



Species differ in worker body size effects on critical thermal limits in seed-harvesting desert ants (*Messor ebeninus* and *M. arenarius*)

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Abstract

Extreme temperatures can constrain foraging behavior, and individual differences in thermal tolerances may affect foraging performance within and among species. Ambient temperatures may thus mediate competitive interactions among species that share resources. Different species of desert seed-harvesting ants (genus *Messor*) forage for similar food resources, and colonies can overlap in foraging areas. Because *Messor* species differ in body size distributions, and thermal tolerance is often size related in ants, we hypothesized that body size differences within and between *Messor* species would predict individual variation in worker thermal tolerances. Body size effects on thermal physiology could have implications for interspecific competition. We measured tolerances of extreme high (maximum critical temperature or CTmax) and low temperatures (CTmin) in two *Messor* species simultaneously at the same study site, smaller bodied *M. ebeninus* and larger bodied *M. arenarius*. Although the species did not differ significantly in CTmin or CTmax, tolerance of high temperatures was significantly size dependent for *M. ebeninus*: worker tolerances of high temperatures decreased with body size in this species. The patterns suggest the foraging activity of the smallest workers of smaller bodied species could be more constrained by high ambient temperatures, which could impact the division of labor within colonies as well as interspecific interactions.

Keywords C_{max} · C_{min} · Polymorphic workers

Introduction

Species differences in thermal physiology can affect inter-specific ecological interactions. For example, when ambient temperatures approach or exceed a species' thermal limits, that species may suffer decreased competitive ability relative to more thermally robust sympatric species. In some animal communities, species partition their activity periods

depending on current thermal conditions (Cros et al. 1997; Kronfeld-Schor and Dayan 2003). The evolution of distinct species thermal physiologies is one mechanism that could favor species coexistence by reducing interspecific competition.

Desert seed-harvesting ants (genus *Messor*) are an excellent model system for testing how species differences in thermal physiology can affect resource use (Cerdeña and Retana 1994). Several *Messor* species co-occur in the northern Negev desert in Israel (Steinberger et al. 1991; Avgar et al. 2008). *Messor* species share food resources: the seeds of desert plants, with some overlap on harvesting from the same plant species (Steinberger et al. 1991). Although species' nest sites can be statistically spatially segregated on a local scale (Warburg and Steinberger 1997), nests of different species often interdigitate, and the foraging areas used by colonies of different species often overlap (Avgar et al. 2008; Saar et al. 2018b). Therefore, these desert ants confront a high potential for interspecific competition for food among congeners. We hypothesize that species differences in thermal physiology could contribute to species coexistence among Negev desert *Messor*

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ants, and that species differences in thermal physiology could play an important role in regulating *Messor* species' access to shared food resources.

Measuring thermal performance is an important first step in predicting how ambient temperatures can affect species differences in access to shared resources. Ants are small-bodied ectotherms, and ant workers do not socially thermoregulate when outside their nests. Across many environmental temperature ranges, ant workers' bodies equilibrate with ambient temperature over the course of several seconds (Kaspari et al. 2015; O'Donnell unpub. data). Ant workers are, therefore, highly sensitive to ambient thermal conditions when they are foraging for food (Segev and Ziv 2012).

Species' accessible thermal environments are bounded by low-temperature limits on activity (minimum critical temperature, or CT_{min}) and high-temperature limits (maximum critical temperature, or CT_{max}). Animals have an array of thermal performance curves that can differ within individuals: locomotion, digestion, etc. (Stevenson et al. 1985). CT measures set boundaries on organismal performance: at the extreme (high or low) temperatures where an organism loses the ability respond behaviorally, its diverse thermal performance curves effectively converge. CT measures provide a convenient bounding metric on subcaste thermal physiology differences, but low and high ambient temperatures that do not surpass CT values can negatively affect physiological performance in insects (Kaspari et al. 2015; Terblanche 2014; Sinclair et al. 2016). Therefore, CT differences can reflect individual variation in thermal physiology even at relatively moderate temperatures (Mesas et al. 2019).

