Received: 11 February 2022 | Revised: 19 July 2022 | Accepted: 21 July 2022

DOI: 10.1002/ecy.3855

REPORT

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Temperature–habitat interactions constrain seasonal activity in a continental array of pitfall traps

Michael Kaspari[1] | **Michael D. Weiser**[1] | **Katie E. Marshall**[2] | **Cameron D. Siler**[1,3] | **Kirsten de Beurs**[4]

[1]Geographical Ecology Group, Department of Biology, University of Oklahoma, Norman, Oklahoma, USA

[2]Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada

[3]Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma, USA

[4]Department of Geography and Environmental Sustainability, University of Oklahoma, Norman, Oklahoma, USA

Correspondence
Michael Kaspari
Email: mkaspari@ou.edu

Funding information
U.S. National Science Foundation, Grant/Award Number: DEB 1702426

Handling Editor: Nicholas J. Gotelli

Abstract

Activity density (AD), the rate at which animals collectively move through their environment, emerges as the product of a taxon's local abundance and its velocity. We analyze drivers of seasonal AD using 47 localities from the National Ecological Observatory Network (NEON) both to better understand variation in ecosystem rates like pollination and seed dispersal as well as the constraints of using AD to monitor invertebrate populations. AD was measured as volume from biweekly pitfall trap arrays (ml trap^{-1} 14 days^{-1}). Pooled samples from 2017 to 2018 revealed AD extrema at most temperatures but with a strongly positive overall slope. However, habitat types varied widely in AD's seasonal temperature sensitivity, from negative in wetlands to positive in mixed forest, grassland, and shrub habitats. The temperature of maximum AD varied threefold across the 47 localities; it tracked the threefold geographic variation in maximum growing season temperature with a consistent gap of *ca.* 3°C across habitats, a novel macroecological result. AD holds potential as an effective proxy for investigating ecosystem rates driven by activity. However, our results suggest that its use for monitoring insect abundance is complicated by the many ways that both abundance and velocity are constrained by a locality's temperature and plant physiognomy.

KEYWORDS
activity density, habitat, temperature, thermal performance curve, thermal performance theory

INTRODUCTION

Evidence on insect declines in the Anthropocene continues to accumulate (reviewed in Wagner et al., 2021). Much of the evidence relies on methods that measure activity density (AD), the rate at which organisms collectively move through their environment (Kaspari & de Beurs, 2019). AD is the product of the abundance (numbers or biomass) and the velocity of individuals (Kaspari & de Beurs, 2019) and is frequently used as a proxy for rates of population interactions like predation rates and seed dispersal (Kaspari, 1993a, 1993b; Roslin et al., 2017; Sam et al., 2015). However, when AD is used to infer changes in abundance—as fluctuations in numbers from pitfall traps, malaise traps, windowpane traps (Gibb et al., 2019; Hallmann et al., 2017; Montgomery et al., 2021; O'Connell et al., 2010; Seibold et al., 2019; Southwood, 1978)—its interpretation requires circumspection.

Specifically, the challenge in monitoring programs using AD arises when changes in velocity alone—with or without changes in abundance—generate changes in AD. This is particularly true when comparing changes in AD across habitats. In two studies from monitoring networks in Germany (latitude range: 3°) AD trended with time or temperature in ways that differed (Seibold et al., 2019) or were invariant (Uhler et al., 2021) among a handful of habitat types. Likewise, in a continent-scale study across North America (latitude range: 46°), the thermal sensitivity of annual AD varied across four habitat categories, from positive linear (scrub), positive decelerating (grassland), unimodal (forests), to invariant (wetlands, Kaspari et al., 2022). Plant physiognomy appears to be a cause: temperature effects on insect velocity can vary systematically when habitat structure influences movement. This is particularly true when comparing flying insects (as in most of the German data referred to earlier) with cursorial insects that move along the ground (like those of the North American study). In the latter, seasonal variation in ground cover and stem density can add significant noise to monitoring efforts. Given the investment required in long-term monitoring (Montgomery et al., 2021; Wagner et al., 2021), understanding when and at what seasonal temperature to sample during the growing season is likely key to designing an effective monitoring program and interpreting its results.

