Predicted Asymmetrical Effects of Warming on Nocturnal and Diurnal Soil-Dwelling Ectotherms

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ABSTRACT: Climate is expected to have broad effects on ecological communities, but this occurs in the context of significant daily temperature variation in many localities. Because many ectotherms can restrict activity to thermally suitable places and times, daily temperature variation offers the potential to buffer impacts of warming. Using thermal activity data from a montane ground-nesting ant community, we explore how a simulated increase in temperature is expected to alter the duration of suitable activity windows. Counterintuitively, we found that simulated warming lengthens activity times for cold-active species and shortens activity times for warm-active species. We explain this result through a simulation model in which time elapsed within a range of suitable temperatures is considered as an additive resource. Fundamentally, our model results rely on the fact that the mathematical function that relates time to temperature through a day (the Parton-Logan function) is concave before and after noon and convex through the night. These properties are common across terrestrial environments with characteristic deceleration in temperature near both the daily maximum and the daily minimum. Our results suggest that the time of day during which an animal's activity temperatures occur may be an important but rarely considered feature of natural history that contributes to the predicted impact of climate change. Thermally restricted diurnal species may need to compensate for shortened daily activity windows through means such as seasonal shifts or expansions, broadened activity temperatures, or range shifts.

Keywords: climate change, ectotherm, behavioral thermoregulation, thermal refuge, ant.

Introduction

Environmental temperature has pervasive effects on ecological communities across scales, affecting organismal physiology and behavior (Gillooly et al. 2001; Kingsolver 2009), interspecific interactions (Dell et al. 2014; Ohlund et al. 2014), and geographic range limits (Parmesan et al. 1999; Parmesan 2006). In light of climate change, a body of theoretical and empirical work has developed in an effort to predict the effects of climate warming on individuals, populations, and communities (Bale et al. 2002; Petchey et al. 2010; Kingsolver et al. 2011; Uszko et al. 2017). Most theoretical work has focused on changes in mean temperature, despite the fact that warming occurs in the context of diel temperature fluctuations from day to night.

Because daily temperature variation in many localities is substantial and many organisms use thermal refuges to avoid unsuitable temperatures, many assumptions made by theoretical models of the effects of increasing mean environmental temperature on organisms are likely violated. Thermal refuges, defined here as thermally buffered microhabitats within the broader landscape, allow organisms to avoid physiologically stressful conditions (Kearney et al. 2009). When thermal conditions become suitable, organisms can emerge from refuges into the broader environment. However, the buffering effects of thermal refuges against climate warming are limited because organisms still need sufficient time in the external environment to satisfy energetic needs (Amo et al. 2007; Fey and Vasseur 2016; Post 2019). Within a temporal window of thermal suitability, organisms can venture out from their refuges to forage, mate, and interact with their environment. During times of year or in locations where this temporal window is too short or nonexistent, organisms may have difficulty fulfilling energetic needs and possibly starve (Fey and Vasseur 2016). For such organisms, relatively short periods of the day that are within a narrow range of suitable temperatures may be significant for fitness outcomes. In this situation, daily temperature trajectories are significant to organismal fitness, and climate change–driven changes may have important consequences for organisms and communities.

Despite obvious local differences (Dai et al. 1999), there are several characteristics of daily ground, air, and boundary-layer temperature trajectories that are nearly universal in

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terrestrial ecosystems. The sun's local zenith results in a peak of incoming radiation at solar noon. Air temperature typically lags behind this peak solar radiation, as infrared radiation from the ground also contributes to warming of the air (Karl et al. 1991). Because of the continuously changing angle of the sun, a function relating time (x) to temperature ($f(x)$) is concave (negative second derivative) during the day. Furthermore, temperatures surrounding solar midnight are, on average, convex (positive second derivative), as nighttime cooling results from a decelerating loss of heat that was accumulated during the day. Another broad geographic trend in terrestrial environments is that nighttime low temperatures are increasing faster than daytime high temperatures (Karl et al. 1991). This diurnal asymmetry, represented by proportionally more warming occurring during the night, reduces the daily range of temperatures at any given site. Diurnal asymmetry of temperature increase may result in differential outcomes of warming for organisms depending on when during the day optimal temperatures occur.

Ants (Hymenoptera: Formicidae) are a prominent example of restricted daily thermal activity because of their ubiquity across terrestrial environments, their construction of social nests, and the frequent use of soil and plants as thermal refuges. The boundary layer above surfaces can be particularly volatile in temperature, with daytime extremes nearing critical thermal temperatures of ants (Kaspari et al. 2015). The thermal ecology of ants exemplifies the diversity of strategies ectotherms can use to exploit variable environments. Seasonal acclimation is common among ants and interacts with both strict and flexible preferences for light and dark conditions, depending on species identity (Heatwole and Muir 1989). Individual ant nests can contain workers with varying thermal physiology, allowing foraging to continue as temperatures change (Esch et al. 2017). Across communities, there are many examples of thermal hierarchies in which subordinate ant species must forage at more extreme local temperatures while behaviorally dominant species occupy more moderate conditions (Cerdá et al. 1997, 1998; Bestelmeyer 2000). Finally, body size is of particular importance for small arthropods, with size strongly influencing the thermal dynamics of body temperature in the sun (Pincebourde et al. 2021). Many other factors shape ant activity, including prey availability (Raimundo et al. 2009) and predator avoidance. These factors together shape realized ant thermal activity windows, a realized local thermal niche that is often consistent for an ant species between successive days (Caut et al. 2013).

