

Weak links: how colonies counter the social costs of individual variation in thermal physiology

Kaitlin M Baudier¹ and Sean O'Donnell^{2,3}



Social insect nestmates often differ in thermal tolerance (the range of temperatures at which an individual functions). Worker thermal physiology can covary with body size, development, genetics and gene expression. Because colonies rely on the integration of diverse colony members, individual thermal tolerance differences can affect group performance. The weak link hypothesis states that if workers differ in thermal sensitivity, then in variable thermal environments colonies can incur performance costs due to thermal stress effects on the most thermally sensitive worker types. We discuss possible adaptive colony responses that ameliorate the costs of thermal weak links. Individual differences in thermal tolerance have profound implications for the effects of temperature variation and climate change on animal societies. Social implications of worker weak links potentially drive macroecological patterns in caste ergonomics.

Addresses

¹ School of Life Sciences, Arizona State University, Tempe, AZ, USA

² Department of Biology, Drexel University, Philadelphia, PA, USA

³ Department of Biodiversity, Earth and Environmental Science, Drexel University, Philadelphia, PA, USA

Corresponding author: Baudier, Kaitlin M. (kmbaudier@gmail.com)

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Introduction

Temperature variation is a major selective force on the physiology of biota worldwide, driving diversification across latitudes, elevations, and microhabitats [1,2,3**]. Thermal tolerance metrics of critical thermal maximum (CT_{max}) and critical thermal minimum (CT_{min}) bound the upper and lower thermal functioning range of organisms, and are frequently used to estimate physiological fitness in relation to climate change [4]. Particular attention has been paid to thermal tolerance differences among small-bodied ectotherms whose body temperatures are near ambient [5,6,7*,8,9]. Thermal tolerance metrics have been applied to assess the potential impacts of climate

change on social insect populations and communities [10–14]. We suggest an important limitation of these analyses is that they do not account for the effects of individual thermal tolerance differences within colonies.

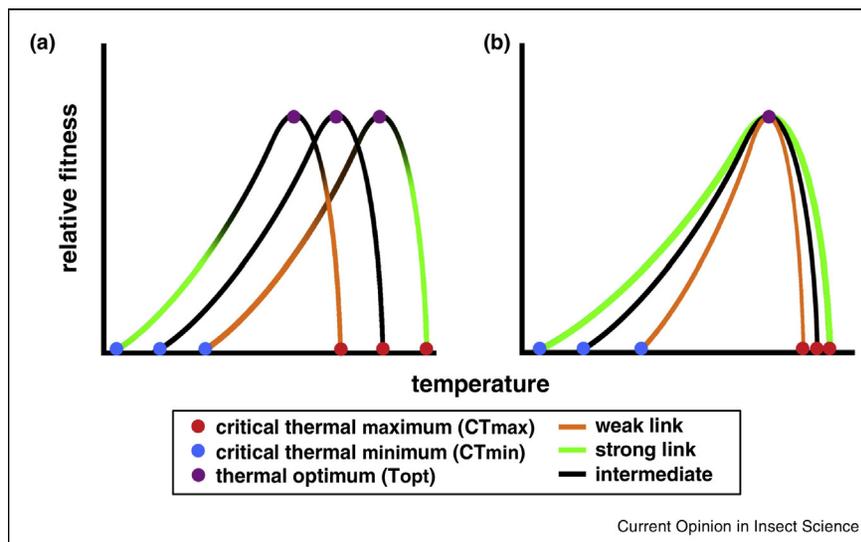
Here we show that negative fitness effects of both heat and cold stress can be amplified in social species. Improved understanding of the dynamics of thermal tolerance in colonies is important not only to predicting responses of social species to rapid anthropogenic climate change, but also to interpreting the evolution of colony structure and behavior across climate gradients.

Individual workers can differ significantly in thermal tolerance within social insect colonies; these differences can be associated with variation in body size, genetics, or developmental stage [15–19]. If the colony's thermal environment varies spatially and/or temporally, some workers can be thermally stressed while their nestmates are not. We refer to thermally vulnerable, temperature-stressed workers classes as 'weak links'. The existence of weak links can impose costs to insect societies only if the thermal environment differentially stresses subsets of workers.

