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Using metabolic and thermal ecology to predict temperature dependent ecosystem activity: a test with prairie ants

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Abstract. As ecosystems warm, ectotherm consumer activity should also change. Here we use principles from metabolic and thermal ecology to explore how seasonal and diel temperature change shapes a prairie ant community's foraging rate and its demand for two fundamental resources: salt and sugar. From April through October 2016 we ran transects of vials filled with solutions of 0.5% NaCl and 1% sucrose. We first confirm a basic prediction rarely tested: the discovery rate of both food resources accelerated with soil temperature, but this increase was typically capped at midday due to extreme surface temperatures. We then tested the novel prediction that sodium demand accelerates with temperature, premised on a key thermal difference between sugar and sodium: sugar is stored in cells, while salt is pumped out of cells proportional to metabolic rate, and hence temperature. We found strong support for the resulting prediction that recruitment to NaCl baits accelerates with temperature more steeply than recruitment to 1% sucrose baits. A follow up experiment in 2017 verified that temperature-dependent recruitment to sucrose concentrations of 20% (mimicking rich extrafloral nectaries), while noisy, was still only half as temperature dependent as recruitment recorded for 0.5% NaCl. These results demonstrate how ecosystem warming accelerates then curtails the work done by a community of ectotherms, and how the demand and use of fundamental nutrients can be differentially temperature dependent.

Key words: *ants; ectotherms; foraging; grasslands; metabolic theory of ecology; stoichiometry; thermal ecology.*

Introduction

A key goal of ecology is to predict when and where resource shortfalls are likely to constrain consumer activity, and hence the work consumers perform in ecosystems (Sterner and Elser 2002, Kaspari et al. 2008, Anderson-Teixeira and Vitousek 2012). Consumer performance is often limited by shortfalls of sodium and sucrose (Galef 1996, Mayntz et al. 2005, Raubenheimer et al. 2009, Snell-Rood et al. 2014). Here, we explore the premise that temperature drives ectotherm foraging for salt and sugar based on temperature's effects on physiological demand and perceived risk of environmental shortfall (Danger et al. 2008, Geerling and Loewy 2008, Kaspari et al. 2010). We do so by exploiting seasonal and daily temperature variation in a sodium-limited prairie ant community (Kaspari et al. 2008). Ants are a model system for this question as they are ubiquitous in terrestrial ecosystems (Hölldobler and Wilson 1990, Kaspari et al. 2000), and most ant communities consist of herbivores that feed on sugary exudates, predators and scavengers that feed on animal tissue, and omnivores that feed on both (Blüthgen et al. 2003, Tillberg et al. 2006, Roeder and Kaspari 2017).

Temperature dependent foraging: insights from metabolic and thermal ecology

Foraging activity in ectotherms has long been linked to temperature via temperature's effect on metabolic rate (Gillooly et al. 2001, Andrew et al. 2013, Stuble et al. 2013, Baudier et al. 2015). Two links are relatively well explored. First, metabolic rate measures the ability of an organism to do work. In ectotherms, metabolic rate, a constraint on activity, increases exponentially over a range of environmental temperatures (Gillooly et al. 2001, Brown et al. 2004). Accelerating performance with temperature has been documented at the scale of organisms and their tissues (Dell et al. 2011) and for ecosystem processes like respiration and photosynthesis (Anderson-Teixeira and Vitousek 2012). Second, beyond some critical temperature, the decline of metabolic rate and organismal performance is well documented, even as the mechanisms are not well-understood (Kingsolver and Huey 2008, Angilletta 2009). Combined, both the acceleration and abrupt decline of activity with temperature should apply to the collective action represented by an ecosystem's insect community (Losey and Vaughan 2006, Kaspari et al. 2015). This powerful prediction is rarely tested, despite the importance of arthropod actions such as pollination (Garibaldi et al. 2013), decomposition (Nichols et al. 2008), and seed dispersal (Hughes and Westoby 1990).

A third link between temperature and foraging activity is temperature's effect on nutrient demand relative to supply (Kay 2002). Two nutrients, sodium and sucrose, differ in their consumer demand based on their storage in the body. Sodium is constantly evacuated from cells by ATPases into an organism's intercellular fluid and has no organic storage form, so consumers must constantly harvest sodium to replace their losses through excretion (Maddrell 1972, Kaspari 2014). In contrast, sugars have numerous long chain forms (e.g., glycogen, starches) that can be stored in cells and released on demand. This leads to our third predicted connection between temperature and foraging: if an ectotherm's excretion rate (including its sodium losses) is

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proportional to its metabolic rate (Peters 1986) then as metabolic rate increases exponentially with temperature, demand for sodium should also increase exponentially with temperature to balance increasing losses. As sucrose is easily stored in the body, we predict demand for sodium will accelerate at a faster rate as temperature increases, compared to the demand for sucrose, which will show a weaker and noisier temperature sensitivity.

