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Karl A. Roeder
USDA-ARS, karl.roeder@usda.gov

Skylar Drey
USDA-ARS, skylar.drey@usda.gov

Jesse D. Daniels
USDA-ARS, jesse.daniels@usda.gov

Diane V. Roeder
Augustana University, dianevroeder@gmail.com

Jackson A. Helms IV
jacksonhelmsiv@gmail.com

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New Record of the Pavement Ant, *Tetramorium immigrans* (Hymenoptera: Formicidae), in South Dakota with Notes on its Thermal Tolerance and Geographic Distribution

Karl A. Roeder[1,*], Skylar Drey[1], Jesse D. Daniels[1], Diane V. Roeder[2], and Jackson A. Helms IV[3]

[1] USDA, Agricultural Research Service, North Central Agricultural Research Laboratory, Brookings, SD 57006, USA.

[2] Augustana University, Biology Department, Sioux Falls, SD 57197, USA.

[3] Westlake, OH, USA.

[*] Corresponding author: (e-mail: karl.roeder@usda.gov)

Abstract

The pavement ant, *Tetramorium immigrans* Santschi, is an abundant and widespread species across large portions of the United States. Yet despite its current distribution in Northeastern, Midwestern, Pacific, and Western states, there is a surprising lack of records from the Great Plains. Here we present an updated county list of *T. immigrans* from museum collections and research grade observations (459 counties; ~15% of US counties), highlighting the first records from one Great Plains state—South Dakota. Observations on community science platforms since 2006 have undoubtedly increased the awareness of *T. immigrans* (+329 counties; ~72% of all county records), however we posit that such platforms may also highlight the dispersal limitations of this species into the less urban, colder Northern Great Plains states of Montana, Nebraska, North Dakota, South Dakota, and Wyoming (~5% of 291 counties). As such, we offer novel information on *T. immigrans*' thermal biology including measurements of critical thermal limits, knock-down resistance, and chill coma recovery. While *T. immigrans* can likely tolerate the warm summer temperatures found in South Dakota due to its heat tolerance hovering around 46 °C, its lower ability to tolerate cold winter conditions may be a possible mechanism for its limited dispersal.

Keywords: ants, community science, distribution record, introduced species, museum collections, thermal biology

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Ants are an abundant, diverse, and conspicuous clade of insects that are present in almost every terrestrial ecosystem globally (Guénard et al. 2017, Kaspari et al. 2019, Schultheiss et al. 2022). From lowland deserts to montane forests, there are approximately 14000 species of ants currently described that vary in size, shape, and function (Kaspari and Weiser 1999, Del Toro et al. 2012, Parr et al. 2017). While many of these species fill important ecological niches within their native range, several others are described as invasive, including five of the top one hundred worst invasive species—*Anoplolepis gracilipes* (Smith), *Linepithema humile* (Mayr), *Pheidole megacephala* (Fabricius), *Solenopsis invicta* Buren, *Wasmannia auropunctata* (Roger)—due to their serious impact on biodiversity and human activities (Lowe et al. 2004). Many less invasive, but still non-native ant species have also been relocated around the globe either on purpose or inadvertently by humans; 200 of which have seen their global ranges increase (Bertelsmeier et al. 2017, Bertelsmeier 2021, Gippet et al. 2023).

The pavement ant, *Tetramorium immigrans* Santschi, is one such species that was introduced into the United States over 100 years ago. Since 1903, *T. immigrans* has been expanding from the east coast of the United States and now occupies at least 40 states (Helms et al. 2019, Zhang et al. 2019, Maxcer et al. 2023). In contrast to many of the invasive ants found in the southern United States, *T. immigrans* excels in disturbed habitats of the more urbanized eastern seaboard as well as more rural agricultural areas in the Midwest (Helms et al. 2020, Roeder and Harmon-Threatt 2022, Moss et al. 2022). Indeed, *T. immigrans* is quite adaptable as a species and colonies can shift their dietary needs to resource availability as a true generalist (Penick et al. 2015, Helms et al. 2021). Queens of *T. immigrans* colonies are thought to be monogynous and polyandrous, producing enough eggs to maintain approximately 15000 workers per colony (Cordonnier et al. 2020, Moss et al. 2022).

Such colony sizes are larger than ~88% of the records from one of the largest recent compilations of ant colony sizes (Burchill and Moreau 2016). Yet despite these life history traits and the expanding range of *T. immigrans* in the US, there is a surprising lack of records from the Great Plains.