Co-occurring *Messor* species differ in average worker body size and in the magnitude of size differences among nest mate workers (Segev et al. 2014). Although the relationship between body size and CT_{max} varies among ant taxa (Oberg et al. 2012), body size often correlates positively with CT_{max} both among and within ant species (Cerdá and Retana 1997; Ribeiro et al. 2012; Verble-Pearson et al. 2015; Wendt and Verble-Pearson 2016). Less is known about the relationship of CT_{min} with body size. This is an important consideration because CT_{max} and CT_{min} can vary independently within and among species (Hoffmann et al. 2013; Bishop et al. 2016): the patterns of body size effects on CT_{max} may not predict body size effects on CT_{min} within a species (Baudier and O'Donnell 2018). Body size differences in both CT_{min} and CT_{max} could affect patterns of task performance by workers, such as foraging activity times over the course of the day (Baudier and O'Donnell 2017).

To test whether sympatric *Messor* species differ in thermal physiology, we measured body size variation and critical thermal limits (CT_{min} and CT_{max}) in foraging workers of *Messor arenarius* and *M. ebeninus* in the northern Negev desert. We asked whether CT_{min} and CT_{max} differed

between species and whether CT covaried with worker body size within species.

Methods

Subject collections

We collected worker ants and conducted thermal tolerance assays at the Jacob Blaustein Institute for Desert Research in Sde Boker, Israel from 31 July to 7 August 2019 (N 30° 52' 24", E 34° 47' 35"). We surveyed the field station grounds to identify active nests of the seed-harvesting ants, *Messor arenarius* and *M. ebeninus*, recording latitude and longitude coordinates for each colony using hand-held GPS units (Fig. 1). A total of three nests of *M. arenarius* and five nests of *M. ebeninus* were used as sources of research subjects. Workers were collected from near the nest entrances with mouth aspirators. Ants were collected during early morning hours (0556 h to 0815 h local time), when most workers were returning to the nests after nighttime foraging trips. At collection, time and date were recorded, as well as ground temperature at the nest entrance using an infrared thermometer.

We collected sufficient workers each day (50–75 workers) to run simultaneous CT_{max} and CT_{min} trials on separate sets of workers from each colony. We selected workers spanning the apparent range of forager body sizes that were active at each colony. Thermal tolerance assays were initiated within 2 h of field collections to minimize the possibility of physiological acclimation by the worker ants (Oberg et al. 2012). Any collected workers that were not used in CT trials were returned to their nest entrances later the same day.

Thermal tolerance assays

On each day, we ran dynamic heat tolerance assays for CT_{max} and CT_{min} (Diamond et al. 2012; Ribeiro et al. 2012; Baudier and O'Donnell 2020) simultaneously on workers from one to two colonies. Assays were run on *M. arenarius* on August 1st, 2nd and 5th, and on *M. ebeninus* on August 4th, 6th, and 7th. During thermal assays, single workers were placed into capped 1.5-ml microcentrifuge tubes using soft forceps. A small piece of cotton was placed on the top of each tube to restrict the workers to the bottom 1.5 cm of the tube. Tubes were numbered and placed in aluminum blocks in the digital heating and cooling dry baths.