We test these three predictions across a seasonal and diel gradient of temperature in an Oklahoma prairie, surveyed with a grid of 300 salt and sugar baits multiple times during the day over a seven-month period. Specifically, we predict that the overall number of baits that ants discover in an hour will accelerate with soil temperature (a proxy for colony temperature) since colony metabolic rate governs ant activity. Second, we predict that this relationship breaks down at high surface temperatures that impede individual forager performance outside the nest. Finally, since rising colony temperatures increase the loss of sodium relative to sucrose, we predict that the demand for sodium, measured by the number of ants recruited to baits, accelerates faster for NaCl than sucrose baits.

Materials and Methods

We studied two grassland ant communities: one at the University of Oklahoma (OU) Centennial Prairie (35.19° N, 97.45° W) in Cleveland County, Oklahoma, from April through October 2016, and the other at Pigtail Alley Prairie (33.89° N, 96.84° W) in Marshall County, Oklahoma, from May through July 2017. The OU Centennial Prairie is 7.7 ha and is mowed once a year in November, but is otherwise undisturbed. Pigtail Alley Prairie is 24.5 ha and was last farmed >20 yr ago but has been undisturbed since.

The OU Centennial Prairie has 16 ant species and is numerically dominated by *Crematogaster lineolata*, *Forelius pruinosus*, *Formica pallidefulva*, and *Monomorium minimum*. Pigtail Alley Prairie has nine ant species and is numerically dominated by *C. lineolata*, *F. pruinosus*, and *Nylanderia terricola*. At both sites, the dominant plant species are *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Andropogon gerardii* (Kaspari et al. 2016*b*).

Sampling salt vs. sugar discovery

To measure how salt and sugar discovery changed with temperature, we set out labeled 1.5-mL Eppendorf vials half-stuffed with cotton and saturated with either 1% sucrose or 0.5% NaCl solution by weight at the OU Centennial Prairie (Kaspari et al. 2008). We conducted our sampling along three 100-m transects spaced 50 m apart. We flagged each transect every 1 m with white PVC surveyor flags. To run a transect, 50 closed vials of each solution were thoroughly mixed (100 vials total per transect). Walking along the transect, a vial was selected at random, opened, and placed next to a flag, every 1 m. To understand what temperatures were important to ant discovery and recruitment to baits, we recorded three measures of temperature every 20 m along each transect while the vials were out, for a total of six measurement locations per transect. We measured soil temperature (to 0.1°C) at 10 cm depth using a temperature probe (Taylor Precision, Oak Brook, Illinois, USA); surface temperature with an infrared thermometer (to 0.1°C, Nicety, Starmeter Instruments Co., Ltd., Shenzhen, Guangdong, China) next to the vial; and air temperature (to 1°C, AcuRite Chaney Instrument Co., Lake Geneva, Wisconsin, USA) at 85 cm off the ground. After 1 hour, we collected the vials, snapping the cap shut to capture all ants inside, and recorded the location of each vial containing ants. We used the above assay to sample ant foraging behavior three times a day (09:00, 13:00, and 17:00) from April through October 2016, four times a month, allowing us to explore ant response across a wide range of diel and seasonal temperature variation.

Recruitment at different sugar concentrations: a follow-up experiment

Ants obtain sugars from extra-floral nectaries and by tending hemiptera. These sources of sugar may have sucrose concentrations from 10% to 50% by mass (Josens et al. 1998, Paul and Roces 2003, Kim et al. 2011). Our first assay (OU Centennial Prairie, April through October 2016) may not have fully confirmed our hypotheses because it used a low sucrose concentration and thus did not adequately test absolute sucrose demand by the ant community. To remedy this problem, and further explore the relationship between sugar demand and temperature, we performed a second assay at a different location, Pigtail Alley Prairie. Our goal was to see if ant recruitment to sucrose baits at higher temperatures would accelerate as sucrose concentration increased, and if so, whether that acceleration in recruitment was greater than the acceleration in recruitment to NaCl baits.

Similar to our 2016 experiment, we used labeled 1.5-mL Eppendorf vials half-stuffed with cotton and saturated with either a 1%, 5%, 10%, or 20% sucrose solution by mass (Kaspari et al. 2008). We conducted our sampling along two 80-m transects spaced 50 m apart. As before, we flagged both transects every 1 m with white PVC surveyor flags. To run each transect, we thoroughly mixed 20 closed vials of each solution (80 vials total per transect). As in our 2016 experiment, a vial was selected at random every 1 m, opened, and placed next to a flag. After 1 h, we collected vials by snapping the lid shut to capture all ants inside. We performed this assay one time a week, twice a day (08:00 and 16:00) from May through July 2017, to observe ant foraging patterns at the hottest part of the day. In the hour while the vials were out, we measured soil, surface, and air temperature at five spots per transect (every 20 m) using the same equipment as in 2016.

