



Using Physiology to Predict the Responses of Ants to Climatic Warming

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1 Using physiology to predict the responses of ants to climatic warming

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4 Sarah E. Diamond,* Clint Penick,* Shannon L. Pelini,† Aaron M. Ellison,‡ Nicholas J. Gotelli,§

5 Nathan J. Sanders,¶ Robert R. Dunn*

6

7

8 *Department of Biology, North Carolina State University, Raleigh NC 27695

9 †Department of Biology, Bowling Green State University, Bowling Green, OH 43403

10 ‡Harvard Forest, Petersham, MA 01366

11 §Department of Biology, University of Vermont, Burlington, VT 05405

12 ¶Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN

13 37996

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21 Correspondence: Sarah E. Diamond; North Carolina State University; Department of Biology;

22 David Clark Labs, Campus Box 7617; Raleigh, North Carolina 27695-7617; Tel: 919-513-8073;

23 Fax: 919-515-5327; sarah_diamond@ncsu.edu

24 Abstract

25 Physiological intolerance of high temperatures places limits on organismal responses to
26 the temperature increases associated with global climatic change. Because ants are
27 geographically widespread, ecologically diverse, and thermophilic, they are an ideal system for
28 exploring the extent to which physiological tolerance can predict responses to environmental
29 change. Here we expand on simple models that use thermal tolerance to predict the responses of
30 ants to climatic warming. We investigated the degree to which changes in the abundance of ants
31 under warming reflect reductions in the thermal niche space for their foraging. In an eastern
32 deciduous forest system in the United States with ~40 ant species, we found that for some
33 species, the loss of thermal niche space for foraging was related to decreases in abundance with
34 increasing experimental climatic warming. However, many ant species exhibited no loss of
35 thermal niche space. For one well-studied species, *Temnothorax curvispinosus*, we examined
36 both survival of workers and growth of colonies (a correlate of reproductive output) as functions
37 of temperature in the laboratory, and found that the range of thermal tolerances for colony
38 growth was much narrower than for survival of workers. We evaluated these functions in the
39 context of experimental climatic warming and found that the difference in the responses of these
40 two attributes to temperature generates differences in the means and especially the variances of
41 expected fitness under warming. The expected mean growth of colonies was optimized at
42 intermediate levels of warming (2 – 4 °C above ambient), yet the expected variance
43 monotonically increased with warming. In contrast, the expected mean and variance of the
44 survival of workers decreased when warming exceeded 4 °C above ambient. Together, these
45 results for *T. curvispinosus* emphasize the importance of measuring reproduction (colony
46 growth) in context of climatic change: indeed, our examination of the loss of thermal niche space

47 with the larger species pool could be missing much of the warming impact due to these analyses
48 being based on survival rather than reproduction. We suggest that while physiological tolerance
49 of temperature can be a useful predictive tool for modeling responses to climatic change, future
50 efforts should be devoted to understanding the causes and consequences of variability in models
51 of tolerance calibrated with different metrics of performance and fitness.

52

53 *Keywords:* ants, climate change, fitness components, niche loss, temperature, thermal tolerance

54

55 **Introduction**

56 Global changes in land-use and climate ensure that species are increasingly likely to
57 encounter novel environments (Grimm et al. 2008). This places a renewed urgency on
58 understanding biological responses to environmental novelty. However, because these changes
59 are occurring at a global scale with potential impacts on millions of species, it is challenging to
60 develop predictions for how each species might respond. To add to the issue, recent models of
61 global biodiversity suggest that conservation planning based on the patterns of global diversity of
62 well-studied vertebrate taxa including birds, mammals, and amphibians, may not cover the
63 diversity of less-studied invertebrate taxa (Jenkins et al. in press; see also Lawton et al. 1998 for
64 similar findings at the regional scale). Together, these limits on conservation planning demand a
65 predictive framework that reduces the dimensionality of this task by identifying key
66 characteristics of those taxa and regions that are most vulnerable to climatic change. A number
67 of frameworks have been proposed for accomplishing this task (e.g., Williams et al. 2008; Huey
68 et al. 2012). Here, we focus on a promising component of these frameworks: the predictive
69 ability of physiological tolerance of extreme temperatures. We use ants as a model system

70 because they are geographically widespread, ecologically diverse, and have the potential to
71 mediate numerous functions of ecosystems (Dunn et al. 2010; Wardle et al. 2011; Zelikova et al.
72 2011).

73 We build upon previous global-scale analyses showing that despite the greater increases
74 in temperature anticipated at higher latitudes, ants inhabiting lower latitudes tend to be the most
75 vulnerable to climatic change because environmental temperatures are close to their upper
76 thermal tolerances (Diamond et al. 2012a). A pattern similar to the global pattern was
77 recapitulated between two large-scale experimental-warming arrays, positioned at the northern
78 and southern boundaries of temperate hardwood forests in eastern North America (Pelini et al.
79 2011); these chambers mimic the range of warming anticipated by the end of the century, from
80 1.5 to 5.5 °C above ambient temperatures (IPCC 2007). We found that thermal tolerance
81 predicted the responses of ants at the low-latitude site where temperatures routinely exceed the
82 upper thermal tolerances of ants—i.e., ants with low thermal tolerances experienced declines in
83 worker abundance and foraging intensity—but not at the high-latitude site where temperatures
84 remain below the upper thermal tolerances of ants (Diamond et al. 2012b; Stuble et al. 2013).

85 Temperature can have both indirect and direct impacts on fitness. In ants, increases in
86 temperature can limit the amount of time available for foraging if temperatures approach or
87 exceed the thermal tolerances of workers, with subsequent limits on colony growth. In contrast,
88 temperature can directly impact colony growth through physiological constraints on the
89 production of brood and the lifespan of workers (Porter 1988; Calabi and Porter 1989; Asano and
90 Cassill 2011). Theory suggests colony growth should be a strong correlate of fitness in ants
91 (Oster and Wilson 1979), and this has been borne out empirically, as larger colonies maintain
92 larger territories (Adams 1990; Tschinkel et al. 1995), deploy more foragers (Tschinkel 2011),

93 and have a higher probability of producing reproductives (Tschinkel 1993; Cole and Wiernasz
94 2000).