Here, we develop a model to predict how diurnal temperature variation interacts with ectotherm behavioral thermoregulation based on a simple assumption that ectotherm activity is limited by local temperature and that the time elapsed within a favorable temperature range is itself a resource. We estimate the sensitivity of this model to activity distribution type and breadth, diurnally asymmetric warming (more warming at night), and day-to-day variation in maximum and minimum temperature. Finally, we apply this approach to an observational data set of fine-scale ant activity and temperature measurements to estimate the magnitude of these impacts within a community of montane ants.

Methods

Generalized Simulation Model

A generalized simulation model was developed in R (ver. 4.0.0; R Development Core Team 2020) to explore the effects of warming on species that are thermally restricted within the day. Species were assumed to have 10°C activity ranges and were otherwise confined to a thermal refuge. For simplicity, this approach assumes uniformly distributed activity across suitable temperatures. We simulated warming of 2°C and calculated the change in the duration of available activity time between the original daily temperatures and temperatures in the warming scenario. The number of minutes of activity gained or lost per day following 2°C warming is reported in all figures.

To simulate diel variation in temperatures, we used a truncated sine wave for daytime temperatures linked to a negative exponential function for nighttime cooling (Parton-Logan function; eq. [1]; modified from Parton and Logan 1981; Lambrechts et al. 2011). The two functions together describe time-lagged warming, peaking after solar noon, as well as exponential decay of nighttime temperature after the sun has set:

$$\text{daytime temp: } T_i = (T_X - T_N)$$
$$\times \sin\left(\frac{\pi m}{12 + 2a}\right) + T_N, \quad (1)$$

$$\text{nighttime temp: } T_i = T_N + (T_S - T_N) \times e^{-(bn/12)}, \quad (2)$$

where T_X and T_N are maximum and minimum daily temperatures, respectively; m is the number of hours past sunrise; T_S is the temperature at sunset (results from eq. [1] are evaluated at $m = $ day length in hours); n is the number of hours past sunset; a is a lag coefficient for maximum temperature; and b is a nighttime cooling coefficient. The parameters a and b were fitted in R using the nls function for data corresponding to soil surface temperature measurements (see field methods below) and were found to provide a best fit at $a = 1.15$ and $b = 3.37$. This curve shape was then normalized such that minimum temperature $= 0$ and maximum temperature $= 1$ and was scaled to an amplitude specific to the simulation scenario (base simulation minimum $= 10°C$ and maximum $= 40°C$).

To explore the sensitivity of our model to properties of more realistic scenarios, we made five independent modifications of our base simulation (table 1). In the first modification, the effect of day-to-day variation in temperature (temperature variation at a site due to weather) was explored by adding normally distributed values (mean = 0, SD = 3°C or 9°C) to each of 10,000 simulated temperature observations.

In the second modification, to explore the effect of the shape of activity distribution used, we substituted a normal distribution with the same standard deviation as our base simulation (2.5°C) in place of the original uniform distribution. This was accomplished using the function dnorm() in R to create a normally distributed vector of probabilities corresponding to each simulated activity temperature. We then scaled this vector such that the probability of activity at optimal temperature was equal to 1 by multiplying by the inverse of the maximum observed activity probability. Along this vector, we took binomial draws for each of 10,000 individual potential activity times through the day to determine what times of the day activity occurred. We used a normal distribution after finding that empirical ant activity data (described below) was approximately normal for most species with

respect to temperature (species summary statistics are provided in table S1, available online).

In remaining sensitivity analyses, we used uniform activity distributions, for simplicity. In the third modification, to examine the effects of greater warming during nights than during days, we included a scenario in which an average of 2°C warming occurs, but with 1°C during the day and 3°C during the night. In the fourth modification, to determine the effect of varying thermal activity breadth, we included two additional scenarios with species having narrow thermal ranges (5°C) as well as broad thermal ranges (20°C). In the fifth modification, to determine the effect of varying daily thermal range, we included scenarios in which daily temperature range is narrow (20°C) as well as broad (40°C).