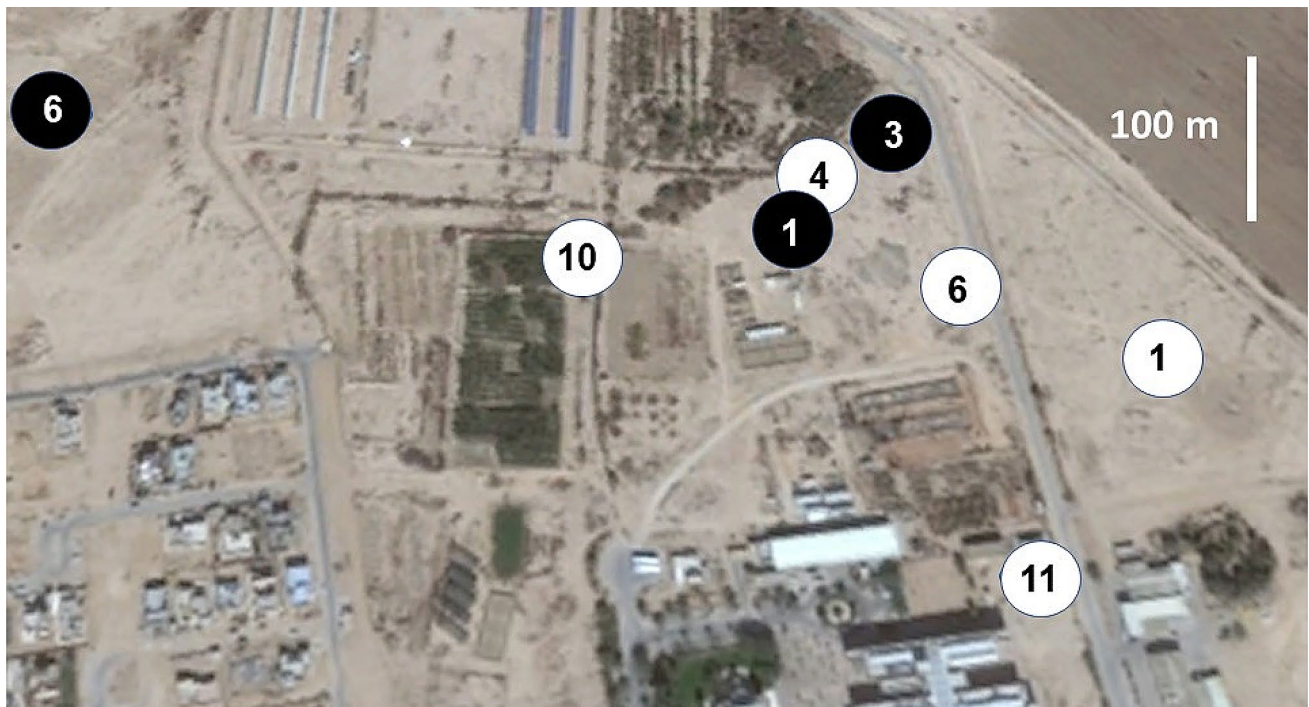


Fig. 1 Satellite image of the study area (GoogleEarth) showing the locations of the subject colony nests, with colony ID numbers indicated. Black circles: *M. arenarius*; white circles: *M. ebeninus*. Distance indicated by scale bar at upper right

CTmax assays

We used a digital dry bath (Benchmark Scientific BSH1002) to manipulate temperatures. The aluminum blocks were pre-heated to a 30 °C starting temperature. After 5 min, each ant was checked for movement by lightly tapping the tube. We then increased the temperature of the heat block by 1 °C every 5 min and checked ants for movement after each 5-min interval at the new temperature. The highest temperature at which an ant responded to tapping with movement of any body part was recorded as its behavior and mobility-based CTmax (Diamond et al. 2012; Ribeiro et al. 2012; Baudier and O'Donnell 2020). We collected CTmax data on 89 *M. arenarius* workers from three colonies and from 90 *M. ebeninus* workers from five colonies.

CTmin assays

Workers for CTmin assays were nestmates of the CTmax workers, collected and assayed simultaneously. Tubes were placed into aluminum blocks in a Tropicooler (model 260014, Boekel Scientific) pre-cooled to 15 °C. After 5 min, ants in tubes were checked for movement, and the temperature was decreased by 1 °C. The lowest

temperature at which an ant maintained movement (as above) was recorded as its CTmin. CTmin data were collected from 64 *M. arenarius* workers from three colonies, and from 65 *M. ebeninus* workers from five colonies.

