# Temperature: Humans Regulating, Ants Conforming

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> *... ants in amazing numbers, whose tiny sparks of life only burn the brighter with the heat, fairly quiver with unquenchable energy as they run in long lines to fight and gather food.*
>
> – John Muir, June 3, 1869

Where there are ants traveling on trails, there are meaningful data easily gathered. These tiny animals–ubiquitous, abundant, orderly–are exceptionally useful for demonstrating an important property of life: the rates of processes are dependent on temperature. Within the temperature range in which each species functions, molecular, cellular, and behavioral events speed up as internal temperature rises. So when ants traveling a set distance are timed at a variety of temperatures, a predictable pattern emerges.

At Santa Rosa Junior College in northern California we are able to find ants year-round as they go about their business on the campus walkways. Students easily gather data on a sample of 10 in about half an hour. The data are surprisingly robust, in spite of all the differences in technique among these newcomers to science.

We study the Argentine ant (*Linepithema humile*), a small (2-3 millimeters) pesty native of South America now introduced worldwide, causing numerous ecological and economic problems. First found in the U.S. in New Orleans in 1891, by 2001 it had been recorded in 21 states, mostly in the South and West (Suarez et al., 2001). Its penchant for walking in lines is due to its use of a trail pheromone. When a wandering worker encounters a rich source of food or water, it produces a chemical trail as it returns to the nest, and this is soon followed by nest mates. Visual cues are not used; flashes of light or moving shadows have no effect. These ants consume a wide variety of animal matter, including other insects; they are especially fond of sweets, particularly flower nectar and honeydew (Markin, 1970; Van Vorhis Key et al., 1981).

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## Procedures

The immediate goal of this experiment is to have students observe the effect of temperature on ant travel time over a set distance. After discussing the ants and their use of trails, I suggest that students work in pairs and search for ants in different locations so we get a range of temperatures. I then indicate that they need to mark off a distance of 30 centimeters next to a trail, without touching it. Using a stopwatch or wrist watch, they time 10 ants as they travel this distance. I explain that because the ants' internal temperature is very close to that of their surroundings, this can be determined by placing a thermometer in contact with the surface next to the trail (see discussion below). We use DiGi-Sense® Type J digital thermometers with a thermocouple probe. Since the data will be pooled and plotted by the entire class, I ask what we might agree on to insure as much uniformity as possible. (I prefer having students participate as much as possible in designing experiments; procedures they have discussed and agreed to are more likely to be followed than mere verbatim instructions.) I manage to guide them to at least the following minimal standards: The trails should be on a smooth hard surface (not dirt), horizontal (not vertical), straight (not curved); data will not be included if an ant wanders, loiters, turns around, or stops and communicates with another ant. I cannot say, however, how well these procedures are followed, for I do not closely observe; presumably there is the normal variability found within any group.

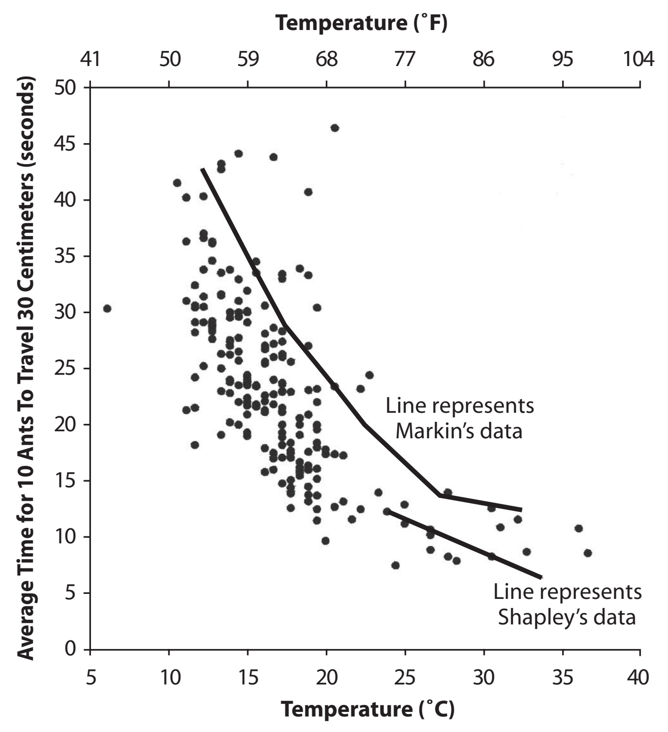
After returning to the lab, each pair of students determines its mean time and writes this and the trail temperature on the board. I then usually provide more data from previous labs to insure that the graphs students make cover a broad range of temperatures.