The status of insect distributions across most of the Great Plains is relatively unknown, as check lists and taxonomic keys often focus on species east of the Mississippi River and West of the Rocky Mountains. For the Northern Great Plains, this knowledge gap is further exacerbated as large portions of land are occupied by a small human population with few historical and contemporary insect bioinventories. However, there have been recent efforts to address these knowledge gaps for charismatic insect groups like bumble bees (Dolan et al. 2017, Bell and Tronstad 2021, Martens et al. 2022, Pei et al. 2022), suggesting high levels of diversity can exist even in these colder, northerly locales. For other less fortunate groups like ants though, little information exists for most species because experts are lacking and the few check lists that do exist (e.g. Wheeler and Wheeler 1944) are in desperate need of updates. Sampling deficiencies limit documentation of non-native species introductions like *T. immigrans* as no records of this species, to our knowledge, exist in museum collections for states like South Dakota (KAR personal communications). Here, we present an updated distribution of *T. immigrans* in the United States from museum collections and research grade observations, highlighting the first records from one Great Plains state—South Dakota. We further offer novel information on *T. immigrans*' thermal biology including measurements of critical thermal limits, knock-down resistance, and chill coma recovery as a possible mechanism for its limited dispersal.

Materials and Methods

Historical specimen and observational records. We compiled *T. immigrans* occurrence records for 3143 county and county equivalent Federal Information Processing System (FIPS) codes from the United States Census Bureau (https://www.census.gov) from 1903 to 2022. Databases queried included the Global Biodiversity Information Facility (GBIF) and the Symbiota Collections of Arthropods Network (SCAN). Combined, these databases contain information from over twenty institutional insect collections and community science platforms like iNaturalist, from which we only used observations that were considered 'Research Grade'. Additional collections in Brookings County, South Dakota were made by the authors from October 2022 to January 2023.

Thermal Biology. We quantified four thermal traits for *T. immigrans* from Brookings, SD: critical thermal maximum and minimum (hereafter CT_{max} and CT_{min}), knock-down resistance, and chill coma recovery. CT_{max} and CT_{min} were determined using a dynamic ramping protocol that is commonly used to measure critical limits in ants (Roeder et al. 2021, Nascimento et al. 2022). We placed 60 individual ants (30 for CT_{max} and 30 for CT_{min}) into 1.5 ml microcentrifuge tubes that had been modified with cotton to remove a thermal refuge in the cap. Microcentrifuge tubes were then placed into a prewarmed/precooled EchoThermTM IC20 heating/chilling dry bath set at 25 °C (Torrey Pines Scientific, Carlsbad, CA, USA). During each thermal assay, we checked ants every 10 min to see if they had reached their critical thermal limit by rotating the vials and looking for a righting response. Dry bath temperature was then increased/decreased by 2 °C (ramping rate = 0.2 °C min^{-1}) and the process was repeated until all ants had lost muscle control.

After determining the critical thermal limits for *T. immigrans*, we used new sets of ants to assess how long individuals could survive at temperatures near their critical thermal maxima (i.e. knock-down resistance) and the length of time it took an ant to recover from a reversible, paralyzed state known as a chill coma (i.e. chill coma recovery). Knock-down resistance was determined by placing 15 individual ants into 1.5 ml microcentrifuge tubes in a dry bath set at a certain temperature. We then checked ants every 10 min for 120 min to determine if and at what time individuals could no longer right themselves. Temperature values tested ranged from 46 °C, the first temperature where all ants lost muscle control in the first 10 min, down to 39 °C, the temperature where all ants survived for the entire 120 min. Chill coma recovery was determined by placing 15 individual ants into 1.5 ml microcentrifuge tubes in a dry bath set to 0 °C for 2, 4, 6, 8, 10, 12, 18, or 24 hours. We then removed ants from the dry bath after the elapsed time and recorded how long it took individuals to right themselves within a 2-hour observation period at ambient room temperature (22 °C). A new set of 15 ants was used for each temperature treatment to determine knock-down resistance (8 temperature treatments) and for each time treatment to determine chill coma recovery (8 time treatments). Knock-down resistance and chill coma recovery were compared using the survdiff function, a log-rank test to compare two or more survival curves, in the "survival" package (Therneau 2020).

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Survival curves were then visualized using Kaplan-Meier plots. All analyses were run in R, version 4.0.1 (2020).