Body size measurements

Head width was used as a measure of ant body size. Body mass and body length are strongly positively correlated with head width in both subject species (head width vs. body length log–log slope approximately 1.3 and linear regression $R^2 > 0.96$ in both cases; Segev et al. 2014). Immediately following completion of thermal tolerance assays, each ant head was dissected from the body at the neck-like junction with the thorax (foramen). Heads were placed individually on a plain flat surface with the foramen facing down. Heads were photographed from directly above using a tripod-mounted digital camera at 4896 × 3672 pixel resolution (Sony Cybershot DSC-TX30). A ruler was included in each photograph to use as reference during head width measurement to convert pixels to millimeters. We measured head width in pixels at the widest point of the head excluding the eyes using the straight line tool in Image J version 153 (NIH 2020).

Statistical analyses

We used SPSS v. 26 software (IBM 2019) and Sigmaplot v. 12 software to analyze the data. We attempted to represent the body size (head width) range of workers we observed at nests in the workers we assayed in each colony. We tested whether the workers sampled for CT values differed in size among colonies within each species for both the CTmax and CTmin data sets. For this analysis, we used General Linear Models (GLM) to test for colony effects (as a random factor) on \log_{10} (head width), we also tested whether head width distributions differed between the species.

We calculated the linear regression relationships of CT (max and min) with head width for each species separately. If the linear relationship was significant, we tested whether adding a curvilinear (quadratic) term to the model significantly improved fit.

To identify significant predictors of CT values, we used GLM analyses. We \log_{10} transformed head widths and CT values to improve linearity of data distributions; temperatures were converted to °K so they could be treated as scale variables. CT (max or min) values were the response variables, species identity was entered in the statistical model as a fixed factor, colony identity (nested within species) was entered as a random factor, and head width was entered as a covariate. We tested for the effects of species, colony, head width, and the (species \times head width) interaction term (ANCOVA, testing whether species differed in the slope of the relationship of CT with head width) on CT (max or min).

Results

Worker body size differences within and between species

Within species, colonies did not differ significantly in head width distributions (*M. ebeninus*: CTmin samples $F_{4,60} = 1.51$, $p = 0.21$; CTmax samples $F_{4,84} = 1.64$, $p = 0.17$; *M. arenarius*: CTmin samples $F_{2,61} = 0.80$, $p = 0.45$; CTmax samples $F_{2,86} = 0.48$, $p = 0.62$). The two *Messor* species differed in worker body size: *M. ebeninus* workers were smaller on average than *M. arenarius* workers, although there was overlap in worker sizes (Fig. 2; for the CT max samples, species size difference $F_{1,175} = 546.4$, $p < 0.001$; for the CTmin samples, species size difference $F_{1,127} = 281.4$, $p < 0.001$).