95 Here we further explore the mechanisms underlying the responses of ants to climatic
96 warming. Specifically, we examine how (1) reductions in foraging time (the amount of thermal
97 niche space for foraging that exceeds the upper thermal tolerance of an ant species) correspond
98 with changes in the abundance of ants under experimental warming, and (2) how estimates of
99 vulnerability of particular species under climatic change are altered by the choice of performance
100 or component of fitness employed, i.e. the survival of workers versus a more comprehensive
101 metric of fitness, colony growth.

102

103 **Materials and Methods**

104 *Warming chambers*

105 The details of our warming chambers are presented elsewhere (Pelini et al. 2011), but
106 briefly, the high-latitude (42° N) site at Harvard Forest and the relatively low-latitude (36° N)
107 site at Duke Forest each contain 12 open-top experimental plots (5 m in diameter). At each site,
108 nine chambers are heated by the addition of warmed air in a regression design of 0.5 °C
109 increasing intervals from 1.5 to 5.5 °C above ambient air temperature, and three chambers are
110 unheated controls. The chambers add a fixed amount of heat (according to the target amount of
111 warming), such that increases in mean temperature are achieved (target and actual differences
112 between chamber temperatures and ambient chambers are on average within 0.3 °C) without
113 alterations to the variance in temperature. Because previous work in this system showed that ants
114 are more vulnerable to climatic change (and exhibit much stronger responses to warming) at the
115 low-latitude site (Duke Forest) than at the high-latitude one (Harvard Forest), we focus

116 exclusively on Duke Forest in the analyses presented here. The chambers at Duke Forest have
117 been heated continuously since January 2010; we present data through January 2013,
118 representing three full years of warming and its impact on the performance of ants.

119

120 *Loss of thermal niche space under warming*

121 We first estimated the thermal niche using kernel density distributions of air temperatures
122 in the chambers during peak activity periods for foraging (hours 10 through 18 during the
123 reproductive season when colonies are growing: May through September). Given that we are
124 focusing on peak periods for foraging, it is likely these temperature distributions estimate the
125 available thermal niches for ants foraging in the chambers. It is possible ants are not actively
126 foraging during this entire period; therefore, we focus our analyses and interpretations on
127 alterations to the time available for foraging, rather than the time of active foraging. We then
128 calculated how much of the thermal niche was lost, specifically how much of the thermal niche
129 (computed using kernel density estimation, which disperses the mass of the empirical cumulative
130 density function over a regular grid, on the air temperatures of the warming chambers)
131 (Silverman 1986) exceeded the upper thermal tolerance of a given ant species (critical thermal
132 maximum, CT_{max} , defined as the temperature at which muscular coordination is lost; see
133 Diamond et al. [2012b] for original data and methods for estimating CT_{max}) (Figure 1 A).
134 Because the air temperature data among the different warming chambers were recorded at the
135 same times and on the same scale (hourly over the course of three years), the total areas under
136 the kernel density curves are the same, ensuring that the loss of thermal niche space can be
137 directly compared among chambers. In general, our thermal-niche-loss models assume that

138 temperature is the major driver of the activity of ants, and do not include the impacts of other
139 abiotic and biotic variables.

140 Finally, we compared the slope of the relationship between the fraction of thermal niche
141 space lost and the degree of warming in the chambers (“thermal-niche-loss slope”) with the slope
142 of the relationship between the abundance of ants (natural log transformed) and the degree of
143 warming in the chambers (“thermal-accumulation slope”). Although the thermal-accumulation
144 slope and thermal-niche-loss slope share the degree of warming as denominators, we present
145 these results as slopes to ensure equal representation among species. Qualitatively similar results
146 were obtained when examining the abundance of ants (natural log transformed) as a function of
147 the loss of thermal niche space as when examining the thermal-accumulation slope as a function
148 of the thermal-niche-loss slope; further, the similarity in results indicates that deviations from
149 linearity of the abundance of ants as a function of the degree of warming do not strongly
150 influence our results. Most species exhibit strong linear components in their responses to
151 warming in the chambers (Appendix F of Diamond et al. 2012b, but see *Temnothorax*
152 *curvispinosus*, described below), so we focus on linear rather than quadratic terms in models of
153 abundance as a function of warming to be able to compare responses among ant species.
154 Abundance data for 20 species were obtained from monthly pitfall trapping from January 2010 to
155 January 2013 in the chambers (most observations occurred during the growing season), and
156 represent the accumulation of individuals in each chamber since the beginning of heating the
157 chambers in January 2010. We expected that species with greater loss of thermal niche space
158 would have flat or negative relationships between abundance and the degree of warming in the
159 chambers.

160

161 *Survival of workers and growth of colonies under warming*

162 For one focal species, *Temnothorax curvispinosus*, we estimated the survival of workers
163 and growth of colonies as functions of temperature in the laboratory. We used Weibull functions,
164 the best-fitting functions among Gaussian and quadratic functions that were also considered
165 (AIC was the basis for comparing fits to the data; see Angilletta [2006]); when the Weibull and
166 Gaussian functions had comparable fits to the data, the Weibull was preferred owing to
167 theoretical predictions of skew in curves describing performance as a function of temperature
168 (Schoolfield 1981). The *T. curvispinosus* colonies originated from North Carolina, USA, at sites
169 near the Duke Forest experimental warming chambers. Colonies were maintained in growth
170 chambers under diurnally fluctuating thermal regimes with mean temperatures of 21, 26, and 31
171 °C for two months (each diurnal range was 10 °C; 14:10 L:D; n = 12, 11, and 12 colonies per
172 temperature treatment, respectively), after which time, we assessed both production of brood and
173 survival of workers within each colony, which served as an estimate of colony growth (see Pelini
174 et al. 2012 for original data and details on rearing ants; all colonies had queens). Both metrics
175 were expressed relative to the initial size of the colony, and the ordinate of each function was
176 determined by the maximum proportion of surviving workers or number of brood produced.