Study Site

Ants were collected across a small (4.2-ha) area of mixed sagebrush shrubs and coniferous forest in the Sierra Nevada mountain range (2,000 m; 39.435583°N, 120.264017°W). Ants within this habitat are ground and litter dwelling, and they forage on the ground, in the leaf litter, and among the local vegetation. Dominant plants include mountain

Table 1: Summary of simulations performed and results

Property investigated	Mean activity temperatures simulated	Model change	Figure	Main result
Base model: activity temperature and activity duration under warming scenario	5°C–45°C	$\Delta T = 2°C$	Fig. 1	Change in activity window duration following warming depends on activity timing within the day
Day-to-day temperature variance	5°C–45°C	Daily SD = 0°C, 3°C, 10°C	Fig. 2A	Day-to-day variation reduces effect size
Normal vs. uniform activity distribution	5°C–45°C	Activity distribution shape (uniform vs. normal)	Fig. 2B	Normal distribution reduces effect size
Diurnal asymmetry of warming	5°C–45°C	$\Delta T_{day} = +1°C$, $\Delta T_{night} = +3°C$	Fig. 2C	Nighttime warming exaggerates nocturnal activity expansion, diminishes daytime effects
Thermal breadth	5°C–45°C	Activity range = 5°C, 10°C, 20°C	Fig. 2D	Effects observed over a condensed range of temperatures with broader thermal activity windows
Daily range	5°C–45°C	Daily min/max = 5°C/45°C, 15°C/35°C	Fig. 2E	Effects observed over a condensed range of temperatures with narrower daily temperature range
Predictions for local species	Observed species activity temperature	NA	Fig. 3D	All species benefit from warming locally, but cold-adapted species benefit more

Note: Each row in the table represents a different sensitivity analysis. From our base model (fig. 1), we individually added daily variation in temperature, substituted uniform activity with normally distributed activity as a function of temperature, simulated diurnally asymmetric warming (3°C at night, 1°C during the day), varied the breadth of thermal activities of species, varied the size of the daily temperature range, and performed warming simulation with empirical temperature data and ant activity observations.

sagebrush (*Artemisia tridentata* ssp. *vaseyana*), wyethia (*Wyethia mollis*), Jeffrey pine (*Pinus jeffreyi*), and white fir (*Abies concolor*).

Field Collections

We collected ground-active ants and ground surface temperature measurements synchronously using automated time-sorting pitfall traps (fig. S1, modified from McMunn 2017; figs. S1–S9 are available online). The robotic traps captured ants active on the surface of the ground and within the surrounding leaf litter. Each trap contained 24 collection vials, filled with 70% ethanol, that rotate on a circular rack, with each vial being positioned under a funnel that is flush with the ground for 1 h, resulting in 24 hourly vials containing ants. We observed ants slipping quickly into the funnel and dying within seconds of submergence in the ethanol.

We imposed a grid of 600 potential sampling sites across the habitat to ensure a minimum of 6 m of separation for all potential collections. We then randomly selected 127 sites for ant collection. We made collections between June 19 and October 14, 2015, concentrated in 1- or 2-week sampling bouts each month. Over the season, this resulted in 3,048-h-long samples of ant abundance (24h × 127sites = 3,048 hourly samples). The traps recorded temperature measurements every 5 min during collections using a K-type thermocouple data logger at a height of 1–3 mm above the surface of the leaf litter or above the surface of the soil if no litter was present (McMunn 2017). To validate measurement from thermocouples, we used thermal photography and confirmed that thermocouples did not heat beyond the temperature of the substrate while in full sun. We also conducted an experiment demonstrating that for this thin thermocouple, the effect size of light absorption is minimal compared with spatial heterogeneity in temperature present at the site (see data and a full description in the supplemental PDF, available online).

To install traps, we carefully removed leaf litter and dug a small hole approximately 20 cm wide, 30 cm long, and 20 cm deep. We then buried the trap, replacing the soil and then the leaf litter, taking care to minimize disturbance to the surrounding litter and soil (fig. S1*C*). After installation, the traps remained closed to ants for 24 h to avoid a "digging-in" effect, when ants are initially attracted to the soil disturbance following pitfall trap installation (Greenslade 1973). We separated ants from all other collected arthropods, identified individuals to the species level, and after confirmation of species identifications by Phil Ward, deposited vouchers at the Bohart Museum of Entomology (University of California, Davis). We estimated critical thermal minimum (CTmin) and maximum (CTmax) of ant workers of common species by exposing individual ants to gradually increasing or decreasing temperatures beginning at 28°C by 1°C every 5 min until they lost the ability to demonstrate coordinated movement (see the full description in the supplemental PDF).

Empirical Activity Distributions and Simulated Warming

The kernel density overlaps between ant species activity distributions (calculated from abundance weighted hourly mean temperatures) and the distribution of measured environmental temperatures was estimated from empirical data. We estimated ant species activity kernels for species that we collected at least 20 individuals. The overlapping area of these two density estimations (observed species activity temperatures and environmental temperatures) was estimated using the R package overlapping (ver. 1.6.0; Pastore 2018). We converted these proportions to available activity time per day by multiplying the area of overlap between active temperatures and all environmental temperatures by the number of minutes occurring within a day. To determine the extent to which simulated warming would affect ant species, we calculated overlap of ant activity temperatures with two environmental temperature distributions: (1) all observed surface temperatures (more than 41,000 measurements) and (2) even heating (adding 2°C to each surface temperature observation). We calculated the difference between these scenarios and performed a linear regression to describe the relationship between median species activity temperature and the change in available activity time per day in response to each warming scenario (effect of warming = time of overlap warming scenario − time of overlap observed temperatures).