## The Students' Data

Figure 1 shows 205 data points obtained by approximately 400 students during 13 semesters. (Nine data points have been omitted from this figure, either because a procedure was not followed or equipment was misread. Such problems become

**Figure 1.**

As temperature rises, the time taken by Argentine ants to travel 30 centimeters declines. For comparison, lines based on data from two other studies are superimposed.



apparent when students report their difficulties or when a measurement is very different from those gathered by others.)

The trend in Figure 1, despite the considerable scatter, is in reasonable agreement with the two other studies on this species. One difference is that George Markin's (1970) times are somewhat longer (his ants were slower at each temperature). A likely reason is that his temperatures were measured in the air "under the canopy of a citrus tree" rather than next to the ants, which were on the tree trunks; presumably the latter were cooler. Indeed, air temperature can differ considerably from nearby surfaces. Commenting on this, Brenda Tremper (1976) notes that in her study "tree trunks were between 18-24° C, in the shade, even when air temperatures were above 30° C." Also contributing to the relative slowness of Markin's ants may have been the vertical trails; indeed, he found that ants ascending were slower than those descending.

Harlow Shapley (1924) timed his ants "on cement and humus" over 30 cm stretches of trail he referred to as "speed traps"; his 21 data points (transformed from cm/sec) closely hugged the line in Figure 1. Shapley, an astronomer famous for discovering that we are located at the outer edge of the Milky Way galaxy rather than in its center, was the first to discover that ant running speed (in *Liometopum apiculatum*) was strongly controlled by temperature and not affected by other meteorological conditions. In his words: "Observation of the time required to run a distance of thirty centimeters, taking an average for ten or twenty individuals, suffices to indicate the air temperature within one degree."

In contrast to Shapley's work, the mean times collected by the students are quite variable at any given temperature. I suspect this may be due to differences among both the trail surfaces and the measurement techniques.

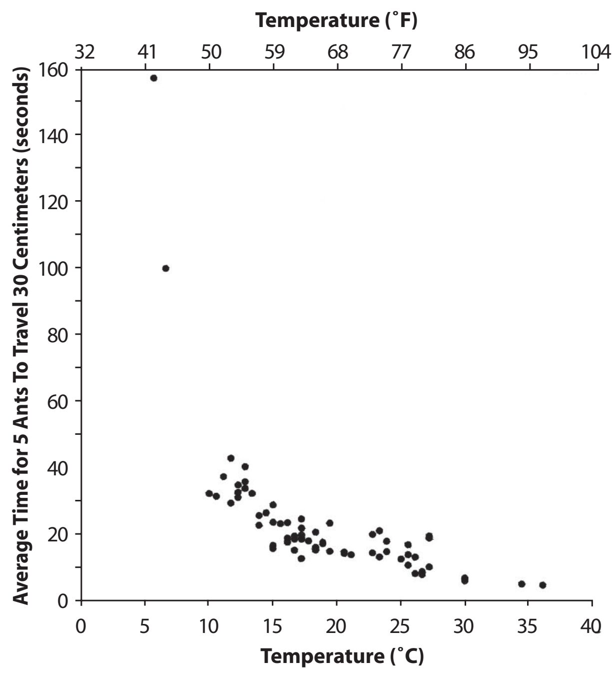
In Figure 2, another set of data shows how slowly these ants travel at low temperatures. (These results are from three earlier semesters when we used a sample size of 5 rather than 10.) Clearly, cold ants are extremely slow; at 5.5° C the mean was 159 seconds. Not included in Figure 2 was a mean of 338 seconds (5.6 minutes) obtained at 4.7° C (the range was broad: 2.5-8.2 minutes). So across the entire temperature range–from 4.7° C to 36° C–the times differ by a factor greater than 60, declining from 5.6 minutes down to 5.3 seconds.