177 Although life-table analyses of ant colonies that would allow the computation of
178 comprehensive measures of fitness, i.e. net reproductive rate (R_0), are relatively nascent for this
179 taxon (Ingram et al. in press), the growth of an ant colony may serve as a useful proxy of the
180 colony's fitness. The probability that a colony will produce reproductives tends to be higher for
181 larger colonies than for smaller ones (Tschinkel 1993; Gordon and Wagner 1997; Cole and
182 Wiernasz 2000). Additionally, larger colonies may provide a buffer against environmental
183 uncertainty (Cassill 2002), and this could lead to higher lifetime fitness benefits. Regardless of

184 the precise mechanism, growth of the colony is almost certainly a more comprehensive estimate
185 of fitness than is the more often studied survival of workers.

186 We evaluated the worker-survival and colony-growth functions with the air temperature
187 data from the experimental warming chambers during the growing season (May through
188 September), available at a temporal resolution of one hour over the course of three years since
189 heating began in the chambers. The resulting distributions of expected survival of workers and
190 growth of colonies were transformed (log-inverse and square root, respectively) to meet
191 normality assumptions for estimating means and standard deviations; we present summary
192 statistics that were back-transformed to the original scale of the data. The natural history of
193 *Temnothorax* sp. ensures that air temperatures are likely to be particularly relevant for this
194 group's physiological performance because *Temnothorax* sp. lives in fallen acorns, walnuts, and
195 twigs, and is intimately tied to its nest, such that the ability of these ants to behaviorally
196 thermoregulate and avoid stressful air temperatures is limited (Mitrus 2013).

197

198 **Results and Discussion**

199 *Global and regional responses to warming*

200 Ants and several other ectothermic taxa are likely to be more vulnerable to climatic
201 change in the tropics compared with more temperate regions (Deutsch et al. 2008; Huey et al.
202 2009; Diamond et al. 2012a; but see Walters et al. 2012). These findings are contrary to previous
203 expectations that ectotherms inhabiting higher latitudes would be more vulnerable owing to the
204 greater amounts of warming anticipated in these regions. The basis of increased tropical
205 vulnerability appears to be related to biogeographic patterns in thermal adaptation; tropical
206 ectotherms have evolved in thermally invariant environments and tend to exhibit narrower ranges
207 of thermal tolerance compared with temperate and higher-latitude ectotherms (Janzen 1967;

208 Brattstrom 1968, 1970). Because tropical ectotherms experience environmental conditions
209 already close to their thermal optima and upper thermal tolerances, even small increases in
210 environmental temperature can lead to population decline or extirpation (Deutsch et al. 2008).

211 Interestingly, this global pattern of increased vulnerability of species living closer to the
212 equator appears to hold even among sites at higher and lower latitudes within the temperate zone.
213 The responses of ants to experimental climatic warming suggest that those from lower temperate
214 latitudes are more vulnerable to warming compared with those from higher temperate latitudes.
215 At our low-latitude site, the critical thermal maximum (CT_{max} , an ecologically relevant metric of
216 thermal tolerance based on the survival of workers in our study) predicted both general activity
217 (Diamond et al. 2012b) and foraging activity (Stuble et al. 2013), such that species with lower
218 CT_{max} values were less abundant and exhibited reduced foraging activity in the warmest
219 experimental chambers. Air temperatures in the warmest experimental chambers can exceed the
220 CT_{max} values of some ant species, but the question arises as to how much of the thermal niche
221 space is lost for the species inhabiting the chambers, and whether this relates to changes in their
222 abundance when subjected to warming?

223

224 *Loss of thermal niche space under warming*

225 Here, we quantified the relationship between the degree of the thermal niche space lost
226 (i.e. how much of the temperature distributions of the chambers exceeded the CT_{max} of a
227 particular ant species) and the changes in abundance of ant species under the experimental
228 manipulations of temperature (Figure 1 B, C). Our models of thermal niche loss are a measure of
229 the reduction of the time available for foraging. Reductions in available foraging time could
230 contribute to reductions in colony performance by reducing the quantity or quality of food
231 retrieved. Reductions in thermal niche space might also lead to an increase in competition since

232 there is less thermal space in which organisms can distribute their activity (Urban et al. in press).
233 Interestingly, even with 5.5 °C of warming, we found that the majority of the 20 species we
234 examined experienced no loss of thermal niche space. However, of the 35% of species that
235 exhibited significant losses of thermal niche space, 71% exhibited significant or trending
236 declines in abundance with experimental warming (Figure 1 C). Thus, for some species with low
237 thermal tolerances, the loss of thermal niche space can be sufficient to drive reductions in
238 foraging and potentially in colony size. It is important to note that these models were constructed
239 with survival-based CT_{max} , and temperature can have differential impacts via different
240 components of performance and fitness. How warming impacts not only survival, but other
241 components of fitness, particularly reproduction, is an important, but open, question in many
242 systems.