A second challenge lies in predicting how and why the temperature of peak AD (T_{ADmax}) varies from place to place. A parallel question in Thermal Performance Theory (Deutsch et al., 2008; Kingsolver & Huey, 2008) seeks to predict the geography of T_{opt} (the temperature of an individual's maximum performance). Given that ectotherm performance tends to first increase then sharply decline with temperature (the thermal performance curve, Angilletta, 2009) Deutsch and colleagues predicted that a population acclimates/adapts its T_{opt} to both (1) track its environment's maximum temperature (T_{max}) and (2) maintain a buffer against the stochasticity of weather and the consequences of being out and about during a $\mathrm{CT}_{\mathrm{max}}$ event. They called this buffer the thermal safety margin (Deutsch et al., 2008). We propose a similar set of constraints to predict the geography of the T_{ADmax}.

Here we use biweekly trap data from the National Ecological Observatory Network's (NEON) North American monitoring array of pitfall traps (Levan, 2020) to test the hypothesis that seasonally varying temperatures predictably constrain and predict AD. We pose two questions: (1) Are biweekly temperatures necessary and sufficient to predict AD, and does this answer vary continentally with habitat? (2) Is the temperature of a locality's maximum AD (T_{ADmax}) also predictable, tracking the locality's maximum temperature? We use our results to clarify best practices when using AD in monitoring insect populations.

METHODS

The NEON (Figure 1a) was rolled out over a 5-year period (2014–2019) for a proposed 30 years of monitoring abiotic and biotic changes across the ecosystems of the United States (Alaska, Hawaii, Puerto Rico, and the 48 contiguous states). At each site, NEON identifies one to four habitat types based on National Land Cover Database land-cover codes, seven of which are used here: deciduous forest, mixed forest, evergreen forest, herbaceous grasslands (henceforth grasslands), pasture/hay, shrub scrub (henceforth scrub), and woody wetlands (henceforth wetlands) (Fry et al., 2008). At each NEON site, 10 pitfall trap arrays are distributed across the habitats (four traps per array from 2015 to 2017, three henceforth) (Levan, 2020) and sampled across the growing season, defined as the weeks when average minimum temperatures exceed 4°C for 10 days and ending when temperatures remain below 4°C for the same period.

Each trap is a 473-ml plastic container containing 150–250 ml of 1:1 deionized water and propylene glycol (summarized in Levan, 2020). Traps are placed flush in the soil with a square cover 1.5 cm above the trap. Traps are emptied and replaced every 14 days, with the contents of all traps from a given array combined and stored in 95% EtOH-filled 50-ml tubes (some arrays required multiple tubes). Here we used data from the 2017 and 2018 field seasons, from each habitat at a site for which we were able to obtain a full season of two pitfall arrays. This produced a total of 47 site–habitat combinations (henceforth "localities"), each representing four full-year array pitfall series (Figure 1; Appendix S1: Figure S1).

We measured biweekly AD (ml invertebrates trap^{-1} 14 days^{-1}) by quantifying the volume of invertebrates in EtOH in each storage tube by sight (repeatability of measure $r^2 = 0.99$, Kaspari et al., 2022). Some samples consisted of multiple tubes of dung and beetles and were judged as outliers in which traps acted as baits. Hence, we excluded the <2% of samples with three or more tubes of material. Our final data set included a total of 1961 biweekly pitfall samples.

For each biweekly sample period we calculated the mean air temperature as the average of the daily minimum and maximum over the 14 days preceding the sample date. We used the Daymet V4 database (Thorton et al., 2020), which provides gridded estimates of daily weather for most of North America. Daymet V4 interpolates and extrapolates daily meteorological station data from the National Oceanic and Atmospheric Administration's Global Historical Climatology Network. The spatial resolution of the gridded data set is 1 × 1 km. This data set was published as version 4 on 8 April 2021.