The two slowest times in Figure 2 (and also the 338-second value) I obtained myself on a clear night when the temperature was falling. I first observed complete cessation of motion in some ants at 4° C. When I resumed observations in the morning ants were immobile in the same location at 3° C; at 5° C two were traveling very slowly. This suggests a threshold for motion of about 4-5° C. (A possible source of error was a rise of about 0.5° C when I got close enough to observe, due to either breath or body heat.) Interestingly, this threshold estimate is close to 7° C, where human nerves stop conducting. This commonly occurs in our extremities, resulting in loss of sensation and motion (Mercer, 1998).

A possible discrepancy is a data point at 6° C in Figure 1. Because no other temperatures this low have been reported during our lab period, and because the time (30 seconds) is far different from those at the similar low

**Figure 2.**

As temperature rises, the time taken by Argentine ants to travel 30 centimeters declines. These data were obtained with a smaller sample size than those in Figure 1. (One data point was omitted due to procedural problems. The data points at the two lowest and four highest temperatures I obtained myself, using a 30-cm mercury thermometer.)



temperatures just discussed, I suspect that an error was made by the reporting students. Tentatively, therefore, I base my conclusions concerning low temperatures on the measurements I made myself.

## Times or Speeds?

Data such as these are often converted to a rate—speed expressed in centimeters per second. This has been done in Figure 3; the times in Figure 2 were divided into 30 centimeters. Clearly, speed increases with temperature. The data suggest a linear relationship; the equation for a regression line is:

$$y = 0.143x - 0.905$$

($r^2 = 0.74$). (When the Figure 1 data are plotted as speeds [not shown], the relationship is similar but not as strong [$r^2 = 0.63$].)

In other studies, the relationship is linear for a seed-harvester ant (Rissing, 1982), although a curvilinear relationship is clear in Shapley's *Liometopum* data (Heinrich, 1993). For linear relationships in other animal behaviors see Bennett, 1980; Chadwick and Rahn, 1954; Walker, 1975; and Block, 1966. See Walker (1975) for a discussion of linear and exponential models.

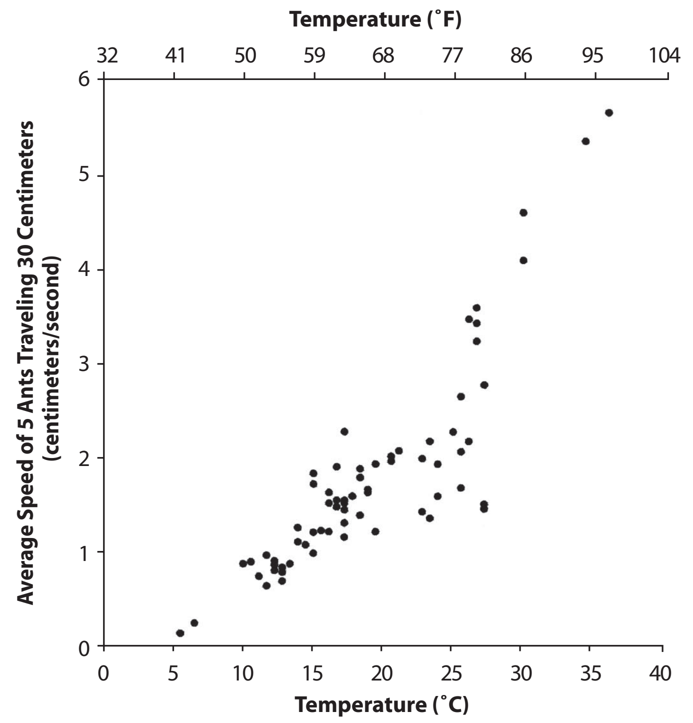
Should students convert their times to speeds? Time as a measure of who is faster is widely used. We all know that 10 seconds in the 100 meter dash is faster than 11 seconds—no need to convert to speeds (10.00 and 9.09 meters per second, respectively). Yet, expressing performance in terms of speed can illuminate other processes. It is fascinating, for example, to convert world record times for running events to speeds and plot these against distance.

My preference with beginning students is to have them plot only their times. Otherwise, I suspect I might jeopardize a primary goal: having students experience the satisfaction of uncovering unsuspected order through their own efforts. It is important that a clear result emerges from their work immediately—no further calculations needed. The more I place additional steps between students and the principles demonstrated by experimental organisms, the more likely it is that some students may not even grasp the basics. For beginnings to be effective, less is more. For more advanced students there is value in doing both graphs; they can puzzle over the striking differences, analyze the speed data by linear regression, and gain experience in interpreting results.