243

244 *Impacts of warming via different fitness components*

245 Estimates of tolerance frequently are based on proxies or components of fitness such as survival,
246 body size, or development time. Few estimates of tolerance are based on more comprehensive
247 metrics such as net reproductive rate (R_0) and intrinsic rate of increase (r), largely owing to the
248 practical limits of obtaining these data (Ingram et al. in press). For example, ideally our models
249 of thermal niche loss would be calibrated with more comprehensive metrics of fitness rather than
250 the survival of workers, but only data on survival are presently available to cover the diversity of
251 ant species present in the experimental warming chambers. Yet importantly, in some cases these
252 more comprehensive metrics of tolerance can have narrower ranges compared with other metrics
253 such as survival (reviewed by Angilletta 2009; Kingsolver et al. 2011). Because many estimates
254 of vulnerability to climatic change are based on survival, we may be misestimating potential
255 impacts: survival functions can determine conditions that are immediately lethal, but populations

256 may stop growing before lethality is reached (i.e. when $R_0 < 1$ or $r < 0$), which over time can
257 contribute to local extirpation.

258 We used the acorn ant, *Temnothorax curvispinosus*, to illustrate how estimates of
259 vulnerability to climatic change might be altered by the choice of tolerance metric used in the
260 context of a colonial ectotherm. *Temnothorax curvispinosus* is a relatively heat-tolerant ant, with
261 a mean CT_{max} of 43.4 °C (using a dynamic-temperature ramping method of assessing thermal
262 tolerance) (Diamond et al. 2012b). As a consequence, this species experienced no reductions in
263 thermal niche space under experimental climatic warming (Figure 1 B). From ant colonies reared
264 in the laboratory under different thermal treatments (Pelini et al. 2012), we were able to estimate
265 the survival of workers and the growth of colonies, a more comprehensive metric of fitness
266 related to R_0 (see above), as functions of temperature. We found that the worker-survival
267 function lies outside the function that describes the growth of colonies; indeed, on the warm end
268 of the function, the upper tolerances of these two attributes differed by 8.3 °C (colony growth
269 $CT_{max} = 34.1$ °C; survival $CT_{max} = 42.4$ °C, an estimate that is relatively close to that using the
270 dynamic-temperature method presented above; Figure 2 A). *Temnothorax curvispinosus* thus
271 appears to survive much higher temperatures than those that colony growth of colonies.

272 When we used these functions to examine the distribution of survival of workers and of
273 growth of colonies in the context of the environmental temperatures in our experimental
274 warming chambers, we found that while expected mean survival began to decline sharply in only
275 those warming chambers that were > 4 °C above ambient conditions (Figure 3 A), expected
276 mean growth of colonies exhibited a somewhat different pattern, with chambers having moderate
277 amounts of warming (2 – 4 °C) yielding the highest growth, and very cool and very warm
278 chambers yielding the lowest growths (Figure 3 B). Because the absolute range of temperatures

279 during the growing season across all chambers (5.9 – 41.5 °C) falls within the limits of the
280 survival function (3.8 – 42.4 °C), the decrease in expected mean survival would appear to result
281 from the skewness of the function, i.e. that survival declines more rapidly on the warm end of the
282 curve above the optimal temperature for survival than on the cool end (Figure 2 A). For expected
283 mean growth, both skewness (again, decreasing more steeply at temperatures higher than the
284 optimum) and breadth—optimal temperatures not being frequently reached in the cool chambers
285 (minimum temperature for colony growth was estimated at 11.6 °C) or being frequently
286 exceeded in the warm chambers (maximum temperature for colony growth was estimated at 34.1
287 °C)—appear to result in moderate amounts of warming leading to the greatest growth.

288 Interestingly, the pattern for expected mean growth of colonies as a function of the
289 degree of warming in the chambers was more functionally similar (optimized at intermediate
290 amounts of warming) to the pattern of observed abundances in the chambers (Figure 3 A,C)
291 compared with expected mean survival, which decreased only at very high levels of warming
292 (Figure 3 B). Principal components (PC) analysis using different amounts of warming as ‘traits’
293 and different types of performance curves as ‘replicates’ revealed that the loadings on PC1 were
294 all of the same sign when comparing the spline fits of colony growth and abundance as functions
295 of warming, but the loadings on PC1 changed signs (both from low to intermediate temperatures
296 and intermediate to high temperatures) when comparing the spline fits of survival and abundance
297 as functions of warming, indicating more substantial differences in curve shape in the latter case
298 (see Izem and Kingsolver 2005 for details of the modeling approach). The similarity in colony
299 growth and abundance patterns as functions of warming suggests that the pitfall trapping method
300 of estimating performance may in fact capture more inclusive metrics of performance such as
301 colony growth. This result is somewhat surprising given the inherent differences between our

302 field and laboratory experiments of ant responses to warming, particularly the differences in
303 timescale (three years of warming in the field versus two months in the laboratory). The field
304 results represent the impacts of warming throughout the colony-growth season and
305 overwintering, whereas the laboratory results represent only the impacts throughout a portion of
306 the colony-growth season. It is perhaps encouraging that the field and laboratory results are in
307 agreement for the responses of *T. curvispinosus* to warming; however, in general, more research
308 is needed on the mechanisms underlying organismal responses to warming throughout ontogeny
309 (e.g. Williams et al. 2012).

310 In contrast to the variance in expected survival which decreased along with decreases in
311 expected mean survival in the warming chambers, the variance in expected colony growth
312 increased with greater warming (Figure 3 A, B). Indeed, while there are more frequent
313 opportunities for achieving the highest levels of colony growth in the warmest (+ 5.5 °C)
314 chamber, *T. curvispinosus* is expected to even more frequently experience temperatures at which
315 the colony cannot grow, leading to an overall reduction in expected mean colony growth in the
316 warmest chambers (Figure 2 C, D). Further, because the experimental chambers alter the mean,
317 but not the variance, of environmental temperature, the anticipated increases in temperature-
318 variance with global climatic change (IPCC 2007) may exacerbate the current pattern of
319 increased variance in expected fitness for *T. curvispinosus*, and possibly for other species.