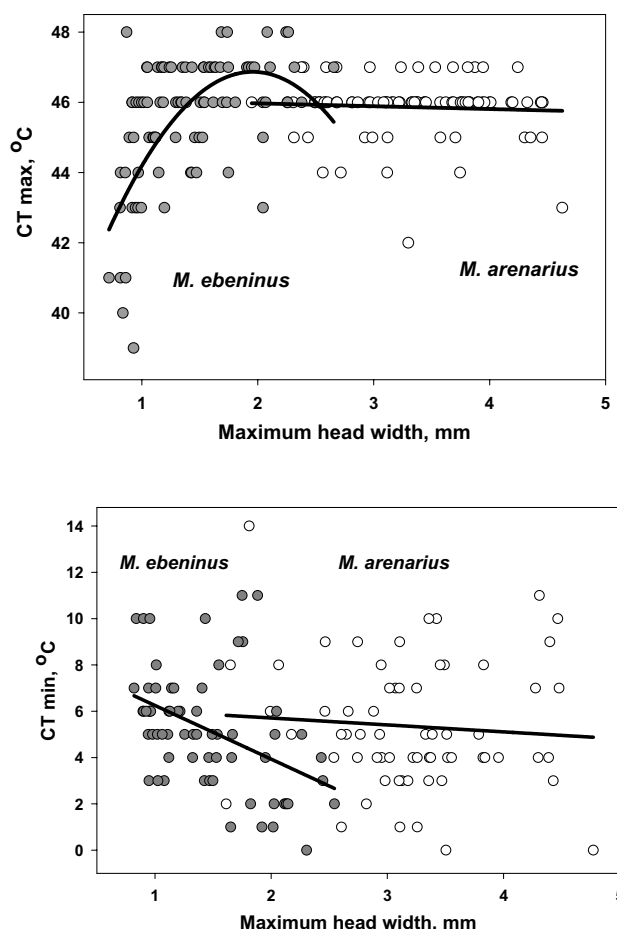


Fig. 2 Relationships of critical thermal limits (top: CTmax, bottom: CTmin) with body size for two species of seed-harvesting desert ants (grey symbols: *Messor ebeninus*; white symbols: *M. arenarius*). Best-fit linear or quadratic regressions for each species are indicated by the solid lines

Within-species body size effects on critical temperatures (CTmin and CTmax)

For the larger bodied species, *M. arenarius*, neither CTmin ($r^2 = 0.006$, $df = 62$, $p = 0.55$) nor CTmax ($R^2 = 0.004$, $df = 86$, $p = 0.57$) was significantly related to body size variation (Fig. 2).

For the smaller bodied species, *M. ebeninus*, CTmin decreased significantly with body size ($R^2 = 0.18$, $df = 63$, $p = 0.004$), but adding a quadratic term did not improve model fit ($R^2 = 0.19$; quadratic term $t = -0.47$, $p = 0.64$). *M. ebeninus* CTmax increased significantly with body size ($R^2 = 0.19$, $df = 88$, $p < 0.0001$), and the relationship was significantly curvilinear (Fig. 2; $R^2 = 0.26$, $df = 87$, $p < 0.0001$; quadratic term $t = -2.77$, $p = 0.007$).

Predictors of maximum critical temperature (CT_{max})

The species did not differ significantly in overall CT_{max} distributions ($F_{1,6} = 0.09$, $p = 0.78$). CT_{max} increased with body size ($F_{1,168} = 17.5$, $p < 0.001$) but the species slopes for the relationship of CT_{max} with head width differed (interaction term $F_{1,168} = 11.3$, $p < 0.005$). One *M. arenarius* worker was identified as a significant CT_{max} outlier (stem-and-leaf analysis, $p < 0.05$) and excluded from the analyses; including this data point did not change any of the conclusions.

Predictors of minimum critical temperature (CT_{min})

The species did not differ significantly in CT_{min} distributions ($F_{1,6} = 0.007$, $p = 0.94$). CT_{min} decreased with body size ($F_{1,119} = 14.5$, $p < 0.001$). The species had statistically similar slopes for the relationship of CT_{min} with head width (interaction term $F_{1,119} = 1.9$, $p = 0.17$).

Colony differences

Colonies differed significantly in CT_{max} values ($F_{6,168} = 6.2$, $p < 0.001$) and in CT_{min} values ($F_{6,119} = 14.6$, $p < 0.001$). Colony sample sizes were small for both species (*M. arenarius*, $n = 3$; *M. ebeninus*, $n = 5$), but there was no apparent relationship between colony mean CT_{max} and CT_{min} values for either species (Supp. Figure 1). Furthermore, the ground temperatures at the nest entrances when the ants were collected were moderate, not approaching worker CT_{max} or CT_{min} values, and ground temperature showed no apparent relationship with colony mean CT values (Supp. Figure 2).

Discussion

Species differences in size-related thermal physiology may be relevant to their ecological interactions. Although the two subject species did not differ significantly in overall mean CT_{max}, the species had different relationships of thermal tolerance with worker body size for CT_{max}. In the larger species, *M. arenarius*, worker body size did not predict CT variation. In the smaller species, *M. ebeninus*, smaller workers were less robust to extreme high temperatures. Within both species, colonies differed significantly in both CT_{max} and CT_{min} distributions. These colony differences were not caused by differences in body size distributions of the workers we sampled. Several factors could contribute to colony differences in thermal physiology, including colony age or developmental stage, short-term effects such as food intake (Bujan and Kaspari 2017), or genetic differences (Saar et al. 2018a).