## Further Opportunities

Experiments give rise to new questions. Students might wonder, or be asked by the instructor, how the amount of scatter among the data points might be reduced. An experiment they might propose and carry out would be to do numerous measurements in the same location as the temperature changes over many hours. Another issue they might pursue is the extent to which sample sizes affect results. Also, students might attempt to determine if speeds are still greater at higher temperatures (the peak in Figure 3 was 5.7 cm/sec at 36˚ C), or if they level off or decline. Argentine ants continue to visit baits up to soil temperatures around 42˚ C, and they survive as high as 45-46˚ C (Holway et al., 2002).

**Figure 3.**
As temperature rises, speed increases. These data are based on those in Figure 2; travel times (in seconds) were divided into 30 centimeters to obtain speeds (in centimeters per second).



## Some Species Regulate, Most Conform

In my teaching, this experiment forms the backdrop for a discussion of organism-temperature relationships. To briefly summarize this topic: We humans, along with the other mammals and the birds, are strikingly different from most other species. By constantly maintaining an elevated body temperature, we can be active year-round, irrespective of external temperatures. In contrast, the majority of species on our planet behave, essentially, like ants; internal temperature rises and falls as dictated by the environment, and functioning speeds up and slows down accordingly. Mammals and birds regulate; most other organisms conform.

Temperature regulation in mammals and birds requires the expenditure of huge amounts of energy to generate heat. Numerous mechanisms adjust gains and losses, and body temperatures are kept within very narrow ranges in spite of threats from environmental extremes. Humans, for example, usually are within about half a degree of 37˚ C, and deviations of just a few degrees outside this range can be life-threatening. (Specifically, this refers to the body core; the skin and extremities are normally much cooler.) (Houdas & Ring, 1982)

In other groups of organisms regulation is sometimes accomplished with externally-derived heat. Butterflies and reptiles, for example, are well-known for basking in the sun. The western fence lizard (*Sceloporous occidentalis*) in the daytime keeps its internal temperature between about 32 and 36˚ C—often far above air temperature—by varying its exposure to sun and shade (Adolph, 1990).

So, specifically defined, temperature regulation is occurring when an organism is actively maintaining its internal temperature within a certain range, one that differs from that which would result if heat energy was merely being passively gained and lost. The ways this is accomplished include generating heat internally and controlling its rate of production and loss, adjusting exposure time in habitats where either a net gain or a net loss of heat energy occurs, and deliberately allowing water to evaporate to unload excess heat. (Excluded is temperature selection, which is the capacity most motile organisms have to escape from extremes or to move into thermally-preferable places. I have observed that Argentine ants appear to do this; when baited into a jar which is then sealed and placed in the sun, they congregate motionless in one region, presumably the coolest.)

In contrast, temperature conformity is occurring when an organism's internal temperature is staying the same as, and fluctuating with, the temperature of its environment. This is the case for most organisms living in water: bacteria, algae, protozoa, invertebrates, and most fish; exceptions include some large fish, and of course, aquatic mammals. Because of its high specific heat and rapid heat conductivity, water readily imparts its temperature to the organisms and surfaces it contacts. Conformity is also true for most organisms living in the soil: bacteria, fungi, protozoa, invertebrates, and plant roots. Their temperatures closely match the soil particles, gases, and water they contact. And similarly, organisms above ground generally have internal temperatures close to, or equal to, the temperature of the air; exceptions, of course, are the mammals, birds, and other temperature regulators.

Importantly, however, when an organism is in direct sunlight, its internal temperature is likely to be quite different from that of the air. For example, leaves fully exposed to the sun are commonly 5-10° C (and sometimes even 15-20° C) warmer than the air (Gates, 1980). Therefore, it is better to say that the temperature of an organism conforms to the inputs of heat energy from its entire thermal environment rather than just to the temperature of its surrounding medium (Withers, 1992).

Conformity, however, does not imply that the cells or bodies of these organisms lack features that affect their temperatures. Heat is a normal byproduct of metabolism, and to varying extents this can elevate internal temperature (as in flying insects, whose muscles are intensely active [Heinrich,1993]); heat is lost when water evaporates, and to varying extents this can depress internal temperature (as in transpiring leaves [Gates, 1980]).