320 *Temnothorax curvispinosus* and the many other species in the genus *Temnothorax*
321 represent somewhat unique cases because their entire colonies are exposed to changes in surface
322 temperature since they nest inside acorns, walnuts, or twigs on the forest floor. This constraint
323 should also be present in ants that nest arboreally, but ground-nesting species generally have
324 more depth to thermoregulate by transporting brood deeper underground to escape excessive

325 temperatures at the surface (e.g. Penick and Tschinkel 2008). While these species should be
326 buffered from negative effects of warming outside their nests, thermophilic species may be able
327 to take advantage of surface-warming by tracking higher temperatures inside their nests to
328 produce brood earlier in the season or to expand the amount of time that optimal brood-rearing
329 temperatures are present at some depth inside their nests. Future work is needed to determine
330 how species with different nesting habits and different temperature preferences for rearing of
331 brood may respond to warming.

332 One component currently missing from these analyses is how generation time varies as a
333 function of temperature. For social ectotherms, generation time may be related to both the age
334 when reproductives are first produced (the ergonomic phase of colony growth, after Oster and
335 Wilson 1979) and to the lifespan of the queen (Ingram et al. in press). While individual workers
336 might be relatively short lived, queens—the functional reproductive unit for social ectotherms—
337 exhibit considerable variability in lifespan, extending from several months of age to nearly 30
338 years (Keller 1998). In addition, the rate of the colony's growth should affect the duration of the
339 ergonomic phase; faster colony growth should correlate with decreases in the amount of time
340 required before the first reproductives are produced. For ants, and perhaps for other social
341 ectotherms, one way to cope with the large variance in generation time is to estimate the
342 longevity of colonies based on other physiological and demographic parameters (Shik et al.
343 2012); however, these models still need to be expressed within a temperature-dependent
344 framework.

345 Because temperature affects the fitness metrics r (intrinsic rate of increase) and R_0 (net
346 reproductive rate) differently owing to generation time (Huey and Berrigan 2001), and because
347 the incorporation of generation time into models of the vulnerability of ectotherms to climatic

348 change has been suggested to produce qualitatively different results from models lacking this
349 component (Walters et al. 2012), estimating generation time is especially important. Our
350 analyses from ants, and others from ectotherms more generally, indicate greater vulnerability in
351 the tropics (Deutsch et al. 2008; Huey et al. 2009; Diamond et al. 2012a). However, Walters et
352 al. (2012) recently suggested that the increased turnover (i.e., shorter generation time) in warmer
353 regions could recoup this increased vulnerability, particularly because shorter generation times
354 could speed adaptive evolution, allowing tropical ectotherms to respond sufficiently rapidly to
355 warming despite their thermal specialization and reduced genetic variation. From the perspective
356 of conservation planning, the qualitative differences in predictions for large-scale regional
357 vulnerability of ectotherms to climatic change is far from ideal, and points to the need to
358 integrate ecological and evolutionary models.

359

360 *Conclusions*

361 In this study, we expanded upon previous work in this system which established a strong
362 positive relationship between changes in the abundance of ants under warming and their upper
363 thermal tolerances. Specifically, we examined the relationship between temperature and
364 performance both in context of alterations to the thermal niches for foraging under experimental
365 climatic warming, and how the choice of tolerance metric—the survival of workers versus a
366 more comprehensive fitness metric, colony growth—influenced expected fitness under warming.
367 Here, we provide results that suggest the loss of thermal niche space for foraging among 20 ant
368 species at one site is somewhat related to decreases in abundance with experimental climatic
369 warming, but that we may be underestimating the loss of niche space when calibrating models
370 with the survival of workers rather than colony growth. In support of this idea, we found that for

371 one well-studied species, the range of thermal tolerance for the survival of workers was much
372 broader than for the growth of colonies. Further, this difference in the range and shape of the
373 relationship between fitness components and temperature induced differences in expected means
374 and variances of fitness under warming.

375 We suggest that understanding how physiological performance is influenced by current
376 and anticipated changes in temperature can serve as a useful baseline model (the focus of our
377 study), with additional effort directed at understanding how this relationship is moderated by
378 physiological acclimation, adaptation, behavior, and alterations to the biotic background (see
379 Table 1 for a summary of the components of thermal-tolerance models for the responses of
380 ectothermic species to climatic warming). Indeed, the models that we explored in this study
381 assume thermal tolerances to be fixed, yet tolerances can be altered via acclimation, adaptive
382 evolutionary responses, or may fail to fully capture organismal vulnerability in the face of
383 behavioral compensatory responses. Further, our models are based on air temperatures rather
384 than on body temperatures, yet in some cases air temperatures may be poor indicators of
385 environmental pressures, as body temperatures can differ substantially from air temperatures
386 (Table 1). Improving estimates of relevant environmental parameters and of components of
387 fitness along environmental gradients will often necessarily trade off with research effort and
388 investment; however, to be able to assess the most useful predictors of the responses of species
389 to climatic change, detailed estimates both of the environment and of organismal responses are
390 critical. We concur with recent calls for increased physiological and demographic data for
391 ectothermic species inhabiting the tropics and lower temperate zone where the impacts of
392 warming may be the greatest, and for which we have the fewest data.

393

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407

408 **References**

- 409 Adams ES. 1990. Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries
410 in colony size. *Anim Behav* 39:321-328.
- 411 Angilletta MJ. 2006. Estimating and comparing thermal performance curves. *J Therm Biol*
412 31:541–545.
- 413 Angilletta MJ. 2009. *Thermal Adaptation: a theoretical and empirical synthesis*. Oxford: Oxford
414 University Press.
- 415 Asano E, Cassill DL. 2011. Impact of worker longevity and other endogenous factors on colony
416 size in the fire ant, *Solenopsis invicta*. *Insect Soc* 58:551-557.