Results

Theoretical Model Results

The results from our generalized simulation model demonstrate that the time of day of thermal activity windows affects whether total activity duration will contract or expand following warming (fig. 1; Wickham 2016). Species whose activity range lies just below the daily maximum temperature experience a contraction in the duration of available activity time within a 10°C temperature window (species 1, fig. 1). Species that are thermally restricted but whose activity range lies just above the daily minimum experience an expansion in the duration of time within a 10°C window (species 2, fig. 1). These effects are generalizable by the Karamata inequality (Karamata 1932) over any interval where the function relating time to temperature is concave or convex, respectively (for concavity, see the supplemental proof in the supplemental PDF). Data and code underlying all figures and analyses have been deposited in the
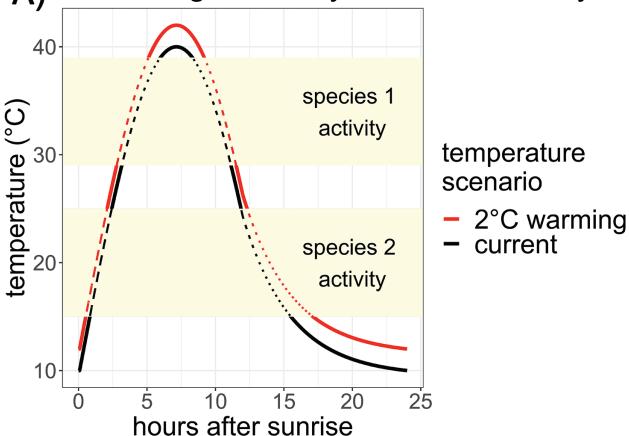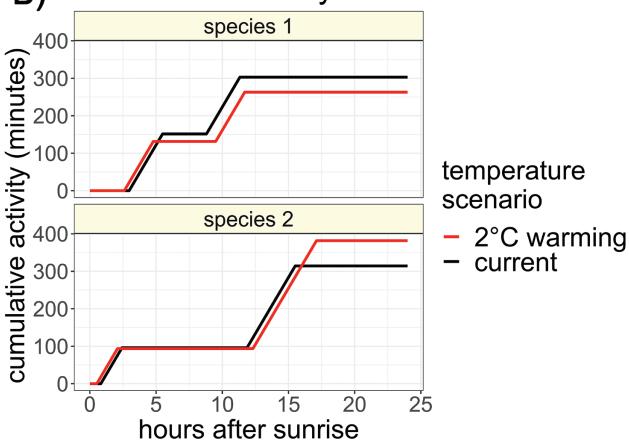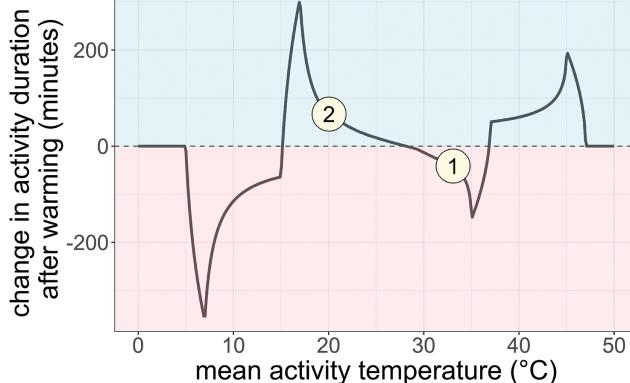
Figure 1: Explanation of the base simulation model and observed asymmetric effects. *A*, Model input for example species with a different mean activity temperature of 33°C (species 1) and 20°C (species 2), each with 10°C broad activity windows superimposed on the daily temperature through one day. Simulations are presented for two daily temperature scenarios, current (black) and 2°C warming (red). Dotted lines in each temperature scenario are times of activity for each species. *B*, Cumulative activity time through the day for each example species. Species 1, a warm-active species near the daily maximum, has decreased duration of activity windows following warming (black line reaches higher daily accumulated activity time), while species 2, a cold-active species near the daily minimum, experiences increased duration of activity windows after warming. *C*, Model results for the net change in activity windows following 2°C warming across species with 10°C activity windows from −5°C to 55°C, with the two example species 1 (activity mean = 33°C) and 2 (activity mean = 20°C) labeled.

Dryad Digital Repository (https://doi.org/10.25338/B84D0V; McMunn and Pepi 2021).

We note that our model predictions also include costs and benefits of warming for species that can be active beyond the range of current daily temperature variation. Species with potential activity windows that include portions above currently observed temperatures greatly benefit from warming as measured by expanded activity opportunities during the heat of the day (mean foraging temperatures above 38°C; fig. 1*C*). Conversely, species with portions of their activity window below the current daily minimum experience a dramatic contraction of activity duration fol-

lowing warming (mean foraging temperatures below 15°C; fig. 1*C*).