So, in a much broader sense, temperature conformity is occurring when an organism is not regulating its gains and losses of heat energy (and thereby not actively maintaining an internal temperature within a particular range). Its temperature may be determined entirely by heat energy gained from the environment, or gains from metabolism or losses through water evaporation may also be involved. Given these considerations, perhaps the broader term, *thermoconformity*, is preferable. Another term with similar usage is *poikilothermy*. (Heinrich [1981a] reviews terminology. He cautions, however, that because these phenomena form continua, concise classification is not possible.)

A small point: the wording here is intended to label the processes; organisms are not being categorized as regulators or conformers. Certainly, the latter is usually fine, but keep in mind that some organisms engage in both processes. A lizard regulates in the daytime during the warmer months, but it conforms at night and throughout the winter.

## The Overwhelming Importance of Size

In the words of George Bartholomew (1981): "It is only a slight overstatement to say that the most important attribute of an animal, both physiologically and ecologically, is its size." Thermally, this is particularly relevant.

In direct sunlight a butterfly, a lizard, or a leaf can heat up considerably above the temperature of the surrounding air. An ant cannot. The reason is its size. The smaller the organism, the greater its surface area, relative to volume; in other words, surface-to-volume ratio increases as size declines. Surface area is crucial because heat energy is exchanged with the environment across an organism's surface. So a small organism loses to the air the energy gained from the sun more readily than a larger organism. The small organism, with its greater surface-to-volume ratio, is in contact with more air (relative to volume), so heat is more quickly transferred and carried away—lost by convection. Transfer from a larger organism is less efficient; its temperature rises more than that of a small organism. For example, when desert locust nymphs were exposed to sunlight, the temperature of a small one (first instar) rose and leveled off quickly at about 2° C above air temperature; a large one (fifth instar) rose and leveled off more slowly at about 8° C above air temperature (Casey, 1981).

Likewise, these relationships hold when heat is being produced internally. In flying insects, body temperature will be considerably above air temperatures in the larger ones, but not in the smallest ones. In general, the larger the insect, the greater the elevation of body temperature; in flight, honeybees commonly are 15-20° C warmer than the air, but mosquitoes are elevated less than 1° C (Heinrich, 1981b).

An ant, even in the sun, will be very close to air temperature. Keep in mind, though, that the ant is in the boundary layer—the air that hugs the substrate surface; the temperature of this air is very near that of the substrate. So if the substrate is in the sun, the ant and the air around it are probably much warmer than the air experienced by human observers. A probe, or just a glass thermometer (as used by Shapley, 1924), placed in contact with the substrate surface, provides an adequate measure of ant body temperature (Rissing, 1982). Alternatively, Marsh (1985), working with large desert ants, used a thermocouple inserted into the thorax of a dead individual. However, these were 4 milligram ants; Argentine ants average only about 0.4 mg.

## Fostering & Assessing Performance

To ensure that students give thought to these principles, I have them accompany their graphs with written explanations of 1) temperature regulation and temperature conformity, and 2) how molecules and cells respond as temperature rises. In addition, I have them list and explain two of their own observations on organisms that are thermoconforming. We discuss in class the example I feel is most important: Food is refrigerated to inhibit decomposers. Their examples range widely, and include pets, plants, microbes, and animals in the wild.

I have not experimentally assessed whether the learning of these principles in the students who participate in this experiment is enhanced above that in a similar group who, for example, might be exposed only to a lecture on these topics. Completion of the above assignment is intended to increase learning, but strictly speaking, the grades I give are not measures of learning. So my conclusions on this issue are very tentative and subjective; these, however, are positive. The performance on the above assignment in its present format (n = 156 students) has been relatively good (median, 21 of 25 points; mean, 19.7). Also encouraging is that this experiment is the one that seems to be most frequently mentioned when I encounter students in later semesters.

## Temperature & Life

So … pervading every organism and every cell, temperature is inseparable from life. Easily measured and understood, it provides a ready bridge between curious minds and living organisms. A great range of phenomena vary under its sway, and when quantified and graphed, a high degree of order often unfolds. Just two terms—regulation and conformity—meet basic needs. Their explanatory power goes far beyond great big humans and tiny little ants.

## Acknowledgments

The idea for this experiment and the inspiration to pursue it came from Bernd Heinrich's work, in particular his chapter on ants in *The Hot-Blooded Insects*. Thanks go to the anonymous reviewers for their helpful comments, and of course, to the students for making this lab a pleasure.

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