The weak-link effect is an emergent property of societies, and is relevant to colony performance and colony fitness. Assuming that colonies are selected to optimize efficiency of worker force production and maintenance, and of division of labor, weak-link costs are likely unavoidable. The costs of weak links can take several forms, in part depending on how colonies behave under varying temperature conditions: costs can include production and maintenance of some inactive workers, inefficient division of labor, or loss of some workers to thermal stress. However, individual thermal tolerance differences may confer net benefits to the colony if weak-link costs can be overcome by an adaptive gain in colony performance. For example, the evolution of a new extreme-temperature tolerant worker class may allow exploitation of resources in new thermal environments. Colonies of workers with different thermal abilities potentially have access to a wider variety of temperatures than would an individual animal.

Colonies can mitigate the costs of weak-link effects using different strategies which we outline below. Some of these strategies may yield adaptive benefits that outweigh the costs of weak-link effects [20], in some cases even favoring the evolution of worker forces with diverse thermal tolerances.

Figure 1



Different types of thermal performance variation among social insect colony members; weak links are the most thermally sensitive colony members in either CT_{min} or CT_{max}, strong links are the most tolerant members in either CT_{min} or CT_{max}; (a) hypothetical for thermal specialist classes within a colony performing tasks in different thermal environments, (b) commonly-observed condition of thermal tolerance breadth differences across size-polymorphic castes or across juvenile to adult life stages within a colony.

Causes of thermal tolerance diversity within colonies

Multiple factors can cause within-colony variation in thermal tolerance. Some factors may result in differences in optimal functional temperature (favored temperature differences; Figure 1). At a given temperature, workers that are nearer their thermal optimum, or those that are not thermally stressed, can be considered “strong links”. Whether an individual worker represents a strong or a weak link can be dependent on the thermal conditions. The same colony member that is a strong link at high temperatures may be a weak link at low temperatures. Other factors may cause workers to differ in the range of tolerable temperatures (tolerance breadth differences; Figure 1). Some colony members might be relatively robust in both high and low temperature conditions.

Body size variation

Size-polymorphic worker castes are present in about 10% of ant species, including major ecological players like fire, army, and leaf cutter ants, as well as in termites [21,22]. Within polymorphic social insect colonies smaller workers generally have lower CT_{max} [17,19,23^{*}], higher CT_{min} [24], and narrow thermal tolerance breadths [3^{**}]. Small-bodied workers also have less thermal inertia, experiencing faster heating and cooling and less resistance to short duration heat stress than larger workers [3^{**}]. Thermally robust size castes likely often evolve as a byproduct of responses to other selection pressures. Large-bodied majors of *Solenopsis geminata* are thought to have evolved muscular seed-crushing heads coinciding with a dietary

shift toward granivory [25]. Similarly, the dietary shift from collecting frass to leaf-cutting in higher attines coincided with an increase in worker polymorphism, including the addition of a large worker caste to carry leaves and even larger soldiers providing colony defense [21]. Increased worker body size in *Solenopsis* and *Atta* is also associated with higher CT_{max} [17,23^{*}]. Thus thermally tolerant castes may be an incidental and unavoidable outcome of the evolution of large castes.

Genetic differences and gene expression

Within monomorphic and polymorphic species alike, genetic and epigenetic variation among colony members can cause diverse individual responses to temperature stress. Differences in heat-sensing among genetic patrines in polyandrous *Apis mellifera* colonies cause differences in thermoregulatory responses among nestmates [26]. Differences in gene expression between acclimated and non-acclimated nestmates can also affect worker responses to thermal stress [27]. Up-regulation of heat shock proteins in the Small Hsp, Hsp40, Hsp60, Hsp70, and Hsp90 families is linked to improved thermal performance among temperature-acclimated eusocial Hymenoptera [28,29^{*}]. Heat shock protein synthesis can also be induced by cold stress, aiding cellular function in both directions of extreme temperature exposure [30]. If only some workers are exposed to extreme temperatures while foraging, they may have advantages in future extreme temperature conditions over nestmates. Sequence divergence at thermally responsive loci is responsible for individual differences in thermal tolerance among solitary

insects [31], but whether and to what degree sequence divergence drives thermal tolerance variation within social insect colonies is poorly known. Individual variation in the perception of temperature can affect individuals' thresholds for responding to temperature variation, a trait associated with within-colony genetic variation [26,32,33]. Whether and how thermal perception is related to individual thermal tolerance is not known.