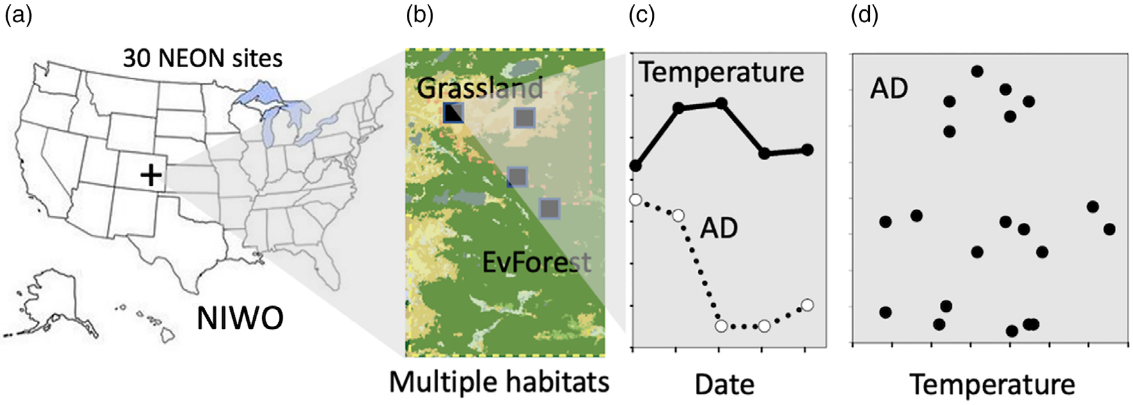

FIGURE 1 How we generate activity density (AD) data from National Ecological Observatory Network's (NEON) array of pitfall traps. (a) We relied on samples from 30 NEON sites for which at least two pitfall arrays are available for each habitat (here, Niwot Ridge Long-Term Ecological Research program LTER, a high-elevation site in Colorado). (b) Pitfall arrays (squares) for each site's National Land Cover Database class (here, herbaceous grasslands and evergreen forests) were loaned from the NEON repository from 2017 to 2018 for a total of four array samples per habitat. (c) Each year/array yields a trajectory of average air temperature (°C) and AD (ml trap^{-1} 14 days^{-1}) across biweekly sample periods (circles). (d) These are compiled to describe, for each locality (i.e., site habitat), the relationship between AD and temperature (e.g., 2 arrays × 2 years × 5 samples = 20 data points).

We used SAS 9.4 (SAS Institute, 2013) for all statistical analyses. To test the first hypothesis—that temperature constrains AD consistently across the six habitat types—we used two complementary analyses. First, we used a generalized linear mixed model (SAS Proc GLIMMIX), assuming a Gaussian distribution, to quantify variation in biweekly AD as a function of habitat (as a class variable) average biweekly temperature (a continuous variable), and we used year and array as a random variable. Second, because the scatterplot of AD versus temperature for the 1961 samples suggested a triangular constraint function, we analyzed the AD–temperature plot using quantile regression (Proc QuantReg), identifying the best fit linear relationship for the 0.9, 0.5, and 0.1 quantiles. Then we used a generalized linear mixed model as previously to test the hypothesis that the average biweekly T_{ADmax} of a locality (the mean from 2 years × 2 arrays) increased with the mean biweekly $T_{\max}$, consistently across the six habitat types, and that the gap between T_{ADmax} and $T_{\max}$ was consistent across habitats. Data are available online at Kaspari (2021).

RESULTS

Across 47 NEON localities (Appendix S1: Figure S1) the mean daily growing season temperature ranged threefold from 11–29°C in two of its grasslands: in Colorado (NEON site NIWO, 40° N) and Oklahoma (OAES, 35° N). The average maximum AD over the same area ranged fourfold, from 5.9 ml trap^{-1} 14 day^{-1} in an Alaska evergreen forest (DEJU) to 22.4 ml trap^{-1} 14 day^{-1} in a North Dakota grassland (NOGP). Broken down by the 47 localities, we observed considerable variation in plots of biweekly temperature with AD (Appendix S1: Figure S1).

Given the triangular scatterplot of AD versus temperature across the NEON network (Figure 2a) we analyzed the relationship—and the influence of habitat—in two complementary ways. First, a generalized linear model using all the biweekly data (Figure 2a) revealed very strong evidence for temperature effects on AD ($F_{1,1849} = 14.4$, $p < 0.0002$), strong evidence for its interaction with habitat ($F_{6,1849} = 3.1$, $p < 0.0051$), and moderate evidence for differences in average AD among habitats ($F_{6,1849} = 2.7$, $p < 0.012$). Analyzed individually with least-squares (LS) regression, AD increased with temperature in three habitats and decreased in a fourth (Figure 2a):

1. Grassland; AD ~ 0.13 T; $t_{1,308} = 2.6$, $p < 0.0091$; $r^2 = 0.02$;
2. Mixed forest; AD ~ 0.20 T; $t_{1,144} = 3.2$, $p < 0.0019$; $r^2 = 0.07$;
3. Scrub; AD ~ 0.37 T; $t_{1,253} = 6.5$, $p < 0.0091$; $r^2 = 0.14$;
4. Wetlands; AD ~ −0.18 T; $t_{1,110} = -2.8$, $p < 0.0070$; $r^2 = 0.07$.

The three remaining habitats revealed no clear relationship between AD and temperature.