Our sensitivity analyses broadly demonstrate that the expansion of activity windows for species active closer to the daily minimum following warming is robust to changes in parameters. However, the magnitude of this effect can be reduced by several realistic assumptions if they are added to the model. Adding a small amount of day-to-day variation (SD = 3°C) diminished the magnitude of observed differences (fig. 2*A*). Adding a large amount of day-to-day variation (SD = 9°C) led to a scenario where all species with ranges bound by the daily minimum and maximum
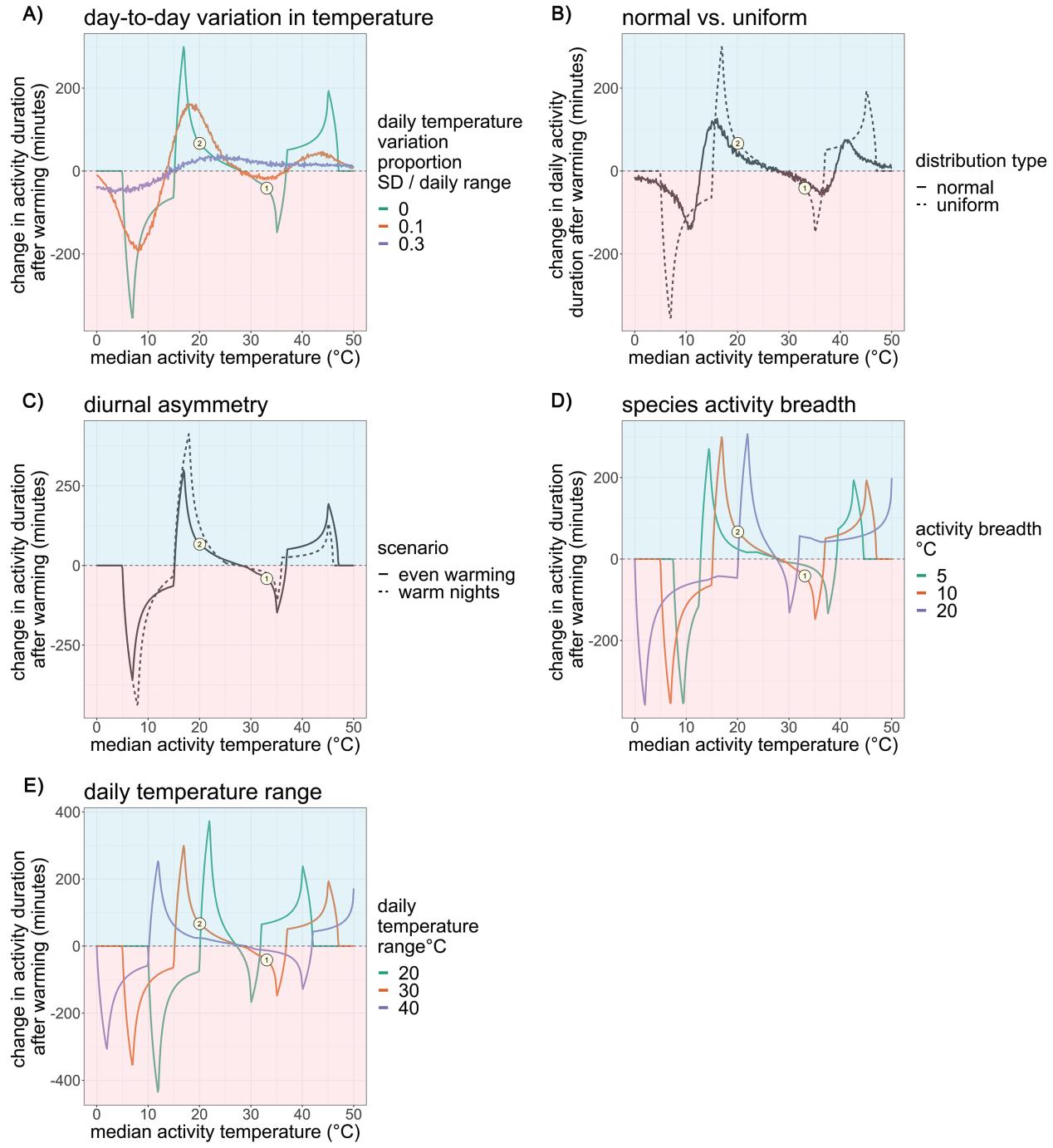
Figure 2: Model results for sensitivity analyses. *A*, Daily activity window duration following 2°C warming with no day-to-day temperature variation (green), weak day-to-day temperature variation (orange; SD/daily range = 0.1), and strong day-to-day variation (purple; SD/daily range = 0.3). We see diminished effects of activity temperature on net change in activity duration following warming as the day-to-day variation increases (lower amplitude in orange and purple lines). *B*, Comparing uniform (dashed line) versus normally distributed (solid line) activity distributions in their relative change in activity window duration following warming. We see diminished effects of activity temperature on net change in activity duration following warming after substituting a normal distribution. *C*, Model results comparing the effect of diurnally asymmetric warming (1°C day, 3°C night; dashed line) versus even warming (2°C day/night; solid line) in their relative change in activity window duration following warming. Warmer nights would tend to exaggerate the expansion of activity windows occurring at temperatures closer to the daily minimum. *D*, Model results comparing broad and narrow activity windows and the effect

temperatures expanded activity durations following warming. This is due to the stability of overnight temperatures near the daily minimum, which following this addition of substantial random noise overcomes the smaller negative effects that are the focus of these analyses. The relative difference between warm- and cold-active species persists (species 1 and 2, fig. 2*A*).