Developmental changes

Worker age is another important determinant of thermal tolerance among nestmates. Juvenile, young adult, and senescing individuals have different thermal tolerance ranges and acclimation response across many insect species [34]. In the harvester termite *Hodotermes mossambicus*, increasing sclerotization of the cuticle over time is associated with increased thermal tolerance breadth [18]. Similarly, workers of the army ant *Labidus praedator* have a higher CT_{min} immediately following eclosion from the pupal stage as compared to after several days of cuticle hardening [35].

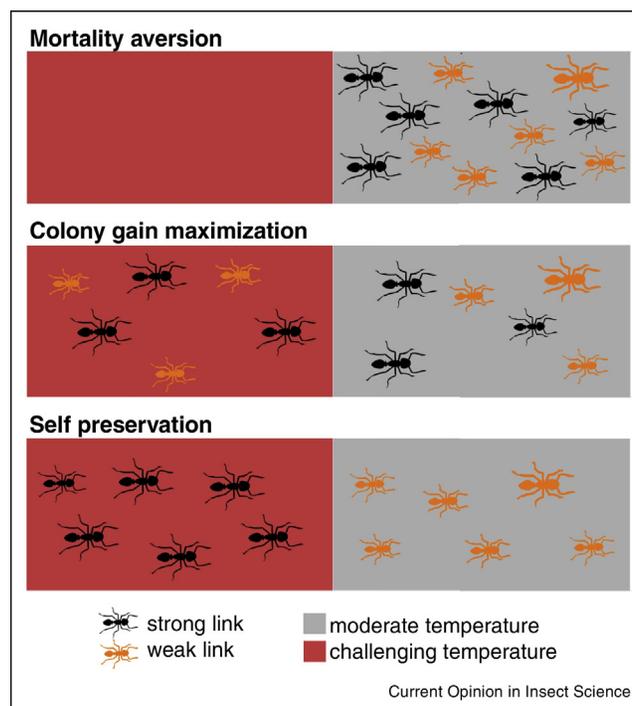
Behavioral countermeasures

A variety of colony-level pressures select for behavioral division of labor among social insects. If there are meaningful worker thermal tolerance differences in a given thermal environment, and assuming colonies are selected for efficient division of labor, weak-link workers will impose costs on colony performance. Here we propose three plausible alternative behavioral strategies social insects could employ in response to challenging thermal conditions, given weak-link pressures (Figure 2). We note the putative group-level costs and benefits of each strategy. Which strategy colonies employ will affect how social insect populations can respond to temperature variation.

1. Mortality aversion: Groups or teams of workers avoid exposure to temperatures that would stress the most sensitive workers in the group/team. If observed, this would suggest some individuals' behavioral responses to temperature are mismatched from their own physiological aptitude. The colony benefit would be protection of weak-link workers from physiological stress/mortality. The cost would be not exploiting some resources in thermal environments that are accessible to the more tolerant individuals (the strong links).