Hypothesis testing

We tested the prediction that increasing temperature accelerates discovery rates to both NaCl and sucrose baits but accelerates recruitment to NaCl baits at a higher rate relative to sucrose baits. To do this, we first compared the average discovery of NaCl and sucrose baits against the average temperature across the three transects for a given date and time of day. We found no consistent temperature difference among the three 100-bait transects, but consistent differences in temperature with time of day (09:00, 13:00, and 17:00). Thus, the value reported for each nutrient is the

response to 150 vials, averaged over three transects of 50 vials (expressed, for example, as the average number of NaCl baits (of 50) discovered at 09:00, 13:00, and 17:00). We generated 82 estimates of ant discovery and recruitment from April through October 2016.

We focus on two responses of the ant community to temperature. A vial was considered discovered if any ant was present in the vial after the 1-h sampling period. The number of salt and sugar vials containing ants per transect, averaged across transects, represented the average ant activity during a sampling period. While ants may have discovered a vial and abandoned it prior to pick-up, we observed vials while taking temperature measurements and vials containing ants after 10–30 min often still contained ants after 1 h. Next, we assumed the demand for a nutrient would be reflected by more worker ants being recruited, and hence accumulating in the vial. Therefore, we assume that recruitment, and hence colony demand, is the number of ants found in a vial (of those containing an ant) at the end of an hour (while acknowledging that factors such as worker size and colony size may also play a role). Moreover, while this method risks occasionally scoring two or more conspecific ants from different colonies as recruitment, we assume intercolony competition makes this rare.

Statistical analysis

To examine the seasonal change in discovery and recruitment to NaCl and sucrose vials we first performed four separate Kruskal-Wallis tests using month as the predictor and either average discovery to NaCl and sucrose baits or recruitment to NaCl and sucrose baits as the response. We tested Pearson correlation coefficients to check for a relationship between average soil and surface temperatures, average air and surface temperatures, and average air and soil temperatures. We also checked for multicollinearity among the different temperature measures using a variance inflation factor cutoff of 3. Next, we examined the relationship between average soil and average surface temperature and average discovery and recruitment using multiple regression, leaving out air temperature because of multicollinearity. Because the multiple regression showed soil temperature had a stronger relationship to ant discovery and recruitment to vials relative to surface temperature, we used only soil temperature in our remaining analyses. To test the influence of temperature, nutrient, and temperature and nutrient interactions on ant discovery and recruitment to baits we performed an ANCOVA (using type III sum of squares) with either average discovery or recruitment as our response, nutrient (NaCl or sucrose) as our predictor, and average soil temperature as our covariate. To better partition the coupled effects of temperature promotion and inhibition on foraging activity, our analysis separated the 09:00, 13:00, and 17:00 trials, resulting in six separate ANCOVAs. We also used an ANCOVA to test the separate and interactive influence of temperature and sucrose concentration on average discovery and recruitment to four sucrose concentrations (1%, 5%, 10%, and 20%) at Pigtail Alley Prairie. Again, we used average discovery and recruitment as our responses, sucrose concentration as our predictor, and average soil temperature as our covariate. Our statistical analyses were conducted in R version 3.3.2 (R Development Core Team 2016).

To estimate the curve fit across the range of temperatures in the study linking temperature to discovery and recruitment of ants to baits, we used a non-linear iterative damped least squares algorithm initiated by a random number seed (Marquardt 1963, Press et al. 1986) and implemented by SigmaPlot version 14.0 (Systat Software, San Jose, California, USA). This algorithm fits a non-linear curve with parameter values that minimize the sum of squares differences between observed and predicted values of the response variable. We used the curves generated by SigmaPlot to calculate the Q_{10} values for average discovery and recruitment to vials. Q_{10} is a descriptive statistic and is a standard measure of the temperature dependence of a process (Angilletta 2009). Q_{10} is calculated as $\left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2-T_1}\right)}$ where R_2 is the rate (i.e., discovery or recruitment) at a higher temperature (T_2) and R_1 is the rate at a lower temperature (T_1). Because we calculated Q_{10} values for a 10°C temperature change at each site, the exponent equals 1. Specifically, we calculated Q_{10} values for average discovery and recruitment rates to vials between 20° and 30°C at OU Centennial Prairie and between 24° and 34°C at Pigtail Alley Prairie because soil temperatures there did not drop to 20°C. Because Q_{10} maps on to the activation energy of metabolic theory (Dell et al. 2011), we use it as a descriptive statistic to compare the temperature dependence of the processes of ant discovery and recruitment to NaCl and sucrose vials. Specifically, we use Q_{10}s to corroborate the prediction that recruitment to NaCl baits has a higher Q_{10} than recruitment to sucrose baits.