Tetramorium immigrans Santschi, 1927 (Hymenoptera: Formicidae)

Material examined: Specimens were collected from October 2022 to January 2023 at the USDA-ARS North Central Agricultural Research Laboratory in Brookings, South Dakota (Latitude 44.34°, Longitude -96.79°, Elevation 503.10m). Ants were initially discovered foraging on dead insects and sunflower chaff in buildings. We then used a combined tuna/honey bait to lure hundreds of individuals out of multiple holes near the base of walls to confirm the presence of full colonies. Ten specimens were pinned and deposited as vouchers in the Severin-McDaniel Insect Research Collection at South Dakota State University and the reference collection at the North Central Agricultural Research Laboratory (Specimen codes: E2022-41-1 to E2022-41-10). Specimens were identified using keys and compared with reference material in the authors' personal collection from other Midwestern states (Fisher and Cover 2007, Wagner et al. 2017).

Results and Discussion

Our search resulted in 4295 records of *T. immigrans* across 459 counties in the United States (Fig. 1). Recent observations from community science platforms (n = 3032) accounted for most new county records (+329 unique counties) compared to museum collections that were more historical in nature (n = 1263 records; 130 counties occupied). The increased use of community science platforms between 2015 and 2020 coincided with a ~9.6-fold increase in known distribution as observational records alone rose from 29 to 277 occupied counites. However, few records exist for the Northern Great Plains states of Montana, Nebraska, North Dakota, South Dakota, and Wyoming (~5% of 291 possible counties in these states). Our collection of *T. immigrans* in Brookings, SD during the winter of 2022 represents not only a new county record, but the first specimens vouchered and deposited for the state. Only three prior research grade observations have been made thus far: two in June/September of 2022 in Minnehaha County and the other in August of 2021 in Douglas County. These results suggest *T. immigrans* may be recently introduced to South Dakota as all confirmed records in the state have occurred in the past two years.

After specimens were identified as *T. immigrans*, we collected ants from buildings in Brookings, SD to quantify various aspects of its thermal biology. CT_{max} ranged from 40 to 48 °C with a mean of 45.7 °C and a median of 46 °C (Fig. 2a). CT_{min} varied slightly less, ranging from 4 to 10 °C with a mean of 6.3 °C and a median of 6 °C (Fig. 2c). Overall, this represents an average thermal range of 39.4 °C, which fits well within commonly reported values across the ant phylogeny and the *Tetramorium* clade specifically (Diamond and Chick 2018, Bujan et al. 2020). Knock-down resistance of ants increased as temperature decreased such that all ants lost muscle control in the first 10 min at 46 °C and all ants survived for 120 min at 39 °C (Fig. 2b; $\chi^2 = 208$, df = 7, $P < 0.001$). As seen with other species, heat tolerance traits like CT_{max} and knock-down resistance are seemingly correlated (Roeder and Daniels 2022, Willot et al. 2022) with knock-down resistance providing additional information on optimal temperatures in which activity can be maximized. We posit that *T. immigrans* can likely perform well in temperatures up to 39 °C. Interestingly, Sioux Falls—the largest urban area in the state—has rarely approached such heat limiting temperatures over the past five years as maximum air temperatures average around 36.8 °C while maximum soil temperatures measured in the surface of bare soil up to 10 cm reside around 28.9 °C (South Dakota Mesonet; mesonet.sdstate.edu).

In contrast to South Dakota's warm summer climate, winter represents a different challenge: minimum air temperatures can drop below –20 °C with soil temperatures routinely below 0 °C (South Dakota Mesonet; mesonet.sdstate.edu). Hostile conditions below the cold tolerance of *T. immigrans* likely limit their distribution to heated buildings and urban environments. This is supported by our observations in which we have yet to collect *T. immigrans* from any ongoing projects in nearby fields of alfalfa, corn, oats, pea, soybean, sunflower, and wheat (KAR personal observation). Yet *T. immigrans* may be able to tolerate some cold as all ants survived exposure to 0 °C for at least 24 hours with chill coma recovery time increasing with exposure time in a linear fashion (Fig. 2d; $\chi^2 = 249$, df = 7, $P < 0.001$).

