to prevent re-sampling of the same colony. In cases where the bivouac site was inaccessible, raids encountered in excess of 300 m from each other within 24 h were assumed to be from different colonies, as this exceeded the longest recorded raid distances for the species (Rettenmeyer, 1963). Latitude/longitude coordinates and elevation of each colony was recorded from a hand-held GPS unit (GPSmap62, Garmin). A total of 40 worker ants were collected from each colony and assayed within 2.5 h of collection. Subject workers were collected from raid columns or from outside the bivouac at the bivouac site. We aimed to sample the full range of worker subcaste body sizes from each colony.

2.2. Thermal tolerance assays

We used standard dynamic methods for estimating thermal tolerance limits (Baudier et al., 2018; Diamond et al., 2016; Oberg et al., 2012; Ribeiro et al., 2012). Half of the workers from each colony sample (n = 20) were used for critical thermal maximum (CT_{max}) assays and the other half (n = 20) used for critical thermal minimum (CT_{min}) assays; workers were size-matched across CT_{max} and CT_{min} assays within colonies. Ants were placed individually in 1.5 mL microcentrifuge tubes stoppered with cotton. Tubes were then placed in either a digital dry heat block (Thermal-Lok 1 and Thermal-Lok 2, USA Scientific, Orlando, FL) or a digital Tropicooler® cold block (Benchtop Hot/Cold Block Incubator, Boekel Scientific, Feasterville, PA). Subject ants were either heated (CT_{max}) or cooled (CT_{min}) by 1 °C every 10 min. At the end of each 10-min interval, subject ants were assessed for mobility loss by 10 s of visual observation following light tapping. Those ants that did not show movement were considered to have surpassed their individual critical thermal limit.

2.3. Identifying worker subcastes

After thermal tolerance assays were complete, we collected all subjects into 95% EtOH. We photographed the head of each worker in the frontal plane using a digital camera mounted on a dissecting microscope. We examined the head capsule photograph of each subject worker to identify subcastes. Workers with dark (sclerotized) head capsules were categorized as minims and media. To delineate minims from media, micrometer-calibrated head width across the antennal insertions (Baudier et al., 2018) was measured from photographs using ImageJ software. For both the CT_{max} and CT_{min} collections, and in both elevation categories, there were relatively low frequencies of workers with head widths of 1.11–1.12 mm; all workers at or below 1.11 mm head width were classified as minims and larger workers with dark head capsules were classified as media. Workers with pale head capsules and non-toothed, sickle-shaped mandibles were classified as soldiers; workers with pale head capsules and flat or toothed mandibles were classified as porters.

2.4. Statistical analyses

Analyses were performed with SPSS v. 24 software. We used General Linear Models (GLM) to test for subcaste differences in CT_{max} and CT_{min}. We categorized colonies into low elevation (below 1000 masl) and high elevation (above 1000 masl) collections. We included elevation category and (colony identity nested within elevation) as predictors in the statistical models. We conducted Tukey post-hoc comparisons among for subcaste means with critical $\alpha = 0.05$. We used the interaction term (elevation category X subcaste) to test whether the pattern of subcaste differences in CT_{max} and CT_{min} depended on elevation.

To analyze differences in thermal tolerance ranges among the subcastes in each elevation zone, we used only those subject colonies where both CT_{max} and CT_{min} had been measured for a given subcaste. We subtracted each colony's mean CT_{min} from that colony's mean CT_{max} to obtain a colony-specific estimate of thermal tolerance range. We used these values as the response variable in a GLM analysis with subcaste, elevation zone, and the (subcaste X elevation zone) interaction term as predictor variables. We used Tukey post-hoc tests to identify subcastes that differed in overall mean thermal tolerance range.

3. Results

We measured head sizes and either CT_{max} or CT_{min} on a total of 1167 *E. b. parvispinum* workers. Subcastes differed in head sizes, but there was substantial size overlap between the three largest subcastes

Table 1

Results of GLM analyses testing relationships of ecological and biological covariates with thermal tolerance limits (top table: CTmax, bottom table: CTmin) for *Eciton burchellii parvispinum* army ant workers. All tests results are type III sums of squares. Predictor variables that were significantly related to variation in CT are indicated in bold text.