2. Colony gain maximization: Groups or teams of workers are relatively insensitive to extreme temperatures, exposing weak-link workers in the group/team to harmful thermal environments. Colony level costs of this strategy include higher risk of mortality or thermal stress of the weak-link workers. However, colonies benefit from the full worker force exploitation of resources in extreme thermal environments. Foragers of several army ant species have been observed raiding over short distances at temperatures which exceed the CT_{max} of small

Figure 2



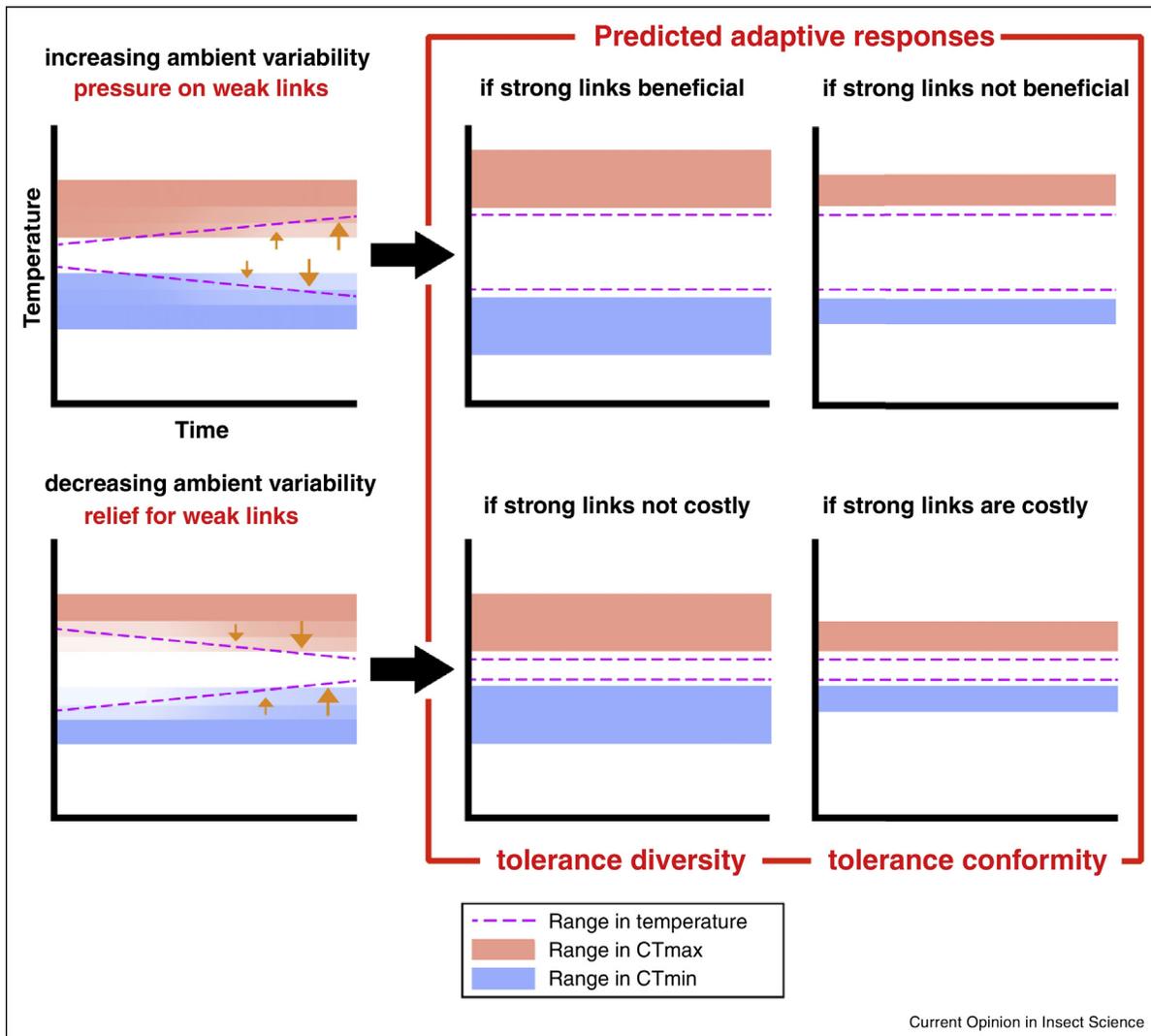
Predicted alternative behavioral response strategies to weak-link effects: Mortality aversion, Colony gain maximization, and Self preservation; within a colony orange nestmates ('weak links') are more sensitive to extreme temperature than strong link nestmates (depicted in black).

castes [36**], suggesting that this response occurs in nature.