Future spread into the Northern Great Plains. At the end of 2022, the world's human population was rapidly approaching eight billion with the United States maintaining the third largest populace at over 300 million individuals (United States Census Bureau; https://www.census.gov/). Projections suggest that a large proportion of these people will reside in ever growing urban areas that often provide habitat for introduced species like the pavement ant, *T. immigrans*. We were curious, though, if data existed to support the hypothesis that *T. immigrans* was

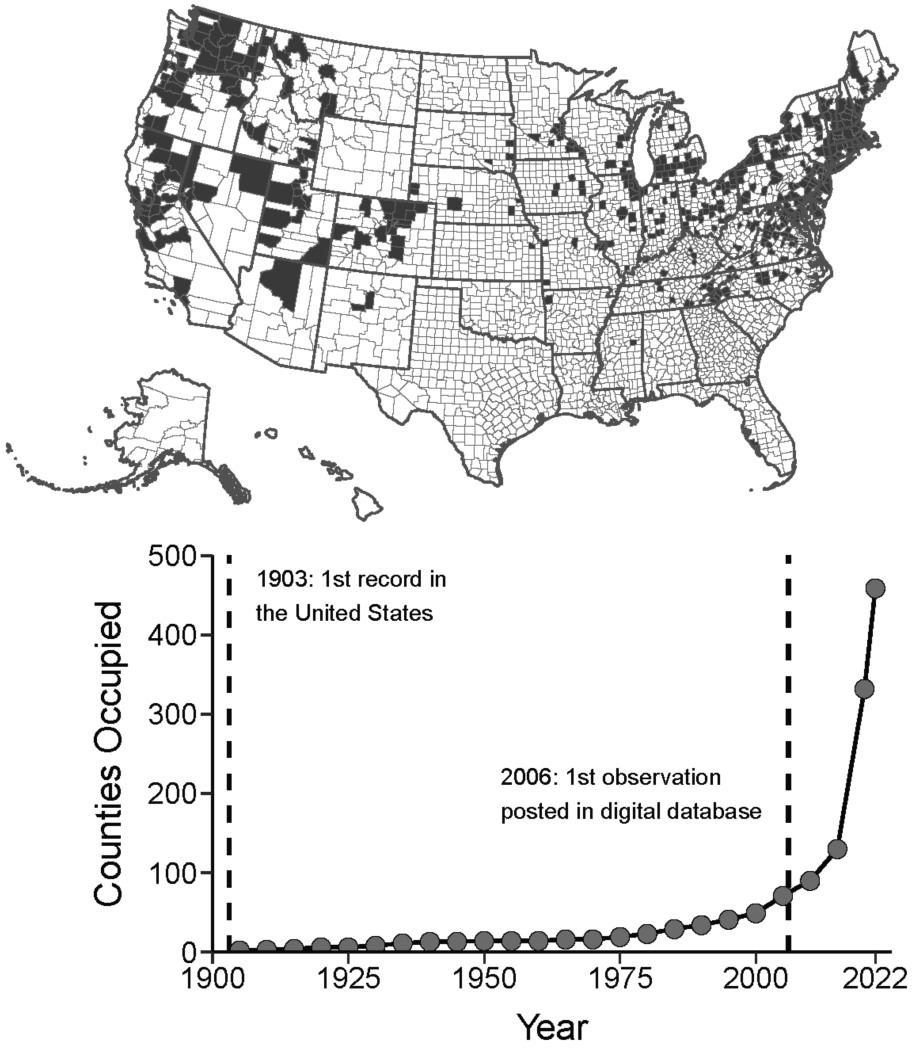

Figure 1. Spatial and temporal distribution of *Tetramorium immigrans*, the pavement ant, based on museum collections and research grade observations for county and county equivalents across the United States from 1903 to 2022. Dark grey counties in the map represent presence of *T. immigrans*.

likely to be found in locations with a higher density of people. Using the United States Census Bureau, we compared population estimates for county and county equivalents where *T. immigrans* was present or absent. In doing so, we found that locations with *T. immigrans* present averaged 339655 people while locations where *T. immigrans* has not been reported averaged 65638 people—an order of magnitude difference. In addition to the climatic limitations, perhaps this is another reason for the lack of *T. immigrans* observations across the Northern Great Plains. The five states that encompass this region are ranked 50th, 47th, 46th, 44th, and 37th in population size, averaging just over a million people each. Thus, it is currently unknown if the lack of *T. immigrans* records are due to reduced urbanization, a lower population size, lack of human dispersal, or harsh climate. However, as the populations of these regions increase along with their urban footprint, we posit that *T. immigrans* records will continue to increase and be first documented by community scientists across the Great Plains.