To further explore whether temperature was necessary, but not sufficient, to predict AD, we ran quantile

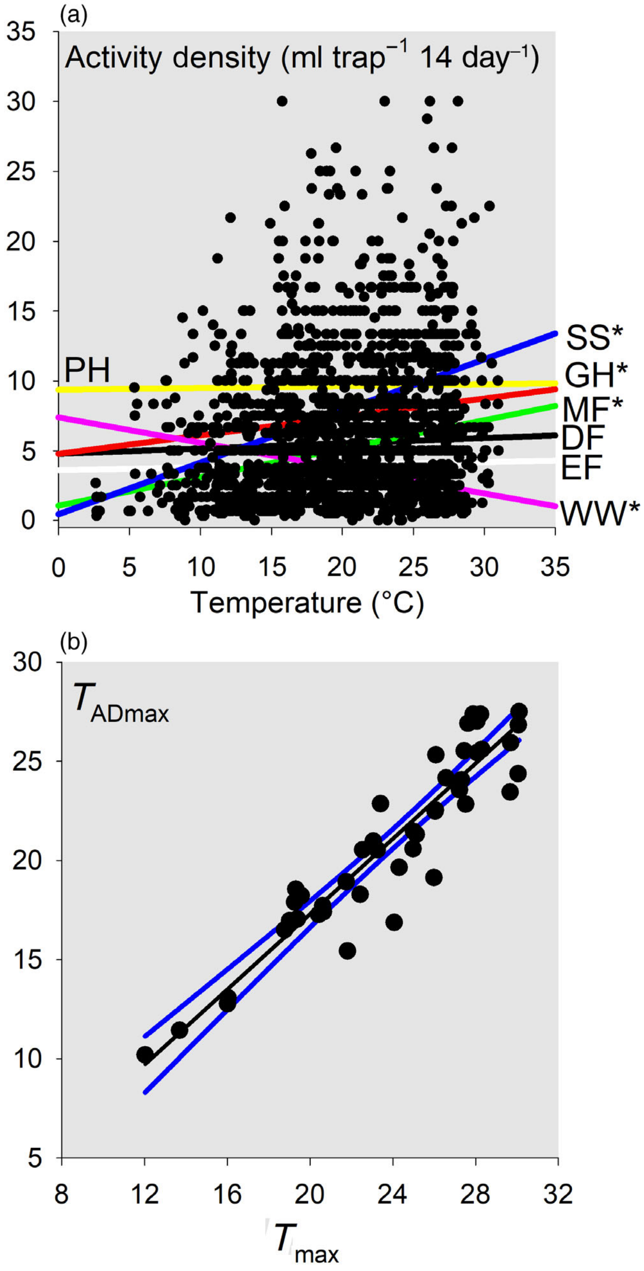

FIGURE 2 Drivers of activity density (AD) at National Ecological Observatory Network pitfall traps. (a) All biweekly data (circles) plotted against locality average temperature in that period. Colored lines represent best-fit linear regressions for each of seven habitat (National Land Cover Database class) types: SS, shrub scrub; GH, grassland herbaceous; MF, mixed forest; DF, deciduous forest; EF, evergreen forest; WW, woody wetland; PH, pasture hay. Asterisks indicate $p < 0.05$ for slope. (b) The temperature of maximum AD at the 47 localities increases linearly with a given locality's average maximum temperature (°C). Black line is best-fit least-squares regression, blues lines are the 95% confidence intervals.

regressions (quantiles 0.1, 0.5, 0.9) with slopes varied across the quantiles:

1. Quantile 0.1; AD ~ 0.03 T; $t = 3.14$; Pr > $|t| = 0.0017$;
2. Quantile 0.5; AD ~ 0.12 T; $t = 4.19$; Pr > $|t| = 0.0001$;
3. Quantile 0.9; AD ~ 0.23 T; $t = 4.23$; Pr > $|t| = 0.0001$;

Although all three quantiles provided strong to very strong evidence for temperature constraints, the 0.1 quantile was much flatter (i.e., a 1-ml increase in AD requiring a 33°C increase in temperature), whereas the median quantile required an 8° increase in temperature toward the same end, and the 90th quantile required a 4°C increase.