3. Self preservation: Individuals respond to environmental temperature in a manner appropriate to their own thermal tolerance; weak links avoid working in temperatures stressful to their own physiology. This could be costly to the colony by reducing efficiency if all worker classes contribute useful labor to the tasks performed by the group/team. An example of self-preservation behavior is the evolution of especially thermally tolerant castes in desert *Cataglyphis* which exploit high-temperature resources independently of other workers, often foraging at different times of day than sensitive nestmates [15,20]. A cost to the colony is incurred because an inactive worker force is maintained under some thermal conditions.

Perhaps one of the most striking examples of behavioral self preservation in social insects is facilitated by social thermoregulation. Though many social insects are poikilotherms as individuals, homeostasis can be emergent at the colony-level [37]. Social insect colonies typically house sensitive members such as juveniles or recently molted individuals in different parts of the nest that experience less thermal variation, creating for them an

Figure 3



Predictions of weak link and strong link thermal tolerance responses to increasing and decreasing environmental variation over an evolutionary time scale.

environment to endure their sensitive developmental stages while sometimes performing specific tasks within the nest [35,37,38].

Physiological countermeasures

Over an evolutionary time scale, we predict that changes in the magnitude of extreme ambient temperatures can result in changes to selection pressure against weak-link workers (Figure 3). Examples of evolutionary timescale shifts in climatic variability include biogeographic dispersal from tropical to temperate regions, or the evolution of a canopy nesting species among a clade of ground-nesting species.

There are two key issues that affect a species' persistence in a thermal environment: thermal tolerance breadth (the

temperature range between CT_{max} and CT_{min}) and thermal tolerance diversity (variation among workers in CT_{max} or CT_{min}). While many studies have focused on thermal tolerance breadths in predicting species thermal sensitivity [5,39,40], thermal tolerance diversity is poorly understood. We suggest this diversity has high relevance for social species, where interactions among individuals with different thermal sensitivities can affect group performance.

We can also consider the potential social benefits of individuals with high CT_{max} and low CT_{min} , or "strong links." Environmental temperature challenges are less likely to affect these individuals compared to weak links, but the colony-level net benefits of producing strong-link individuals depend on both physiological and abiotic

factors. Colony production of large-caste individuals requires more nutrient provisioning [41]. Heat or cold acclimation may increase short-term survival in extreme temperatures, but it also can decrease long-term survival and reduce efficiency of task performance [42,43].

If in a given species strong links and weak links are both of net cost to the colony (for potentially different reasons), then the evolution of low thermal tolerance diversity is predicted as a result of stabilizing selection (Figure 3). If the sum colony-level benefits of both strong links and weak links outweigh their costs, then high thermal tolerance diversity is predicted. However, if colony-level costs and benefits are equal for strong links and weak links, then thermal tolerance diversity is predicted to be dependent on physiological limits due to phylogenetic constraints. There is evidence for high weak-link costs and possible net gain from strong links among surface-active Neotropical army ants [36**]. In this study, obligate below ground species of army ants encountered little diel variation in temperature and solar input relative to surface-active species. Above-ground species, which evolved from a subterranean ancestor [44,45], not only had wider mean thermal tolerance breadths, but also had lower thermal tolerance diversity than below-ground species. Body size was positively related to CT_{max} in all species sampled, but the size- CT_{max} slope was steeper in below-ground species, suggesting that weak links were more costly in variable surface environments. This partial decoupling of body size and thermal tolerance suggests factors other than size act to set thermal tolerance diversity, but that variable size also likely imposes an inherent weak-link effect.