Finally, to examine consistency of temperature sensitivity among common species, we compared the temperature dependence of species discovery rates for the four numerically dominant species at the OU Centennial Prairie. To do this, we first summed NaCl and sucrose discovery for a given species/sampling period then binned sampling events by integer temperature (e.g., 15°C = all observations from 14.5 to 15.49°C) and finally expressed the temperature–discovery curve of each species as a proportion of the highest discovery rate across all soil temperatures recorded (i.e., with a maximum of 1.0). We again used SigmaPlot to fit a curve on discovery rates for each species and used this curve to calculate the Q_{10} value for discovery.

Results

In the 2016 experiment, the average number of NaCl and sucrose baits discovered by ants varied monthly, although there was a larger seasonal change in the discovery of NaCl than sucrose baits (Kruskal-Wallis $\chi^2 = 44.8$, df = 6, $P < 0.0001$ and K-W $\chi^2 = 29.0$, df = 6, $P = 0.0001$ respectively; Appendix S1: Fig. S1). The average recruitment of ants showed a similar pattern, varying sevenfold within a month for NaCl, while sucrose recruitment was lower and varied less (K-W $\chi^2 = 52.4$, df = 6, $P < 0.0001$ and K-W $\chi^2 = 13.7$, df = 6, $P = 0.0336$; Appendix S1: Fig. S1).

Prediction: rising soil temperatures enhance activity, extreme surface temperatures suppress it

Three measures of environmental temperature covaried with month and time of day in the 2016 experiment, but to

varying degrees (Appendix S1: Fig. S2). Soil temperature averaged 26.2°C across June and July, and increased about 8°C from 09:00 to 17:00 every day. In contrast, surface temperatures were highly variable, fluctuating up to 30°C in a given day with a peak at 13:00. Dynamics of air temperature were intermediate. Across the 82 sampling events, all temperature measurements were correlated (average soil and surface temperature Pearson $r = 0.43$, $P < 0.0001$; average air and surface temperature Pearson $r = 0.65$, $P < 0.0001$; and average air and soil temperature Pearson $r = 0.81$, $P < 0.0001$; Appendix S1: Fig. S3). As stated above, we tested for multicollinearity (average soil temperature VIF = 1.29, average surface temperature VIF = 1.35, average air temperature VIF = 4.82) and removed air temperature from analyses because of multicollinearity.

Soil, surface, and air temperatures differed in their association with discovery and recruitment (Appendix S1: Fig. S4). Multiple regression revealed that average discovery rates of NaCl roughly doubled with increasing soil temperature ($P < 0.0001$; Table 1) and were suppressed as surface temperatures rose ($P = 0.0095$; Table 1), accounting for about half the variation in NaCl discovery. Sucrose discovery rate showed a similar pattern of increasing with soil temperature ($P = 0.002$; Table 1), accounting for about one-third of the variation in discovery.

Prediction: discovery rates accelerate with soil temperature

We next test the prediction that activity of ant foragers should accelerate with the temperature they experience. Our ANCOVAs showed that average discovery rate of NaCl baits accelerated at all three times of day, with power law exponents >2.8 and Q_{10}s from 3.2 to nearly 14 (Fig. 1, Appendix S1: Table S1). Average discovery of sucrose baits showed a similar accelerating pattern at 09:00 and 17:00. At 13:00 and 17:00, average NaCl and sucrose discovery rates increased similarly (temperature effects $P = 0.0359$ and $P < 0.0001$ respectively, nutrient and interaction effects not significant; Table 2). However, inconsistent with our implicit assumptions that discovery rates of both nutrients would increase with temperature, the average discovery rates were higher for NaCl than for sucrose at 09:00 ($P = 0.0033$; Table 2), with almost four times the Q_{10} (Fig. 1). This inconsistency disappears in the other two time samples.

Table 1. Results of multiple regression quantifying whether average soil or average surface temperature better account for average discovery (number of vials discovered per 50 ants) and average recruitment (number of ants per vial) to NaCl and sucrose vials at the OU Centennial Prairie.