Replacing uniform ant activity distributions with a normally distributed activity function lowered the magnitude of the effect of diurnal asymmetry (fig. 2*B*), although results were in the same direction using both distributions.

Diurnally asymmetric warming (3°C warming at night, 1°C during the day) allowed species active at cool temperatures to further extend nighttime activity, but we saw a less dramatic reduction in daytime activity (fig. 2*C*).

Modifying activity breadth expands the range of temperatures over which we observe diurnal asymmetry in response for narrowly active species (thermal breadth of 5°C) but contracts the range of temperatures over which we observe diurnal asymmetry of response for broader thermal ranges (20°C; fig. 2*D*). Modifying daily temperature range alters the range of temperatures over which we observe diurnal asymmetry in response. At a location with less diurnal temperature change (20°C daily range), a 2°C temperature increase results in more dramatic effects of asymmetry concentrated within a narrower range. At a location with more diurnal temperature change (40°C range), a 2°C temperature increase results in less dramatic effects of asymmetry for species with activity temperatures falling within a broader range (fig. 2*E*).

Empirical Results

We collected 4,354 ant workers representing 21 species. We include here analyses of only species with more than 20 individuals collected (15 species). Local temperature data varied substantially across collection sites and seasons, but ants demonstrated restrictions to moderate and warm temperatures locally (fig. 3*A*, 3*C*). Species thermal activity ranges are remarkably broad at this site, with large overlap in activity temperatures by species (fig. 3*B*). While overlapping to a large extent, species average activity temperatures varied by nearly 15°C (19°C–35°C). The temperature on the surface of the ground, where ants frequently forage, frequently exceeds species critical thermal maximum temperatures in open habitats, while nighttime temperatures are near species critical thermal minimum temperatures (figs. S2, S3). Species with higher CTmax values were found to be active at higher median temperatures ($t = 2.3$, $P = .039$, $R^2 = 0.27$; fig. S2). We found no relationship between CTmin values and median foraging temperatures (fig. S3).

Simulated warming by 2°C led to greater overlap between environmental temperatures and ant thermal activity distributions following warming for all species. This difference in simulated available activity time was more pronounced for species that on average were active at colder temperatures, as predicted by our theoretical results (fig. 3*D*).

Discussion

Our model shows that the time of day during which thermally restricted activity windows occur determines whether that activity window will expand or contract following warming. Our model gives the nonintuitive result that with climate warming, cold-active species activity windows may expand, while warm-active species activity windows may be reduced in some circumstances. This is due to general properties of terrestrial daily temperature trajectories—specifically, the decelerating rate of warming as temperatures approach the daily maxima and slowly begin to cool—and the exponential decline in temperatures during overnight cooling. The concavity of the daily temperature trajectory at high temperatures and convexity at low temperatures cause asymmetric effects on species that are active on the concave versus convex part of the trajectory. We substantiate our model result using empirical activity data from an ant community, in which we demonstrate that ants active at temperatures occurring closer to the daily minimum are expected to have available activity times expanded by warming to a greater degree than species that are active closer to the daily maximum. Simulated warming of 2°C results in approximately a 20–30-min daily advantage for the most cold-active species compared with the most warm-active species.

Our results have significant implications for the effects of climate warming on ectotherm communities, suggesting asymmetric effects of thermal window expansion and contraction on cold- versus warm-adapted species with the