Latitudinal gradients: linking climate and caste diversity

Latitude is the best-studied ecological cline in thermal variation. Globally, ants follow Bergman's rule of increasing body size toward high latitudes both in terms of individual worker size [46] as well as colony size [47]. According to the size-complexity hypothesis, worker size polymorphism among social insects is more likely to evolve in larger colonies [48,49], which would lead to the prediction that worker physical polymorphism in ants would be more common at high latitudes. However ant colonies are more size-polymorphic in the tropics [22]. We suggest that increasing worker size polymorphism is more likely to evolve in the tropics where environmental temperature variation pressures against weak-link castes (i.e., small bodied workers) are relieved. Ants tend to be larger in mean body size [46] as well as more uniform in size [22] in temperate regions. We propose the evolutionary loss of small bodied heat- and cold-susceptible castes accompanied the invasion of temperate latitudes: lower and more variable seasonal temperatures drove the increase in worker size and the decrease in worker size diversity.

Climate change

Anthropogenic climate change is expected to cause rapid increases in global mean temperature and in climatic variability for many regions [50,51]. Under these changing conditions weak-link individuals are the first colony members to incur physiological costs, and these costs may affect social insect colony fitness. Due to the weak-link effect, climate change costs to social species can occur before the mean critical thermal limits of a species are exceeded. These social costs are poorly assessed by previous climate change models, as standard practice is to use species means and not colony outliers to predict the impacts of directional increase and variation increase on social species.

Tropical sites experience relatively little seasonal variability in temperature. Tropical species often have narrow thermal tolerance breadths, causing them to be more vulnerable than high-latitude species to small changes in temperature [5,52]. Despite climate change being larger in magnitude at high latitudes, tropical species therefore experience more dramatic metabolic shifts than temperate and polar species [53]. Studies of ant responses to predicted warming scenarios in North America found that CT_{max} corresponded closely to species extirpation and success due to warming, particularly at lower latitudes [10]. These changes destabilized ant communities [54], even in temperate regions. Size-polymorphic tropical social insects have the added challenge of potentially magnified weak-link effects due to higher incidence of small, thermally sensitive castes.

Complications and qualifying factors

If the weak-link effect is costly for colonies, why are thermally sensitive colony members present in any environment? The presence of sensitive colony members in thermally uniform environments suggests that there is some benefit to the evolution of thermal diversity in colonies. In relatively benign thermal environments, the benefits of worker heterogeneity may outweigh weak-link costs. Heterogeneity in thermal sensitivity contributes to more stable thermoregulation in nests of *Apis mellifera* [26]. In large colonies task specialization also drives polymorphism [49], causing thermal tolerance diversity independent of thermal adaptiveness.

Although most empirical studies suggest a positive relationship between colony member body size and CT_{max} and a negative relationship between body size and CT_{min} , the exact mechanism of this relationship is the result of a wide variety of factors, some of which are understudied. This is evidenced by between-species body size relationships that contradict within-species predictions of thermal tolerance increase with body size [12,55].

Implications for future research

An important implication of the weak link hypothesis is a reevaluation of how thermal tolerance metrics predict

climate change effects on social species. Most studies investigating vulnerability of social insects to climate change base risk assessments on species and colony averages, disregarding negative effects on thermally sensitive individuals [12,14,17,56]. Models of social insect species' vulnerability to thermal stress should include metrics of colony minimum tolerance and thermal optimum diversity. Incorporating these colony-level metrics in performance assessments will increase accuracy of predictions within and among social taxa.

The general premise of the weak link hypothesis can be tested by comparative studies of social insect colonies differing in thermal tolerance diversity. Studies examining whether and to what degree these colonies differ in worker mortality or task performance under challenging thermal conditions are needed. Empirical studies testing the three behavioral predictions of weak-link pressures are also needed. Whether social species engage in *mortality aversion*, *self preservation*, or *colony gain maximization* relates to tradeoffs in altruism and task specialization. In this manner, the weak link hypothesis introduces a new level of abiotic complexity to discussions of social, biotic interactions.

A broad survey of weak-link effects across social insect taxa can be conducted via experiments that alter the thermal environment of worker tasks, observing behavioral response followed by thermal tolerance assays. Assessment of geographic and microhabitat patterns in colony size polymorphism and thermal tolerance diversity are paramount in testing if and how weak-link factors play into large scale patterns of thermal physiology. Such work would shed light on the interaction between colony size, task specialization, caste differentiation, and abiotic factors.

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