Nutrient and parameter	Estimate	Error	t	Pr > |t|
Discovery				
NaCl ($r^2 = 0.47$)				
Intercept	−28.78	5.84	−4.93	<0.0001
Soil temperature	2.30	0.27	8.53	<0.0001
Surface temperature	−0.32	0.12	−2.66	0.0095
Sucrose ($r^2 = 0.26$)				
Intercept	−6.30	3.08	−2.04	0.0444
Soil temperature	0.56	0.14	3.94	0.0002
Surface temperature	0.10	0.06	1.62	0.1091
Recruitment				
NaCl ($r^2 = 0.49$)				
Intercept	−7.34	1.42	−5.16	<0.0001
Soil temperature	0.56	0.07	8.47	<0.0001
Surface temperature	−0.05	0.03	−1.56	0.1240
Sucrose ($r^2 = 0.02$)				
Intercept	1.22	0.25	4.90	<0.0001
Soil temperature	0.003	0.01	0.26	0.7950
Surface temperature	0.003	0.01	0.63	0.5300

At the OU Centennial Prairie, four species made up 94% of the bait discoveries (Appendix S1: Fig. S5). Average discovery rates of three of the four species increased as a power law with temperature ($r^2 = 0.8$ to 0.93) with Q_{10}s of 4.4–5.0 (Appendix S1: Fig. S5). In contrast, average discovery rates of one species, *F. pallidefulva,* showed a relatively uniform, linear decrease with temperature.

Prediction: demand for salt accelerates faster than demand for sugar

Across all three times of day, a significant interaction between temperature and nutrient reflected stronger temperature dependent recruitment to NaCl compared to sucrose ($P < 0.0008$; Fig. 1, Table 2). In each case, recruitment to NaCl increased exponentially with temperature ($b = 4.4$, 3.0, 3.7 and $P < 0.0008$; Appendix S1: Table S1) and failed to vary for sucrose ($b = 0$, 0.1, 0.4 and $P > 0.05$; Appendix S1: Table S1). Q_{10} values for recruitment to NaCl baits ranged from 3.4 to 6.0 while Q_{10} values for recruitment to sucrose baits ranged from 1.0 to 1.2, further corroborating the prediction that recruitment to NaCl baits was more temperature dependent than recruitment to sucrose baits (Fig. 1).

As previously mentioned, a potential bias occurred by our use of 1% sucrose in the 2016 baits. This concentration may have been unattractive compared with other sugar sources such as extrafloral nectaries or exudates, resulting in low ant recruitment (Josens et al. 1998, Paul and Roces 2003, Kim et al. 2011). In a 2017 follow-up experiment, sucrose was offered at four concentrations (1%, 5%, 10%, and 20%). Our ANCOVAs showed average recruitment remained highly sensitive to temperature ($P < 0.0001$; Appendix S1: Table S2) and sucrose concentration ($P < 0.0001$; Fig. 2, Appendix S1: Table S2). However, given the noisy data, there was not a significant interaction between temperature and sucrose concentration for either discovery or recruitment to sucrose vials ($P > 0.05$; Appendix S1: Table S2), and the slopes of the power laws did not approach statistical significance (Appendix S1: Table S3).

Discussion

Temperature can drive the activity of ectotherm assemblages in at least three ways. Higher temperatures release a constraint on metabolism, allowing ectotherms to generate and use more ATP; higher temperatures can increase the rate that resources are used and depleted from the body and hence increase demand; and ultimately higher temperatures cause all metabolic activity to slow then shut down when thermal limits are exceeded (Gillooly et al. 2001, Clarke and Fraser 2004). We generated and tested three quantitative predictions and found that activity in a prairie ant community accelerated with soil temperature consistent with release