ANOVA table			
For CTmax			
Predictor variable	Model DF	F statistic	P-value
Elevation zone	1	0.95	0.34
Colony nested within elevation zone	33	12.3	< 0.001
Subcaste	3	24.5	< 0.001
Subcaste X Elevation zone	3	0.30	0.83
For CTmin			
Predictor variable	Model DF	F statistic	P-value
Elevation zone	1	19.2	< 0.001
Colony nested within elevation zone	16	3.1	< 0.001
Subcaste	3	21.1	< 0.001
Subcaste X Elevation zone	3	0.09	0.97

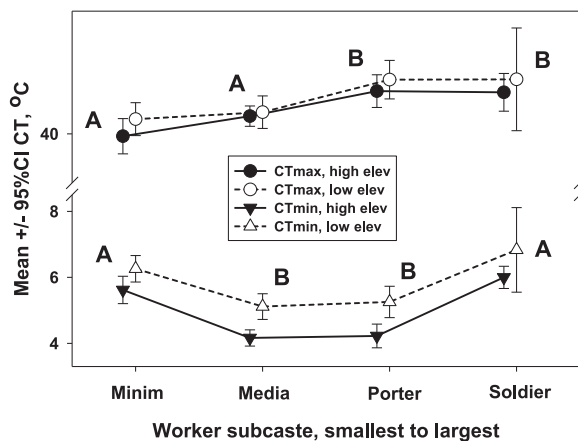


Fig. 1. CTmax (upper plots) and CTmin (lower plots) for *E. b. parvispinum* worker subcastes. X-axis (subcaste category) values for high elevation (filled symbols) and low elevation (open symbols) data points are offset for clarity. Letters represent subcaste overall means that were significantly different for CTmax and for CTmin in post-hoc comparisons (Tukey, critical $\alpha = 0.05$).

(Fig. S2; means \pm SD: minims 0.97 ± 0.11 mm, media 1.35 ± 0.18 mm, porters 1.97 ± 0.28 mm, soldiers 2.79 ± 0.35 mm; $F_{3,1163} = 1951.8$, $p < 0.001$). CTmin values ranged from 1°C to 16°C , and CTmax ranged from 33°C to 43°C . Statistic values and p-values for the analysis of variation in CTmax and CTmin are presented in Table 1 and Fig. 1 (see also Fig. S3). Both CTmax and CTmin differed highly significantly among the worker subcastes. CTmax generally increased with worker subcaste size; in contrast, CTmin was lowest for workers of intermediate size. Post-hoc analyses suggested minims and media had similar, lower CTmax and porters and soldiers had similar, higher CTmax. For CTmin the pattern was different, with minims and soldiers (the smallest and largest workers, respectively) sharing similar higher CTmin, and media and porters sharing similar lower CTmin. These patterns of differences among subcastes did not differ significantly among elevations for either CTmax or CTmin. CTmin differed significantly between the low and high elevation zones; CTmin was consistently lower in the cooler high elevation zone. CTmax did not differ significantly between elevation zones.

The subcastes differed significantly in thermal tolerance ranges (Fig. 2; $F_{3,72} = 13.5$, $p < 0.001$). Estimated thermal tolerance ranges were higher for intermediately-sized workers at both low and high elevations (Fig. 2). Post-hoc analyses (Fig. 2) suggested minims had lower thermal tolerance ranges than media and porters; porters had higher thermal tolerance ranges than both minims and soldiers.