We did not see evidence for temporal (or temperature-related) separation of species' activity periods during our

observations: all *Messor* species were foraging mainly at night during our data collection period, and foraging activity appeared to begin and end at similar times for the two subject species. Workers of both species, therefore, avoided the highest diurnal temperatures when foraging, minimizing the potential effects of species differences in CT_{max} on inter-specific competitive interactions. However, both species forage during the day in other seasons when temperature effects on foraging may be stronger. When examined on an annual cycle, the two species exhibit substantial phenological overlap in their above-ground activity (Steinberger et al. 1992), but on a finer scale there is a clear temporal partitioning of activity across the diel cycle. In the spring and in the fall, *M. ebeninus* is mainly nocturnal whereas *Messor arenarius* forages mainly from dawn to early morning and from later afternoon until dusk (Avgar 2007; Giladi unpublished observations). Assuming the species differences in size–physiology relationships, we measured are not seasonally dependent (Bujan et al. 2020), this pattern suggests *M. ebeninus* may avoid foraging in conditions that could challenge the most vulnerable workers.

Messor arenarius workers were uniformly thermally robust across their entire body size range, but worker size variation could be important to thermal effects on behavior and division of labor in *M. ebeninus*. Social insect workers are often differentiated into specialized subcastes that perform distinct but complementary roles in colony function (Wills et al. 2018); in worker polymorphic species such as *Messor* ants, worker behavioral specialization is often associated with body size (Segev and Ziv 2012). Different thermal sensitivities among colony members, such as size subcastes, can cause conflicts over acceptable ambient temperature conditions. The most thermally vulnerable colony members may represent physiological weak links, and they may constrain some aspects of colony performance (Baudier and O'Donnell 2017). For example, smaller *M. ebeninus* workers may have a narrower tolerated range of ambient temperatures than their larger nestmates, as well as potential interspecific competitors. The relevance of within-colony size-related differences in thermal tolerance to *M. ebeninus* colony performance is not known, but worker size variation could be adaptive for other reasons that offset the thermal vulnerability of small workers. One possibility is that the more thermally vulnerable small workers bring competitive advantages, such as the ability to harvest seeds of different (presumably smaller) sizes or species, or the ability to collect seeds from different microhabitats.

An important caveat to interpreting our results is that the data were collected during a relatively hot and dry season in the Negev desert. Physiology data from other seasons are important to collect: some ant species workers show changes in thermal tolerances over time, such as across seasons (Bujan et al. 2020). However, the body size patterns we

documented, particularly the greater thermal robustness of the larger species, accord well with findings on other ants. Several studies documented temperature-sensitive responses of the subject species well within the range bounded by the CT values. For example, Avgar (2007) found differences in running speed between *M. arenarius* and *M. ebeninus* with the former being faster overall (as might be expected based on body size) but also more temperature sensitive. The increase in running speed with ground temperature in *M. arenarius* was twice as fast as the increase in *M. ebeninus*. In another study, it was found that in both winter and summer, the range of temperatures at which *M. arenarius* visited seed baits was wider than that of *M. ebeninus* (Segev and Ziv 2012).

Two other aspects of these species' foraging behavior may be related to their temperature tolerances and to the different size-tolerance patterns. The two species differ in their degree of sociality when foraging (Avgar et al. 2008). *M. arenarius* foragers mainly exhibit solitary foraging, whereas *M. ebeninus* forages in dense columns of workers. The efficiency of *M. ebeninus* foraging depends on the simultaneous activity of many workers which experience similar environmental conditions. Both species exhibit size-matching between forager size and food item size (Segev et al. 2014), a behavior which increases foraging efficiency when colonies encounter a diverse food supply (Traniello 1989; Retana and Cerda 1994). The extent to which these species can perform size-matching across a wide range of environmental conditions may be limited by body size–physiology relationships (Segev et al. 2014).

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