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of 2°C warming. A broad activity window (20°C; purple) only results in diurnally asymmetric expansion/contraction of activity windows in a very narrow range of temperatures (centered between the minimum and maximum daily temperatures). Species with narrow activity windows (5°C; green) experience this expansion/contraction of activity windows following warming over a broad set of mean activity temperatures. *E*, Model results comparing broad and narrow daily temperature ranges and the effect of 2°C warming. A narrow daily range (20°C; green) results in diurnally asymmetric expansion/contraction of activity windows in a narrower range of temperatures (centered between the minimum and maximum daily temperatures). At a location with a broad daily temperature range (40°C; purple), local species experience expansion/contraction of activity windows following warming over a broad set of mean activity temperature. All panels contain yellow badges labeling example species 1 and 2 from figure 1.
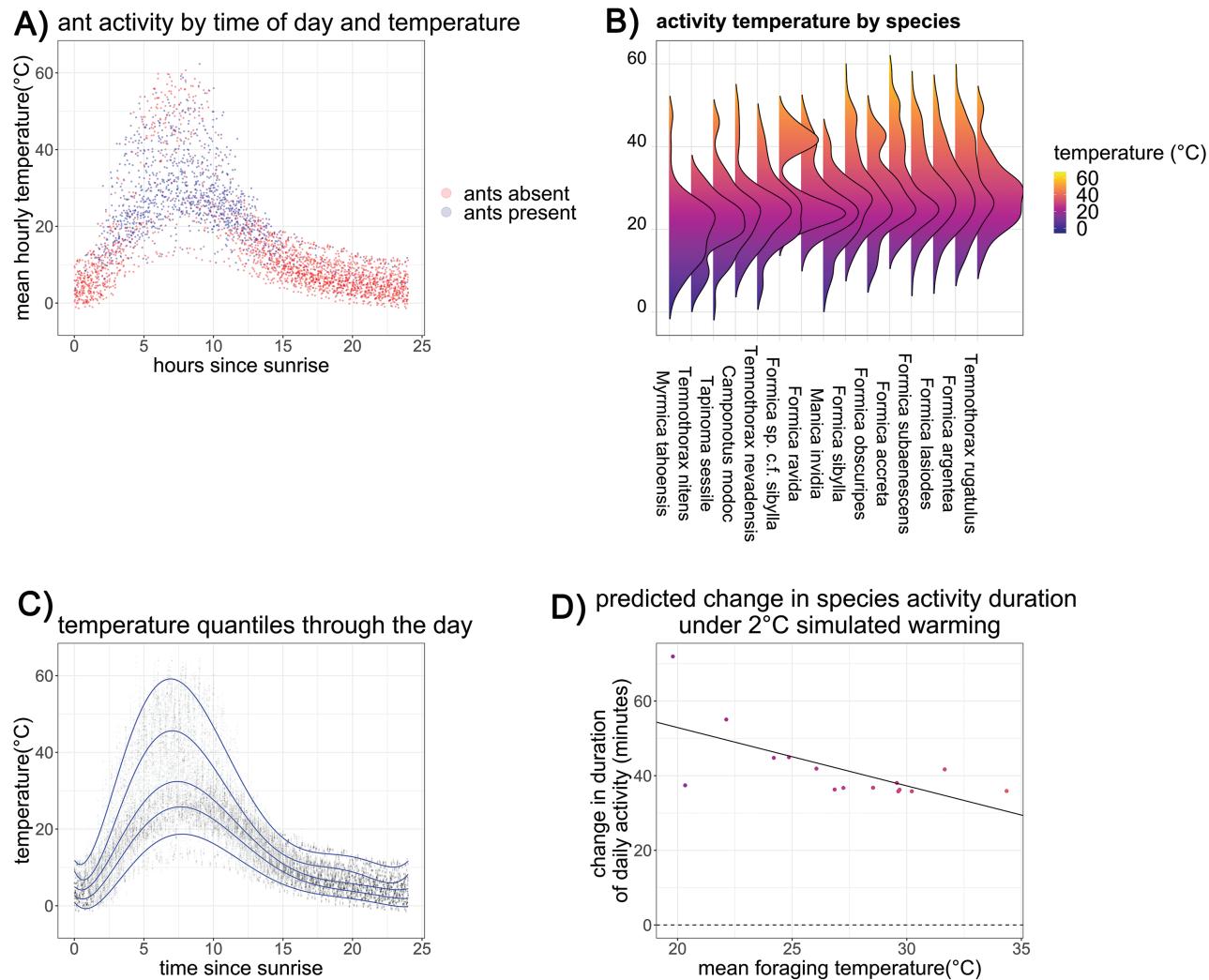
Figure 3: Empirical surface temperature measurements and ant activity with temperature. *A*, Presence and absence of active ants across all collections (137 sites, 24 hourly collections). Ant activity is largely restricted to intermediate temperatures. *B*, Frequency distributions of ant collections for common species by temperature. Species have broad and overlapping activity temperatures. *C*, A quantile regression of surface soil temperature measurements with 5th, 25th, 50th, 75th, and 95th quantile temperatures plotted throughout the day, demonstrating that local surface temperatures are concave and convex, as described using the Parton-Logan daily temperature model. *D*, Change in estimated activity time per day with 2°C warming as a function of mean activity temperature. Each point in *B* is an ant species within the community, collected at least 20 times across a period of 4 months. Available activity time for each species was calculated using an empirical estimation of overlap between environmental and species level temperature observations. A linear regression (change in activity ∼ median activity temperature) is overlaid. Species with higher mean activity temperatures experience a smaller expansion of activity following simulated warming than do species with lower mean activity temperatures.

ability to escape daily thermal extremes (e.g., through refuge use). This suggests that it is important to consider the effects of climate warming in the context of daily temperature fluctuations and behavioral thermoregulation.

The robustness of our primary finding to sensitivity analyses suggests that it is likely to be quite general across communities of organisms that use thermal refuges, which include many ectotherms (e.g., insects [Marsh 1985; Smolka et al. 2012], reptiles [Huey and Slatkin 1976; Huey et al.

1989; Webb and Whiting 2005]). However, the effects of sensitivity analyses suggest some implications of when the effects we document are likely to be more or less dominant. Sensitivity analyses showed that differences between cold- versus warm-active species were less pronounced if we assume a normal as opposed to uniform thermal activity distribution. The empirical activity distributions of ants in our community, while not uniform, showed a tendency toward being more platykurtic than a normal distribution. Species

thermal activity distributions may have a range of shapes, from platykurtic to leptokurtic, which would strengthen or weaken the effects found in our model. Interestingly, our sensitivity analyses of thermal niche breadth suggest that with respect to temperature effects on the length of daily activity windows, species with wider thermal activity niches may be more sensitive to warming compared with those with narrower thermal activity niches. This is because as temperatures shift, species with niches that cover a wider range of the daily temperature range are more likely to experience a change in the available duration of temperatures, as they are more likely to overlap a portion of the daily temperature curve with greater concavity or convexity. If species are preadapted or maladapted to future temperatures, they will experience large magnitude increases or decreases in available foraging time (left and right sides of curve, fig. 1*C*).