Across the 47 localities, the average maximum biweekly AD (T_{ADmax}) was a linear function of the locality's own average maximum air temperature (T_{max}, Figure 2b). Across a threefold range of T_{ADmax}—from 10°C in a Colorado grassland (NIWO) to 28°C in an Oklahoma grassland (OAES)—a generalized linear model found very strong evidence for a constraint of T_{max} that was consistent across habitats (T_{max}: $F_{1,39} = 253$, $p < 0.0001$; habitat: $F_{1,39} = 0.2$, $p < 0.97$). A LS regression ($T_{\mathrm{ADmax}} = -1.7 + 0.95T_{\mathrm{max}}$, $p < 0.0001$, $r^2 = 0.87$) revealed a linear relationship (test of slope = 1, $F_{1,45} = 0.86$, $p = 0.36$). The average gap between T_{ADmax} and T_{max} (median 2.8°C) was remarkably constant across the habitat types (GLM $F_{1,40} = 0.25$ $p = 0.96$), with least-square means revealing T_{ADmax}'s from 2.0°C below T_{max} (wetlands) to 3.4°C (scrub).

DISCUSSION

Ectotherm activity is frequently an increasing function of temperature up to some maximum (reviewed in Angilletta, 2009). Less is known about ectotherm assemblages, even as that collective behavior is key to a range of community interactions and ecosystem services (Del Toro et al., 2012; Ness et al., 2004), including the rate at which predators find their prey (Roslin et al., 2017), herbivores find their host plants, and mutualists find each other. In an earlier analysis of NEON pitfall AD from Alaska to Puerto Rico (Kaspari et al., 2022), annual AD increased linearly with average growing season temperature (scrub), increased but decelerated (grasslands), and was unimodal (forest), accounting for 33% to >92% of the variation. Here we show that this geographic pattern is weakly recapitulated at a biweekly grain over the season, where temperature primarily devolves into a constraint function: as temperatures increase and decrease throughout the growing season, high temperatures are necessary but not sufficient to generate high levels of AD. However, one feature of a locality—the temperature of its maximum AD (T_{ADmax})—was a surprisingly consistent, linear function of the threefold geographic variation in maximum biweekly temperature across the NEON network, with a median of *ca*. 3°C across the seven habitats.

The macroecology of AD

Extending earlier studies that reveal the strong influence of local micro- and macroclimate on the mean and variance in body temperature (Huey & Preston Webster, 1976; Navas et al., 2013), we find that NEON pitfall arrays across North America demonstrate a clear linear relationship between a community's T_{ADmax} and its locality's $T_{\max}$, accounting for 87% of the geographic variation. Although constraint traits like population $\mathrm{CT}_{\max}$s are frequently assumed to be fixed by deep time and phylogeny (Searcy & Bradley Shaffer, 2016; Sibly et al., 2012), the emergent properties of ecosystems like T_{ADmax} appear highly malleable, tracking local temperature.

Such tracking can arise through a variety of mechanisms. For $\mathrm{CT}_{\max}$, ecosystems may filter co-occurring populations, favoring a different suite of species (i.e., those with higher thermal maxima) as ecosystems warm (Bujan, Roeder, Yanoviak, & Kaspari, 2020; Kaspari et al., 2015; Roeder et al., 2021). A second driver is seasonal plasticity in thermal traits, like the community of grassland ants whose population's $\mathrm{CT}_{\max}$ can vary by +5°C across the growing season (Bujan, Roeder, de Beurs, et al., 2020). Understanding the drivers of this threefold variation in T_{ADmax} is a critical next step in predicting Anthropocene changes in species range and abundance, as well as the ecosystem services provided by invertebrates.

Using AD in insect monitoring: Prospects and challenges

Our results contrast with those from a network of 179 localities in German Bavaria spanning 3° latitude (Uhler et al., 2021). Like them, we found the signature of overall linear increases in trap catch with temperature (although they did not, to our knowledge, analyze evidence for a constraint function). However, Uhler et al. (2021) found no effect of habitat (albeit across three types: forest, agricultural, urban). Our broader geographic extent (from 18° to 64° N and seven habitat types) revealed changing temperature sensitivity with habitat, from negative (wetlands) to absent (pasture/hay, evergreen and deciduous forests) to positive (scrub, grassland, and mixed forest). We thus provide further evidence that plant physiognomy (e.g., the plant stems that crowd the soil surface) can obscure temperature sensitivity in pitfall capture rates by interfering with the ease of movement across the soil surface.

Can AD be effective in monitoring changes in abundance, especially after accounting for changes in physiognomy? Two challenges endure: how to factor out the effects of environmental temperature on velocity, and the many factors that drive temperature sensitivity. First an ectotherm's body temperature sums over convective (i.e., air temperature) and radiative (e.g., sun vs. shade) heating (Angilletta, 2009; Kaspari et al., 2015; Prather et al., 2018); our Daymet temperatures reflect only the former (Thorton et al., 2020). As a result, the boundary layer environments commonly found on sunny days at the soil surface can diverge from air temperatures centimeters above (Kaspari et al., 2015; Oke, 1978; Pincebourde et al., 2021; Spicer et al., 2017). Refinements in sensor distribution and biometeorology will undoubtedly improve the precision and accuracy of our AD–temperature curves and, with it, monitoring (Kearney & Porter, 2009; Pincebourde & Casas, 2019; Potter et al., 2013; Sunday et al., 2014).