- 417 Bonebrake TC, Deutsch CA. 2012. Climate heterogeneity modulates impact of warming on
418 tropical insects. *Ecology* 93:449–455.
- 419 Brattstrom BH. 1968. Thermal acclimation in anuran amphibians as a function of latitude and
420 altitude. *Comp Biochem Physiol* 24:93-111.
- 421 Brattstrom BH. 1970. Thermal acclimation of Australian amphibians. *Comp Biochem Physiol*
422 35:69-103.
- 423 Calabi P, Porter SD. 1989. Worker longevity in the fire ant *Solenopsis invicta*: ergonomic
424 considerations of correlations between temperature, size and metabolic rates. *J Insect*
425 *Physiol* 35:643-649.
- 426 Cassill D. 2002. Yoyo bang: a risk-aversion investment strategy by a perennial insect society.
427 *Oecologia* 132:150–158.
- 428 Cole B, Wiernasz D. 2000. Colony size and reproduction in the western harvester ant,
429 *Pogonomyrmex occidentalis*. *Insect Soc* 47:249-255.
- 430 Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008.
431 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Nat Acad Sci*
432 USA 105:6668-6672.
- 433 Diamond SE, Sorger DM, Hulcr J, Pelini SL, Del Toro I, Hirsch C, Oberg E, Dunn RR. 2012a.
434 Who likes it hot? A global analysis of the climatic, ecological, and evolutionary
435 determinants of warming tolerance in ants. *Glob Change Biol* 18:448–456.
- 436 Diamond SE, Nichols LM, McCoy N, Hirsch C, Pelini SL, Sanders NJ, Ellison AM, Gotelli NJ,
437 Dunn RR. 2012b. A physiological trait-based approach to predicting the responses of
438 species to experimental climate warming. *Ecology* 93:2305–2312.

- 439 Dunn RR, Guenard B, Weiser MD, Sanders NJ. 2010. Global ant diversity and conservation:
440 Geographic gradients. In: Lach L, Parr CL, Abbott KL, editors. *Ant Ecology*. Oxford:
441 Oxford University Press.
- 442 Gilman SE, Wethey DS, Helmuth B. 2006. Variation in the sensitivity of organismal body
443 temperature to climate change over local and geographic scales. *Proc Nat Acad Sci USA*
444 103:9560–9565.
- 445 Grimm NB, Faeth S, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM. 2008. Global
446 change and the ecology of cities. *Science* 3019:756–760.
- 447 Gordon DM, Wagner D. 1997. Neighborhood density and reproductive potential in harvester
448 ants. *Oecologia* 109:556-560.
- 449 Huey RB, Berrigan D. 2001. Temperature, demography, and ectotherm fitness. *Am Nat* 158:
450 204–210.
- 451 Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Perez HJA, Garland T. 2009. Why
452 tropical forest lizards are vulnerable to climate warming. *Proc R Soc B* 276:1939-1948.
- 453 Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012. Predicting
454 organismal vulnerability to climate warming: roles of behaviour, physiology and
455 adaptation. *Phil Trans R Soc B* 367:1665–1679.
- 456 IPCC. 2007. *Climate change 2007: the physical science basis*. Cambridge: Cambridge University
457 Press.
- 458 Ingram KK, Pilko A, Heer J, Gordon DM. In press. Colony life history and lifetime reproductive
459 success of red harvester ant colonies. *J Anim Ecol*.
- 460 Izem R, Kingsolver JG. 2005. Variation in continuous reaction norms: quantifying directions of
461 biological interest. *Am Nat* 166:277-289.

- 462 Jenkins CN, Guénard B, Diamond SE, Weiser MD, Dunn RR. In press. Conservation
463 implications of divergent global patterns of ant and vertebrate diversity. *Divers Distrib.*
464 Janzen DH. 1967. Why mountain passes are higher in the tropics. *Am Nat* 101:223–249.
- 465 Kearney M, Shine R, Porter WP. 2009. The potential for behavioral thermoregulation to buffer
466 “cold-blooded” animals against climate warming. *Proc Nat Acad Sci USA* 106:3835-
467 3840.
- 468 Keller L. 1998. Queen lifespan and colony characteristics in ants and termites. *Insect Soc*
469 45:235-246.
- 470 Kingsolver JG, Woods HA, Buckley LB, Potter KA, MacLean HJ, Higgins JK. 2011. Complex
471 life cycles and the responses of insects to climate change. *Integr Comp Biol* 51:719–732.
- 472 Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond PM, Hodda M, Holt
473 RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD. 1998. Biodiversity
474 inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*
475 391:72-76.
- 476 Mitrus S. 2013. Cost to the cavity-nest ant *Temnothorax crassispinus* (Hymenoptera:
477 Formicidae) of overwintering aboveground. *Eur J Entomol* 110:177–179.
- 478 Oster GF, Wilson EO. 1979. *Caste and ecology in the social insects*. Princeton, NJ: Princeton
479 University Press.
- 480 Pelini SL, Diamond SE, MacLean H, Ellison AM, Gotelli NJ, Sanders NJ, Dunn RR. 2012.
481 Common garden experiments reveal uncommon responses across temperatures, locations,
482 and species of ants. *Ecol Evol* 2:3009-3015.