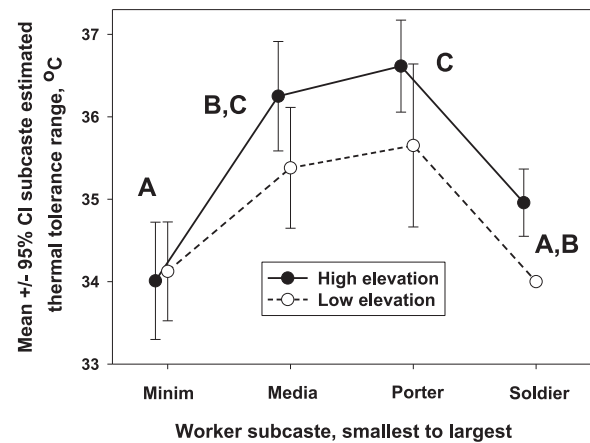


Fig. 2. Estimated thermal tolerance ranges (CTmax-CTmin) for *E. b. parvispinum* worker subcastes. X-axis (subcaste category) values for high elevation (filled symbols) and low elevation (open symbols) data points are offset for clarity. Letters represent subcaste overall means that were significantly different for thermal tolerance range in post-hoc comparisons (Tukey, critical $\alpha = 0.05$).

Thermal tolerance ranges did not differ significantly between the low and high elevation colonies ($F_{1,72} = 2.67$, $p = 0.11$). The patterns of thermal tolerance range differences among subcastes did not differ significantly among the elevation zones (Fig. 2; GLM interaction term, $F_{3,72} = 0.96$, $p = 0.42$).

4. Discussion

There were significant subcaste (body size) differences in CTmin and CTmax, but the relationships of thermal tolerance with body size were complex. As documented previously in polymorphic ants (Ribeiro et al., 2012; Baudier et al., 2015), larger workers had higher CTmax. In contrast, workers of the intermediate size subcastes had the lowest CTmin; in other words, small minims and large soldiers were most vulnerable to low temperature extremes. These subcaste differences were associated with significant subcaste differences in thermal tolerance ranges; minims had the narrowest ranges, while porters had the greatest ranges. The tolerance range values must be interpreted with caution because CTmin and CTmax were measured on different individuals, although the subjects came from the same colonies.

Consistent with the findings of a multi-species comparative analysis on army ants (Baudier et al., 2018), we found a relationship of CTmin with elevation: ants from cooler, higher elevations had lower CTmin; the pattern of the effects of elevation on CTmin did not differ among worker body sizes. However, as shown previously, CTmax did not differ between ants collected at high and low elevation sites (Baudier et al., 2018).

Critical thermal limits, as measured by limits to mobility responses, are relevant to ant colony fitness because they set the boundaries between which workers can perform tasks necessary for colony function, such as foraging and defense (Andersen et al., 2015). CTmax is often close to optimum performance temperatures (Sunday et al., 2011; Huey et al., 2012), while CTmin estimates the limit above which workers can effectively perform labor. CT measurements have proven to be predictive of species' geographic ranges, and predictive of costs associated with local temperature increases resulting from climate change (Sunday et al., 2011; Huey et al., 2012; Kellermann et al., 2012; Kaspari et al., 2014). Relative to CTmax, CTmin limits on individual performance have received relatively little empirical attention, but CTmin can be highly relevant to understanding species geographic ranges and range shifts in response to directional climate change. For example, in *Aphaenogaster* ants, biased species elevation range shifts following global warming corresponded to species differences in CTmin, but not to differences in CTmax (Warren and Chick, 2013).

5. Conclusions

Our findings demonstrate that body size effects on CT_{min} are not well-predicted by size effects on CT_{max}. CT_{max} does not serve as an adequate or straightforward proxy of CT_{min}. A complete understanding of thermal physiology variation in social insect species requires measuring both upper and lower thermal tolerances across the range of worker body sizes. The patterns we documented have important implications. We emphasize that changes in lower extreme temperatures may have important effects on worker performance, and by extension, on colony function, via weak-link effects. We predict increases in low temperature extremes will differentially enable activity for worker ants of different castes, particularly at cool high-elevation sites. Differential subcaste sensitivity to low temperatures could translate into altered colony function at high elevations at low temperatures, for example, at night. The greater vulnerability of soldiers to low temperatures could translate into impaired colony defense at the upper elevation limits of the *E. b. parvispinum* range. The predicted effects of directional climate change will be subcaste-specific, and the subcaste-specific effects will differ between changes in high versus low temperature extremes.

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Conflicts of interest

None.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.jtherbio.2018.10.011](https://doi.org/10.1016/j.jtherbio.2018.10.011).

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