Second, although metabolic rates do generally increase with temperature, they do so at widely varying rate constants (Dell et al., 2011). For example, a review of 24 ant species (Hurlbert et al., 2008) revealed *ca*. a 1 $\mathrm{cm\ s^{-1}}$ increase in velocity for every 8°C increase in temperature, but one varying with starting temperature and species; a second study of 88 tropical ant species revealed a range of (mostly) positive temperature–velocity curves (Kaspari et al., 2015). Moreover, velocity also increases with body size as *ca*. $\mathrm{mass}^{0.25}$ (Hurlbert et al., 2008) and varies with diet (Prather et al., 2018). The volume of the 100+ diverse populations found in a NEON pitfall trap likely integrates over all this variation.

In sum, the NEON pitfall network—given its geographic extent, biweekly resolution, and emphasis on ecological communities—is an unprecedented resource for monitoring invertebrate populations. We conclude that decreases in AD with moderate increases in temperature support a working hypothesis of decreased abundance (and the converse). More difficult to interpret are cochanges in AD and temperature, where, for example, higher temperatures can promote higher velocities, higher abundance, or both. Improvements in temperature mapping and the precision and ubiquity of temperature-sensitivity data in insect populations will undoubtedly help. But so too will ancillary measures aimed at directly quantifying abundance. Two long-term studies of ant communities on two continents (Gibb et al., 2019; Kaspari et al., 2020) are instructive in this regard. Both revealed 20-year increases in AD with warming. However, in one—when square meter plots were used to add an independent measure of abundance—increases in both velocity and abundance became apparent (Kaspari et al., 2020). Such accurate, distributed measures of animal abundance, never easy to obtain, are worth the investment if ecologists are to predict the future of Earth's ecosystems.

ACKNOWLEDGMENTS

This work was supported by a grant from the National Science Foundation, DEB 1702426. KEM is supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant. The manuscript benefited greatly from two anonymous reviewers.

CONFLICT OF INTEREST

The authors report no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Kaspari, 2021) are available in the Open Science Framework at https://doi.org/10.17605/OSF.IO/6EZST.

ORCID

Michael Kaspari https://orcid.org/0000-0002-9717-5768
Michael D. Weiser https://orcid.org/0000-0001-9080-0834
Katie E. Marshall https://orcid.org/0000-0002-6991-4957
Cameron D. Siler https://orcid.org/0000-0002-7573-096X
Kirsten de Beurs https://orcid.org/0000-0002-9244-3292

REFERENCES

Angilletta, M. J. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford, UK: Oxford University Press.

Bujan, J., K. A. Roeder, K. de Beurs, M. D. Weiser, and M. Kaspari. 2020. "Thermal Diversity of North American Ant Communities: Cold Tolerance but Not Heat Tolerance Tracks Ecosystem Temperature." *Global Ecology and Biogeography* 29(9): 1486–94. https://doi.org/10.1111/geb.13121.

Bujan, J., K. A. Roeder, S. P. Yanoviak, and M. Kaspari. 2020. "Seasonal Plasticity of Thermal Tolerance in Ants." *Ecology* 101: e03051.

Del Toro, I., R. R. Ribbons, and S. L. Pelini. 2012. "The Little Things that Run the World Revisited: A Review of Ant-Mediated Ecosystem Services and Disservices (Hymenoptera: Formicidae)." *Myrmecological News* 17: 133–46.

Dell, A. I., S. Pawar, and V. M. Savage. 2011. "Systematic Variation in the Temperature Dependence of Physiological and Ecological Traits." *Proceedings of the National Academy of Sciences* 108(26): 10591–6.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. "Impacts of Climate Warming on Terrestrial Ectotherms across Latitude." *Proceedings of the National Academy of Sciences* 105(18): 6668–72. https://doi.org/10.1073/pnas.0709472105 http://www.pnas.org/content/105/18/6668.abstract.

Fry, J. A., M. J. Coan, C. G. Homer, D. K. Meyer, and J. D. Wickham. 2008. "Completion of the National Land Cover Database (NLCD) 1992–2001 Land Cover Change Retrofit Product." *US Geological Survey Open-File Report* 1379: 18.