- 483 Pelini SL, Bowles FP, Ellison AM, Gotelli NJ, Sanders NJ, Dunn RR. 2011. Heating up the
484 forest: opentop chamber warming manipulation of arthropod communities at Harvard and
485 Duke Forests. *Methods Ecol Evol* 2:534–540.
- 486 Penick CA, Tschinkel WR. 2008. Thermoregulatory brood transport in the fire ant, *Solenopsis*
487 *invicta*. *Insect Soc* 55:176-182.
- 488 Porter SD. 1988. Impact of temperature on colony growth and developmental rates of the ant,
489 *Solenopsis invicta*. *J Insect Physiol* 34:1127-1133.
- 490 Schoolfield RM, Sharpe PJH, Magnuson CE. 1981. Non-linear regression of biological
491 temperature-dependent rate models based on absolute reaction-rate theory. *J Theor Biol*
492 88:719–731.
- 493 Shik JZ, Hou C, Kay A, Kaspari M, Gillooly JF. 2012. Towards a general life-history model of
494 the superorganism: predicting the survival, growth and reproduction of ant societies. *Biol*
495 *Lett* 8:1059-1062.
- 496 Silverman BW. 1986. *Density Estimation*. London: Chapman and Hall.
- 497 Somero GN. 2010. The physiology of climate change: how potentials for acclimatization and
498 genetic adaptation will determine ‘winners’ and ‘losers’. *J Exp Biol* 213:912-920.
- 499 Stuble KL, Pelini SL, Diamond SE, Fowler DA, Dunn RR, Sanders NJ. In press. Foraging by
500 forest ants under experimental climatic warming: a test at two sites. *Ecol Evol*.
- 501 Tschinkel WR. 1993. Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta*
502 during one annual cycle. *Ecol Monogr* 63:425-457.
- 503 Tschinkel WR, Adams ES, Macom T. 1995. Territory area and colony size in the fire ant
504 *Solenopsis invicta*. *J Anim Ecol* 64:473-480.

- 505 Tschinkel WR. 2011. The organization of foraging in the fire ant, *Solenopsis invicta*. *J Insect Sci*
506 11:1-30.
- 507 Tylianakis JM, Didham RK, Bascompte J, Wardle DA. 2008. Global change and species
508 interactions in terrestrial ecosystems. *Ecol Lett* 11:1351-1363.
- 509 Urban MC, Tewksbury JJ, Sheldon KS. In Press. On a collision course: competition and
510 dispersal differences create no-analogue communities and cause extinctions during
511 climate change. *Proc R Soc B*.
- 512 Walters RJ, Blanckenhorn WU, Berger D. 2012. Forecasting extinction risk of ectotherms under
513 climate warming: an evolutionary perspective. *Func Ecol* 26:1324–1338.
- 514 Wardle DA, Hyodo F, Bardgett RD, Yeates GW, Nilsson MC. 2011. Long-term aboveground
515 and belowground consequences of red wood ant exclusion in boreal forest. *Ecology*
516 92:645-656.
- 517 Williams CM, Hellmann J, Sinclair BJ. 2012. Lepidopteran species differ in susceptibility to
518 winter warming. *Climate Res* 53:119-130.
- 519 Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G. 2008. Towards an integrated
520 framework for assessing the vulnerability of species to climate change. *PLoS Biol*
521 6:e325.
- 522 Zelikova TJ, Sanders NJ, Dunn RR. 2011. The mixed effects of ants on above and belowground
523 processes in a temperate forest. *Ecosphere* 2:63.
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528 **Figure legends**

529 *Figure 1.* The relationship between the degree of loss of the thermal niche space and the density
530 of ant workers, each expressed as a function of the degree of warming of the chambers. (A)
531 Conceptual diagram for the loss of thermal niche space when temperatures exceed CT_{max} ; the
532 temperature profile in the warmest chamber (+5.5 °C) and the CT_{max} of *Nylanderia faisonensis*, a
533 species with one of the lowest CT_{max} values (37 °C) that occurs in our warming chambers, are
534 shown; the remaining CT_{max} values (19 species) are indicated by hash marks along the x-axis;
535 note that some species exhibit no loss of thermal niche space. (B) A sample calculation of the
536 loss of thermal niche space as a function of the degree of warming in the chambers using *N.*
537 *faisonensis*. (C) The thermal-accumulation slope (± 1 SE) as a function of the thermal-niche-loss
538 slope (± 1 SE).

539
540 *Figure 2.* Laboratory-estimated colony-growth and survival functions for *Temnothorax*
541 *curvispinosus* in the context of air temperatures from the warming chambers. (A) Colony growth
542 (solid line) and survival (dashed line) as functions of temperature (°C), with the estimated critical
543 thermal maximum for each indicated as G CT_{max} and S CT_{max} , respectively. (B) Distributions
544 (using kernel density estimation) of air temperatures of the +0 and +5.5 °C warming chambers.
545 (C) Distributions (using kernel density estimation) of the colony-growth function evaluated using
546 air temperatures of the chambers, with results from the +0°C (light grey bars) and +5.5°C (dark
547 grey bars) chambers shown. (D) Distributions (using kernel density estimation) for the worker-
548 survival function evaluated using air temperatures of the chambers, with results from the +0°C
549 (light grey bars) and +5.5°C (dark grey bars) chambers shown.

550

551 *Figure 3.* Expected colony growth and survival of *Temnothorax curvispinosus* under the
552 temperatures measured in the experimental climatic-warming chambers and observed changes in
553 abundance in the warming chambers. (A) Expected mean and standard deviation of colony
554 growth, obtained by applying air temperatures of the chambers to the laboratory-estimated
555 colony-growth function, expressed as a function of the degree of warming in the chambers. (B)
556 Expected mean and standard deviation of survival, obtained by applying air temperatures of the
557 chambers to the laboratory-estimated survival function, expressed as a function of the degree of
558 chamber warming in the chambers. (C) The natural log of abundance of *T. curvispinosus* as a
559 function of the degree of warming of the chambers. In each panel, smoothing splines are used to
560 visualize the patterns of responses.

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574 **Table 1** Components of predictive models of the responses of ectothermic species to climatic
 575 warming based on thermal tolerance.