The results of our model depend on the properties of daily temperature range, which varies with latitude, peaking in daily range near 30°N/S (Wang and Dillon 2014). In addition, daily temperature range of habitats vary as a result of local vegetative cover, continental versus maritime influence, and a number of other climatic factors (e.g., cloud cover, humidity). Sensitivity analyses found that adding random variation to temperature decreased the main effect of the model, suggesting that these effects are less likely to be observed in areas with greater variability in temperature between days. Greater warming at night versus during the day lessened the observed negative impact on warm-active species while increasing the positive impact on cold-active species. This suggests that warming at night is likely to have less severe impacts on ectotherm communities that use thermal refuges to escape daytime warming, meaning that regional differences in the strength of daytime versus nighttime warming may be important for the overall impact of warming on these communities. Last, our model results are sensitive to the relative magnitudes of daily variation in temperature and ectotherm thermal niche breadth, which covary by biome. For example, daily temperature fluctuations are generally smaller in humid, low-latitude tropical regions (Wang and Dillon 2014), and ectotherm thermal niche breadths are expected to be narrower in these same regions because of lower interannual temperature variation (Deutsch et al. 2008). In our own preliminary analysis, we suggest that this balance may lead to a larger per-degree change in ectotherm activity window duration in the tropics than in temperate regions, although this outcome depends on the relative magnitudes of both thermal niche breadth and daily temperature range (fig. S6). Larger diel asymmetries in the effect of warming on activity time in the tropics could counteract the greater expected vulnerability of some cold-active tropical ectotherms to warming because of narrow thermal safety margins (Deutsch et al. 2008), at least among species that can use thermal refuges.

In this study, negative consequences of temperature outside the activity range were not estimated. While this assumption is perhaps reasonable for ground-nesting ants or bees, many animals are incapable of eliminating exposure to diel fluctuation in temperature. Exposure to temperature during periods of nonactivity can have large effects on fitness. For example, nighttime warming increases egg production in a temperate diurnal lizard species through enhanced energy budgets (Clarke and Zani 2012). Conversely, nighttime warming reduces the ability of an aphid to recover from heat stress during warm days (Zhao et al. 2014). These divergent findings emphasize the importance of considering, when available, detailed life histories in modeling the impacts of temperature on ectotherms.

Negative effects of exceeding the critical thermal maximum temperature in species without effective thermal refuges have strong negative impacts on fitness due to the steep decline in fitness once enzyme denaturation begins (Martin and Huey 2008). Exposure to increased daily maximum temperatures could override broadened activity time for species with imperfect thermal refuges. Small ectotherms, particularly insects, are notoriously hard to find if they do not return to a nest, and thus the quality of many ectotherms' thermal refuges are not known. Even for the present study, ants can remain active during warm periods by moving through slightly deeper portions of the leaf litter. Exploitation of very small-scale thermal heterogeneity is one of many contributors to the broad thermal activity ranges observed according to temperature measurements above the surface of the soil or leaf litter. The interaction between time of activity and continuously varying habitat quality could play an important role in determining the net effect of climate change on populations. For example, behavioral thermoregulation of a nocturnal gecko does not only depend on use of a shady thermal refuge; the geckos also use body positioning and posture to enhance thermoregulation within the refuge, with strategies varying by season to maintain stable body temperatures (Kearney and Predavec 2000).

A framework that incorporates additional factors of how species interact with temperature, beyond availability of activity time, is necessary to accurately predict fitness outcomes of climate change for individual species of ectotherms. Tolerance of environmental temperature can result from a large number of traits, including behaviors and body plans (e.g., long legs, large body mass, rapid movement) that allow ectotherms to decouple internal body temperature from their local environment. Ectotherm microhabitat choice and time devoted to thermoregulatory behaviors, such as basking, can extend activity times at a cost of decreased efficiency in foraging, hunting, mating, or any other behavior contributing to fitness.

Conclusion

The time of day during which an animal's activity window occurs determines whether suitable activity temperatures will increase or decrease in duration following warming. This result is generalizable to many species that utilize high-quality thermal refuges to persist in variable environments and suggests important differences in the effects of warming on communities dependent on local daily temperature variation. The framework suggested here is appropriate for ground-nesting diurnal ectotherms, such as many ants and bees, but a more nuanced incorporation of natural history characteristics is certainly necessary to account for the complexities of behavioral thermoregulation. An improved understanding of the interactions between behavioral thermoregulation and local properties of diel temperature variation are a critical component in predicting the impact of climate change on ectotherms.

Statement of Authorship

M.M. designed and built the experimental equipment, designed collection methods, conducted fieldwork, identified ants, and conducted initial data analysis. M.M. and A.P. wrote the manuscript, designed figures, and conducted final data analysis.

Data and Code Availability

All data and code have been posted and are available in the Dryad Digital Repository (https://doi.org/10.25338/B84D0V; McMunn and Pepi 2021). Their use in future research is encouraged.

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