Gibb, H., B. F. Grossman, C. R. Dickman, O. Decker, and G. M. Wardle. 2019. "Long-Term Responses of Desert Ant Assemblages to Climate." *Journal of Animal Ecology* 88: 1549–63. https://doi.org/10.1111/1365-2656.13052.

Hallmann, C. A., M. Sorg, E. Jongejans, H. Siepel, N. Hofland, H. Schwan, W. Stenmans, A. Müller, H. Sumser, and T. Hörren. 2017. "More than 75 Percent Decline over 27 Years in Total Flying Insect Biomass in Protected Areas." *PloS ONE* 12(10): e0185809.

Huey, R. B., and T. Preston Webster. 1976. "Thermal Biology of Anolis Lizards in a Complex Fauna: The Christatellus Group on Puerto Rico." *Ecology* 57(5): 985–94.

Hurlbert, A. H., F. Ballantyne, IV, and S. Powell. 2008. "Shaking a Leg and Hot to Trot: The Effects of Body Size and Temperature on Running Speed in Ants." *Ecological Entomology* 33: 144–54.

Kaspari, M. 1993a. "Body Size and Microclimate Use in Neotropical Granivorous Ants." *Oecologia* 96: 500–7.

Kaspari, M. 1993b. "Removal of Seeds from Neotropical Frugivore Droppings." *Oecologia* 95: 81–99.

Kaspari, M. 2021. "Seasonality of Activity Density." OSF. https://doi.org/10.17605/OSF.IO/6EZST.

Kaspari, M., J. Bujan, K. A. Roeder, K. de Beurs, and M. D. Weiser. 2020. "Species Energy and Thermal Performance Theory Predict 20-Yr Changes in Ant Community Abundance and Richness." *Ecology* 100: e02888. https://doi.org/10.1002/ecy.2888.

Kaspari, M., N. A. Clay, J. Lucas, S. P. Yanoviak, and A. Kay. 2015. "Thermal Adaptation Generates a Diversity of Thermal Limits in a Rainforest Ant Community." *Global Change Biology* 21(3): 1092–102.

Kaspari, M., and K. de Beurs. 2019. "On the Geography of Activity: Productivity but Not Temperature Constrains Discovery Rates by Ectotherm Consumers." *Ecosphere* 10(2): e02536.

Kaspari, M., M. D. Weiser, K. E. Marshall, M. Miller, C. Siler, and K. de Beurs. 2022. "Activity Density at a Continental Scale: What Drives Invertebrate Biomass Moving across the Soil Surface?" *Ecology* 103(1): e03542. https://doi.org/10.1002/ecy.3542.

Kearney, M., and W. Porter. 2009. "Mechanistic Niche Modelling: Combining Physiological and Spatial Data to Predict species' Ranges." *Ecology Letters* 12(4): 334–50.

Kingsolver, J. G., and R. B. Huey. 2008. "Size, Temperature, and Fitness: Three Rules." *Evolutionary Ecology Research* 10: 251–68.

Levan, K. 2020. "NEON User Guide to Ground Beetle Sampled from Pitfall Traps." https://data.neonscience.org/documents/10179/2237401/NEON_beetle_userGuide_vC/39803cdd-4278-e23e-6ea7-958cbb44329f.

Montgomery, G. A., M. W. Belitz, R. P. Guralnick, and M. W. Tingley. 2021. "Standards and Best Practices for Monitoring and Benchmarking Insects." *Frontiers in Ecology and Evolution* 8: 513.

Navas, C. A., J. M. Carvajalino-Fernández, L. P. Saboyá-Acosta, L. A. Rueda-Solano, and M. A. Carvajalino-Fernández. 2013.

"The Body Temperature of Active Amphibians along a Tropical Elevation Gradient: Patterns of Mean and Variance and Inference from Environmental Data." *Functional ecology* 27(5): 1145–54.

Ness, J. H., J. L. Bronstein, A. N. Andersen, and J. N. Hollandc. 2004. "Ant Body Size Predicts Dispersal Distance of Ant-Adapted Seeds: Implication of Small-Ant Invasions." *Ecology* 85: 1244–50.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2010. *Camera Traps in Animal Ecology: Methods and Analyses*. Berlin: Springer Science & Business Media.

Oke, T. R. 1978. *Boundary Layer Climates*. New York, NY: Methuen and Co.