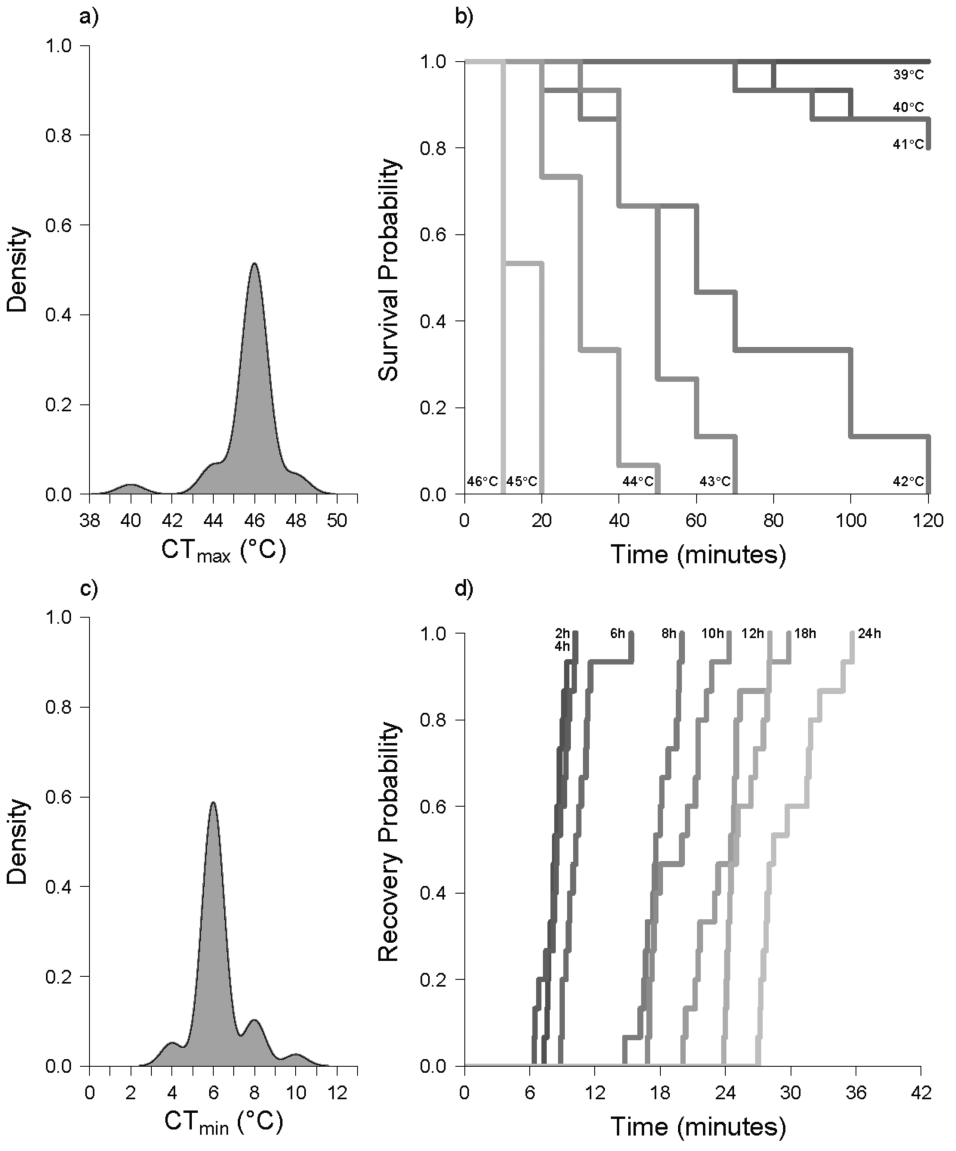

Figure 2. Thermal trait measurements for *Tetramorium immigrans*, the pavement ant. Panel (a) depicts critical thermal maximum (CT_{max}), panel (b) depicts knock-down resistance, panel (c) depicts critical thermal minimum (CT_{min}), and panel (d) depicts chill coma recovery. Kernel density plots are used in panels (a) and (c), while Kaplan-Meier survival curves are used in panels (b) and (d). For both survival curve plots, treatments are arranged from less stressful conditions in dark grey (39 °C, 2h exposure) to more stressful conditions in light grey (46 °C, 24h exposure).

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