IN MEMORIAM

James Edward Heath

Just as the ability to devise simple but evocative models is the signature of the great scientist so overelaboration and overparameterization [are] often the mark of mediocrity. (Box 1976, p. 792)

James Edward Heath (1935–2017) devoted his career to thermal biology. He was an outstanding scientist who advanced our understanding of the physiological ecology of ectotherms and endotherms, advised 20 PhD students and many undergraduates, and served for 35 years as Editor-in-Chief of North America for the *Journal of Thermal Biology*. But Jim Heath will be forever remembered—and appropriately so—for his legendary and influential beer can experiment (Heath 1964*b*), published in *Science*.

To put that experiment in context, we must first depict the state of thermal biology leading up to the early 1960s. In 1944, Cowles and Bogert published a pioneering monograph that proved foundational for physiological ecology. That monograph documented the fact that desert reptiles gain some behavioral control over body temperature (T_b) by adjusting posture and position within their thermal environments and also by altering the timing of their daily activity. Specifically, Cowles and Bogert showed not only that the body temperatures of desert reptiles diverged from ambient temperatures but also that they remained relatively constant (nearly as constant as the body temperatures of endotherms) during the daylight activity periods. Cowles and Bogert (1944) effectively established the concept of behavioral homeostasis and put reptiles front and center on the map of physiological ecology.

The next two decades saw many herpetologists charging to the field, armed with Schultheis rapid-reading thermometers (Brattstrom 1965). They made a cottage industry of taking of cloacal temperatures of reptiles and amphibians ("grab and jab," "noose and goose," "blast and shaft"). These researchers typically reported the mean and variance of body temperatures of active lizards and sometimes included a regression of body temperature on air temperature. They then interpreted observed patterns (e.g., of relatively constant body temperatures, even in the face of changing ambient temperatures) as evidence of behavioral thermoregulation, but rarely did they report direct observations of regulatory behavior itself (Christian et al. 2016).

Enter James Heath, who was a PhD student at UCLA mentored initially by Raymond B. Cowles but finished his degree in 1962 with Kenneth S. Norris after Cowles retired. UCLA at that time was a major breeding ground for new data and ideas in physiological ecology, with other highly influential scholars such as George A. Bartholomew, Bayard Brattstrom, Warren P. Porter, R. C. Lasiewski, and Malcolm Gordon—all of whom have made major contributions to thermal biology.

Heath's thesis (Heath 1965) included laboratory and field studies of temperature regulation in horned lizards (*Phrynosoma*). His thesis is a treat to read even a half century later. For example, Heath designed and introduced the "herpetothermoplanoclinotron," which was a simple apparatus (but with a 10-syllable name) that records the shadow cast by a horned lizard. Heath used this apparatus to quantify how horned lizards adjust posture (and thus alter rates of heat exchange) in response to T_b. Throughout his monograph, Heath cleverly monitored both behavioral switches and associated body temperatures. So, he knew whether change in posture (or other behaviors) really affected thermoregulation. His ethogram of thermoregulatory behaviors of horned lizards (his fig. 17) is still used as an examplar in textbooks. In our view, his monograph is still

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probably the most careful and thorough experimental study of behavioral thermoregulation ever conducted. Remarkably, Heath was only 26 years old when he submitted his thesis.

Not surprisingly, Heath was justifiably bothered by the lack of rigor in contemporary "grab-and-stab" studies of thermoregulation. For him, merely observing a narrow distribution of body temperature—or calculating shallow regression slopes of body temperature on air temperature—was insufficient evidence, by itself, that lizards were thermoregulating. As he noted, "A problem arises when the field records are used to try to elucidate thermoregulatory mechanisms when no true regulation has been observed" (Heath 1964*b*, p. 784).

Heath then chose to make his point by examining whether the distribution of temperatures of "inanimate objects" (water-filled beer cans[1]) would be distinguishable from temperatures measured for reptiles. He set out 13 beer cans into the desert and recorded temperatures of beer cans and of air at hourly intervals over most of a day. His figure 1 showed a distribution of beer can temperatures, which was left skewed and looked remarkably like the distributions of body temperatures of (purportedly) thermoregulating lizards. In his figure 2, he plotted beer can temperature against air temperature, finding that beer can temperatures were elevated above air temperatures, especially at low air temperatures: this plot looked remarkably like plots of body temperatures versus air temperatures for (purportedly) thermoregulating lizards. Obviously, pattern does not always imply process. And as Heath (1964*b*, p. 765) aptly concluded, "Body temperature randomly collected in the field need not reflect regulation."

We were graduate students in the late 1960s and early 1970s when we first read Heath's *Science* paper. For us, his paper was important and certainly unlike anything we had ever read. For several reasons, we saw it as a monumental and concept-changing paper.

First, the project was elegant, simple, and humorously told. And it took only one day of field work (we will ignore the prep time involved in emptying 13 cans of beer!). How many other papers in *Science* are based on only one day of data collection?