Pincebourde, S., and J. Casas. 2019. "Narrow Safety Margin in the Phyllosphere during Thermal Extremes." *Proceedings of the National Academy of Science USA* 116(12): 5588–96.

Pincebourde, S., M. E. Dillon, and H. Arthur Woods. 2021. "Body Size Determines the Thermal Coupling between Insects and Plant Surfaces." *Functional Ecology* 35(7): 1424–36. https://doi.org/10.1111/1365-2435.13801.

Potter, K. A., H. Arthur Woods, and S. Pincebourde. 2013. "Microclimatic Challenges in Global Change Biology." *Global Change Biology* 19: 2932–9.

Prather, R. M., K. A. Roeder, N. J. Sanders, and M. Kaspari. 2018. "Using Metabolic and Thermal Ecology to Predict Temperature Dependent Ecosystem Activity: A Test with Prairie Ants." *Ecology* 99(9): 2113–21.

Roeder, K. A., J. Bujan, K. M. de Beurs, M. D. Weiser, and M. Kaspari. 2021. "Thermal Traits Predict the Winners and Losers under Climate Change: An Example from North American Ant Communities." *Ecosphere* 12(7): e03645.

Roslin, T., B. Hardwick, V. Novotny, W. K. Petry, N. R. Andrew, A. Asmus, I. C. Barrio, Y. Basset, A. L. Boesing, and T. C. Bonebrake. 2017. "Higher Predation Risk for Insect Prey at Low Latitudes and Elevations." *Science* 356(6339): 742–4.

Sam, K., B. Koane, and V. Novotny. 2015. "Herbivore Damage Increases Avian and Ant Predation of Caterpillars on Trees along a Complete Elevational Forest Gradient in Papua New Guinea." *Ecography* 38(3): 293–300.

SAS_Institute. 2013. *SAS (R) 9.4 Statements: Reference*. Cary, NC: SAS Institute Inc.

Searcy, C. A., and H. Bradley Shaffer. 2016. "Do Ecological Niche Models Accurately Identify Climatic Determinants of Species Ranges?" *The American Naturalist* 187(4): 423–35.

Seibold, S., M. M. Gossner, N. K. Simons, N. Blüthgen, J. Müller, D. Ambarlı, C. Ammer, J. Bauhus, M. Fischer, and J. C. Habel. 2019. "Arthropod Decline in Grasslands and Forests Is Associated with Landscape-Level Drivers." *Nature* 574(7780): 671–4.

Sibly, R. M., J. H. Brown, and A. Kodric-Brown. 2012. *Metabolic Ecology: A Scaling Approach*. New York, NY: John Wiley & Sons.

Southwood, T. R. E. 1978. *Ecological Methods*, 2nd ed. London, UK: Chapman and Hall.

Spicer, M. E., A. Y. Stark, B. J. Adams, R. Kneale, M. Kaspari, and S. P. Yanoviak. 2017. "Thermal Constraints on Foraging of Tropical Canopy Ants." *Oecologia* 183(4): 1007–17.

Sunday, J. M., A. E. Bates, M. R. Kearney, R. K. Colwell, N. K. Dulvy, J. T. Longino, and R. B. Huey. 2014. "Thermal-Safety Margins and the Necessity of Thermoregulatory Behavior across Latitude and Elevation." *Proceedings of the National Academy of Sciences* 111(15): 5610–5.

Thorton, P. R., R. Shreshtha, M. M. Thornton, S. C. Kao, Y. Wei, and B. E. Wilson. 2020. *Gridded Daily Weather Data for North America with Comprehensive Uncertainty Quantification - Daymet Version 4*. Oak Ridge, TN: Oakridge National Laboratory.

Uhler, J., S. Redlich, J. Zhang, T. Hothorn, C. Tobisch, J. Ewald, S. Thorn, et al. 2021. "Relationship of Insect Biomass and Richness with Land Use along a Climate Gradient." *Nature Communications* 12(1): 5946. https://doi.org/10.1038/s41467-021-26181-3.

Wagner, D. L., E. M. Grames, M. L. Forister, M. R. Berenbaum, and D. Stopak. 2021. "Insect Decline in the Anthropocene: Death by a Thousand Cuts." *Proceedings of the National Academy of Sciences* 118(2): e2023989118.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Kaspari, Michael, Michael D. Weiser, Katie E. Marshall, Cameron D. Siler, and Kirsten de Beurs. 2022. "Temperature–Habitat Interactions Constrain Seasonal Activity in a Continental Array of Pitfall Traps." *Ecology* e3855. https://doi.org/10.1002/ecy.3855