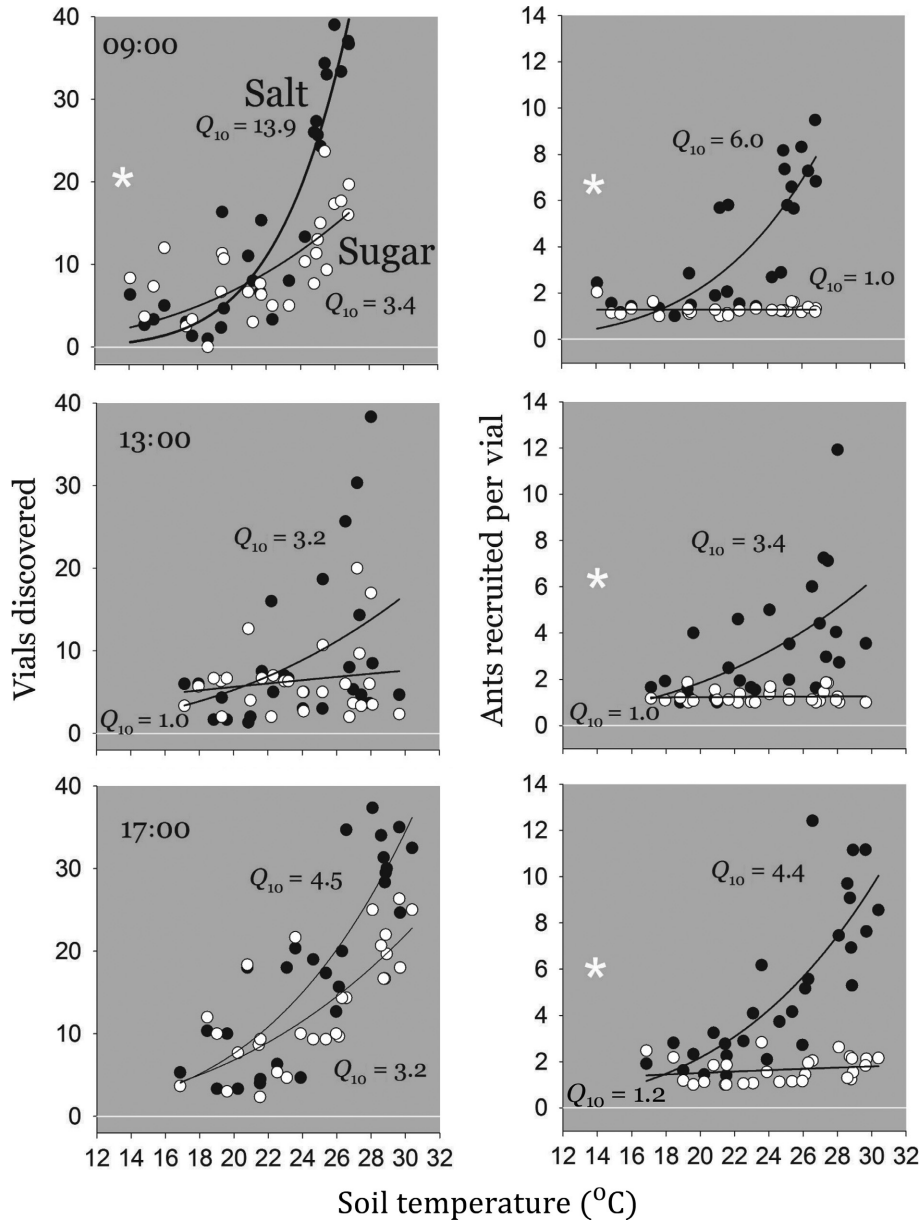


FIG. 1. Responses of an Oklahoma prairie ant community to vials filled with 0.5% NaCl solution and 1% sucrose solution by weight as a function of mean soil temperature in trials from April through October 2016. Each point is the mean response to 150 vials per nutrient, split into three transects of 50 vials run during each time period. Number of vials discovered is a measure of discovery; ants per vial is a measure of subsequent recruitment. Trials were run at 09:00, 13:00, and 17:00, representing gradually increasing soil temperature. Q_{10} values (see *Materials and Methods: Statistical analysis*) listed were calculated as the ratio of the rate of discovery or recruitment at 30°C vs. the rate at 20°C. Curves are best-fit power laws using the Marquardt-Levenberg algorithm and white asterisks represent a significant interaction (i.e., different slopes) using an ANCOVA analyzing $\log(Y) = \log(X)$.

of a basic metabolic constraint before shutting down at high temperatures. We found that demand for 0.5% sodium, a food resource more likely to be lost at higher temperatures, accelerated faster than the demand for 1% sucrose and had higher Q_{10} values than multiple sucrose concentrations (1–20%).

Our most novel discovery arises from the asssumption that two vital foods have different temperature sensitivities. Herbivore and decomposer activity is frequently constrained by sodium shortfall given the need of these trophic groups to enhance their body tissue concentrations 100-fold over the plants they consume (Kaspari et al. 2008, 2014, Clay et al. 2014, Snell-Rood et al. 2014). However, ionic nutrients like K^+, Na^+, and Cl^- that are water soluble (as well as water itself) are all subject to excretion, with dynamics driven by metabolic rate (Peters 1986). As a consequence, higher temperatures create proportionately greater demand for these resources than for those that are more easily stored, like sugars. In this study, we found similar discovery rates for sodium and sucrose at 13:00 and 17:00. However, even when we provided an ant community with sugar akin to that found from rich extrafloral nectaries (Völkl et al.

1999, Kay 2002, Petry et al. 2012) the Q_{10} value for recruitment to 0.5% NaCl was at least double the one for sucrose (Fig. 2), suggesting stronger temperature sensitivity for sodium relative to sucrose.