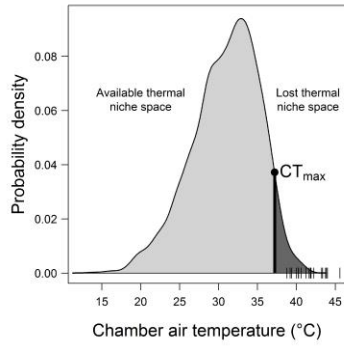
Components of the model		References
Thermal environment	Spatio-temporal resolution of environmental temperature	Finer spatial and temporal resolution allows computation of the variability of fitness Bonebrake and Deutsch (2012)
	Air temperature versus body temperature	Body temperatures are often more reflective of organismal performance than are air temperatures Gilman et al. (2006)
Physiology	Short-term versus long-term population dynamics	Survival can allow estimation of immediate relative vulnerability across space, time, or species, but reproductive output and generation time are needed to understand long-term vulnerability Kingsolver et al. (2011)
Moderators	Phenotypic plasticity	Warmer conditions can increase upper thermal tolerances (within generations) Somero (2010)
	Behavioral plasticity	Behaviorally mediated thermoregulation can avoid body temperatures exceeding upper thermal tolerances Kearney et al. (2009)
	Adaptive evolutionary responses	Warmer conditions can select for increased upper thermal tolerances (across generations) Walters et al. (2012)
	Biotic background	Alterations to resources, competitors, predators, and pathogens can improve or exacerbate responses to warming Tylianakis et al. (2008)

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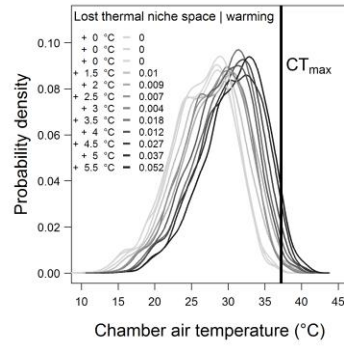
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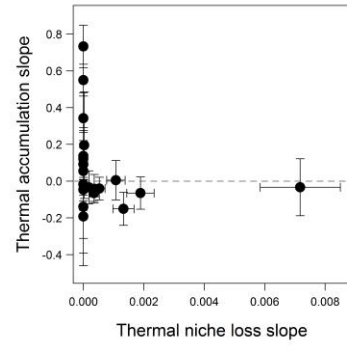
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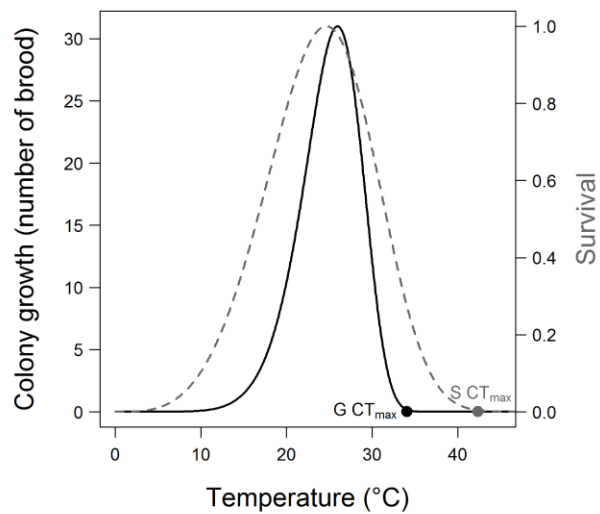


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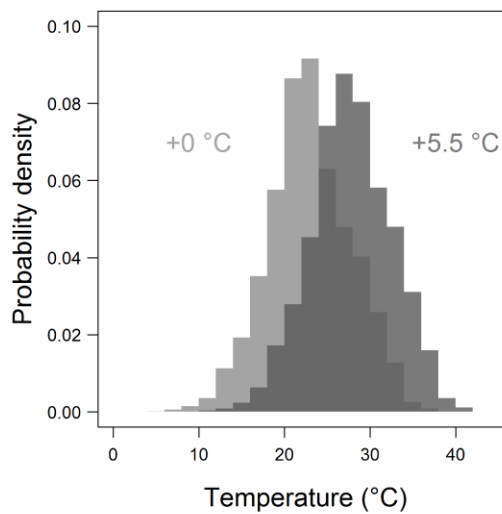


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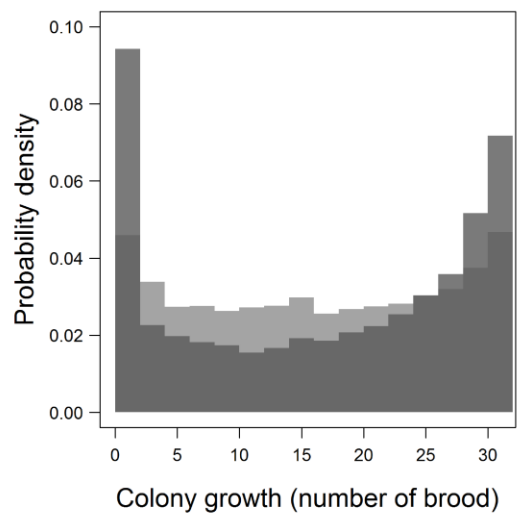
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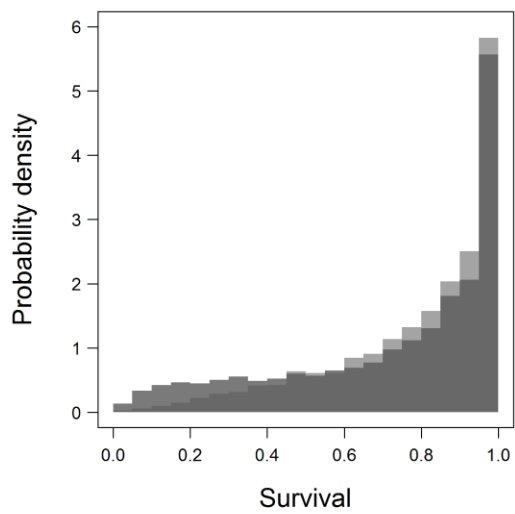
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