Second, it is the first paper that we had read—and possibly the first ever written—that implemented the concept of a "null model" in field ecology. That term is derived from the "null hypothesis" of statistics and represents the expected pattern in the absence of some force, mechanism, or behavior. This approach follows from the philosophies of science proposed by Karl Popper (1959), suggesting that knowledge should be derived from experiments eliminating alternatives to the method being studied. Heath (1964*b*) never used the term "null model," which did not become popular in ecology for two decades (Harvey et al. 1983), but the essence of the concept was in his paper. Importantly, Heath's "inanimate" beer cans (but see below) served as null models for what the distribution of body temperatures (or regression of body temperature on air temperature) would look like in the absence of overt thermoregulatory behavior. That conceptual breakthrough alone should justify a prominent place in biological history for Jim Heath.

Third, Heath's beer cans were effectively "operative temperature models" of the equilibrium temperature of reptiles. Although the term "operative temperature" had previously been introduced via the human thermobiology literature, it did not become widely known by animal ecologists for a decade or more after Heath's paper (Bakken and Gates 1975; Tracy 1982). Importantly, Heath was probably the first field ecologist to use a physical analog (beer can) of an operative temperature model, and such models subsequently became central to understanding field thermal biology (Porter et al. 1973; Christian et al. 1983; Bakken 1992; Hertz et al. 1993), though contemporary models are superior representations of animals (Bakken and Angilletta 2013).

As thermal biologists later began to learn about heat transfer to and from animals, it became clear that Heath's "inanimate" models weren't completely inanimate (see Huey et al. 1977, p. 1067). For example, the cans were out only for part of a day, which implies regulation of activity time—a common thermoregulatory behavior (Stevenson 1985). Moreover, they were upright in the sand: early in the morning or late in the afternoon, the large and painted sides of the beer cans were exposed to the sun's radiation, but at midday, the smaller and more reflective tops of the cans were exposed. Thus, these postural and color "changes" almost certainly caused the cans to receive much more radiant heat in the morning and afternoon while reducing absorption in the middle of the day. In other words, Heath's "inanimate" beer cans were actually—if unintentionally—"passive thermoregulators." But that does not detract from his experiment: rather, it merely reinforces "Heath's . . . still timely message: inferring thermoregulation in the absence of controls or direct observations is risky" (Huey et al. 1977, p. 1067). Moreover, Heath's beer can experiment—especially combined with his own rigorous experimental studies with horned lizards (Heath 1965)—transformed thermal biology, and the entire field has benefited from the wisdom of his remarkable experiments and insights.

Heath (1964*b*, p. 765) recognized that beer cans were not ideal physical models of reptiles (which differed in size, shape, absorptivity, etc.), and so he proposed a second way to generate a null model for thermoregulation: "A simple and useful control might be to tether an animal in the direct sunlight and check its temperature periodically. A deviation of the control temperature from that of an animal collected randomly would be partly attributable to regulation." Today, an equivalent of Heath's suggested "control" is implemented commonly and successfully by using physical manikins rather than living animals (Bakken and Gates 1975; Hertz et al. 1993; Bakken and Angilletta 2013).

Heath did additional research on the thermal biology of reptiles. He documented head : body temperature differences in horned lizards (Heath 1964*a*) and (in another report in *Science*)

1. The beer brand was Schlitz (J. Heath, personal communication), a rice-based beer that has mercifully become nearly extinct. This would have been before pop-top cans, and the highly reflective top could be opened only by a "church key." See http://crtracy.com/Tracy/Nat_Hist_Beer_Cans.html.

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showed that morning emergence of horned lizards was driven by a temperature-insensitive clock (Heath 1962). Also, he did extensive and pioneering work on the thermal biology of insects, first in moths and later in cicadas (often in collaboration with his wife, Maxine S. Heath). He used infrared thermography to study surface temperatures of animals and edited the *Journal of Thermal Biology* for decades. These contributions and others Heath made to science and education have recently been summarized by one of his former students (Gordon 2017).

On a personal level, neither of us knew Jim well. R. B. Huey met with him in person only twice, and C. R. Tracy met with him only once. But both of us corresponded frequently with Jim as a colleague and friend for decades. Both of us appreciate that few people have influenced our thinking more than Jim Heath did and still does. We quickly recognized the importance of his beer can experiment, even though null models were still a foreign concept at the time. We soon realized the power and elegance of his simple experiment, as well as the relevance of his message about the importance of experimental approaches to understanding behavior.

We would be remiss not to cite a paper that Heath coauthored with Polly Phillips (Phillips and Heath 2001) on heat loss in Dumbo the Flying Elephant. Dumbo had giant ears, and—by using biophysical calculations—Phillips and Heath showed that Dumbo may have needed those large ears to dissipate the excess heat produced during flapping flight!

In future decades, James Heath will no doubt be remembered primarily for his beer can experiment. But future scientists who read his paper will always take away two important lessons. First, pattern does not necessarily imply process. Second, and perhaps more importantly, science can be fun (Gordon 2017).

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