A second novel element is our focus on community behavior. A basic prediction from both metabolic and thermal ecology is that constraints on ectotherm activity should ease as an accelerated function of the organism's temperature. This acceleration is often found when measuring the performance of individuals (Dell et al. 2011) and at the scale of ecosystem processes (Anderson-Teixeira and Vitousek 2012). In contrast, the study of communities typically focuses not on the predicted similarities, but on the differences among species traits (Bennett and Lenski 1993, Cerdá et al. 1998, Feeley and Silman 2010). Here we show that the majority of individuals (and three of the four most common species) in a prairie ant community accelerate their foraging activity with temperature (Appendix S1: Fig. S5).

At the same time, this larger trend highlights the behavior of an outlier species, *F. pallidefulva*, which by consistently decreasing its foraging activity with temperature clearly diverges from the foraging pattern predicted by a metabolic approach. This exploration of thermal space "around the edges" of the community points to the role that active competition or species filtering may play in driving this alternate thermal niche (Rosenzweig 1995, Cerdá and Retana 2000, Kaspari et al. 2016*a*). For example, subordinate species can alter their resource preference or the time of day they are active in the presence of a dominant species (Lynch et al. 1980, Savolainen and Vepsäläinen 1988, Andersen 1992, Cerdá et al. 1998, Sanders and Gordon 2003). In our prairies, the numerically dominant *C. lineolata* often filled salt vials, potentially reducing opportunities for *F. pallidefulva* and other species to use these vials when *C. lineolata* is active. If so, then studies of foraging time and bait preferences of *F. pallidefulva* and other subordinate species should converge on those of the dominant *C. lineolata* in the lab or in baits protected from *C. lineolata*.

TABLE 2. ANCOVA tests of temperature sensitivity on average discovery ($\log_{10}$ number of vials with at least one ant) and average recruitment ($\log_{10}$ number of ants per vial) of ants.

Parameter	Discovery		Recruitment	
	F	Pr > *F*	*F*	Pr > *F*
09:00 (df = 1,49)				
$\log_{10}$(mean soil temperature)	48.68	<0.0001	25.08	<0.0001
Nutrient (NaCl vs. sucrose)	9.58	0.0033	21.91	<0.0001
Interaction	9.97	0.0027	27.02	<0.0001
13:00 (df = 1,50)				
$\log_{10}$(mean soil temperature)	4.65	0.0359	13.95	0.0005
Nutrient (NaCl vs. sucrose)	2.85	0.0977	10.32	0.0023
Interaction	2.99	0.0901	12.71	0.0008
17:00 (df = 1,52)				
$\log_{10}$(mean soil temperature)	68.94	<0.0001	43.16	<0.0001
Nutrient (NaCl vs. sucrose)	1.8	0.1860	19.95	<0.0001
Interaction	2.07	0.1562	25.15	<0.0001

Note: Separate ANCOVAs were conducted for each time of day (09:00, 13:00, or 17:00). We test the predictions of (1) more overall bait discovery at higher temperatures (2) higher overall discovery of salt vs. sugar baits, and (3) a steeper increase in discovery and recruitment to salt baits relative to sugar baits at higher temperatures.

Performance integrates over different measures of environmental temperature

During this study, we matched the ants in this prairie to temperatures they actually experience (Kearney and Porter

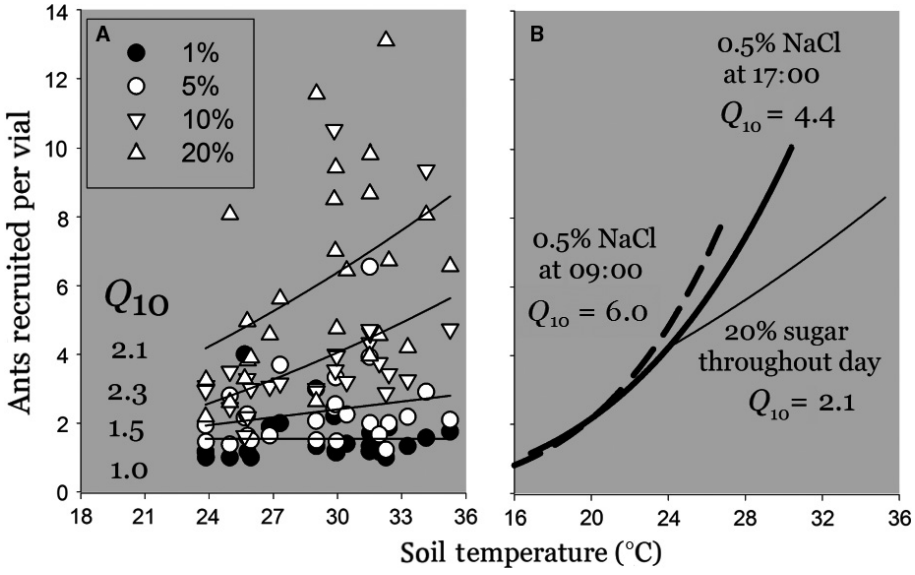


FIG. 2. Response of ant recruitment to different sugar concentrations over a range of soil temperatures. Curves are best fit power laws as in Fig. 1. Q_{10} values are listed next to the line they represent, calculated as the ratio of the rate of discovery or recruitment at 34°C vs. the rate at 24°C. (A) Study of the ant community at Pigtail Alley Prairie, Oklahoma, USA, an ant community composed of species similar to those at the OU Centennial Prairie, Oklahoma, USA, offered baits with four different sucrose concentrations (1%, 5%, 10%, or 20%). (B) Temperature recruitment curves of ants to NaCl baits at 09:00 and 17:00 at the OU Centennial Prairie and the entire-day recruitment curve to 20% sucrose baits at Pigtail Alley Prairie.

2009, Kaspari et al. 2015). Colonies that live in the soil experience a thermal environment that is predictable at a seasonal and daily timescale (Andrew et al. 2013, Stuble et al. 2013, Baudier et al. 2015). Specifically, soil temperature had a unimodal seasonal and daily distribution (Appendix S1: Fig. S2). Soil temperature also appeared to be the most important factor driving ant discovery of, and recruitment to, food (see also Dunn et al. 2007). One confounding factor, however, that may shape the foraging behavior of ants is colony size as both the number of workers produced (Markin 1970, Tschinkel 1993) and the speed at which broods develop (Porter 1988, Penick et al. 2017) changes with temperature throughout the year. In future studies, disentangling how colony size contributes to the nutritional demands of ant colonies across temporal changes in temperature will undoubtedly result in new and exciting insights.

Surface temperature can represent the microclimate worker ants are exposed to while foraging (O'Neill and Kemp 1990) and frequently correlates with the number of ant species foraging (Cerdá et al. 1998, Bestelmeyer 2000, Lessard et al. 2009, Wittman et al. 2010, Stuble et al. 2013). At the OU Centennial Prairie, for example, high surface temperatures were useful in predicting when the ant community began its midday shutdown (i.e., 16 species were recorded at 17:00, only eight at 13:00). Yet surface temperature can often be quite variable (Appendix S1: Fig. S2) and we posit that the resulting noisy foraging data at 13:00 likely arose in two ways, both based on insolation (Kearney and Porter 2009, Kaspari et al. 2015). First, early in the growing season, when soil was most exposed, high surface temperatures were common even when the air was still cool. Second, throughout the year, cloud cover could cool the soil surface and allow for higher midday foraging.

Future directions

Our results have two implications for the ecology of a warming world. First, if the performance of ectotherm consumers accelerates with temperature as predicted by metabolic and thermal ecology, then both the magnitude and starting point of any temperature change is key to predicting magnitude of the response (i.e., the Q_{10} from 10° to 20°C will be lower than that between 20° and 30°C). Put another way, in a warming world, the first response of ecosystem functions driven by consumers in ecosystems far from their thermal maximum (Deutsch et al. 2008) will be an acceleration, not a crash. One conclusion is somewhat paradoxical: that warm ecosystems, when warmed further, may show greater magnitudes of increase in herbivory, decomposition, seed dispersal and other ecosystem services driven by ectotherms than cooler ecosystems (or, perhaps, more variable responses as their thermal performance curves straddle the thermal optima).

Second, if the demand for ionic resources like sodium have strong thermal dependencies (Figs. 1 and 2), this reduces one opportunity for conservation in stressful environments. Consumers can choose to cease foraging to conserve storable resources like sugars; such a tactic is less viable for sodium, which is constantly pumped out of cells and excreted from the body, driving individuals closer to their minimum sodium set point. Thus, higher temperatures may release a community of consumers from a thermal constraint while increasing a sodium deficit in sodium poor environments. The size of an ectotherm community's activity Q_{10} (e.g., rate of herbivory or pollination) should thus, all else equal, be lower in inland ecosystems and higher in Na-rich coastal ecosystems (Kaspari et al. 2008).

In sum, evidence accumulates for the role of sodium shortfall as a constraint on terrestrial ectotherm assemblages (Kaspari et al. 2008, 2014, Clay et al. 2014, Snell-Rood et al. 2014). This study suggests an orthogonal factor, temperature, that can exacerbate or ameliorate the effects of low sodium supply. Increases in atmospheric CO_2 may enhance both temperature and carbohydrate production (Ainsworth and Long 2005). Soil nesting ants are likely to be buffered from the direct effects of increasing temperatures and may benefit from increasing production of exudates. However, the accelerating effects of temperature on sodium demands may constrain ability of ant colonies to exploit these carbohydrates.

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