Dynamics of death by heat

Time at high temperature modulates fly mortality in nature

By **Raymond B. Huey**[1] and **Michael R. Kearney**[2]

I t has been known for a century that mortality from heat depends not only on the exposure temperature but also on the duration of exposure (*1*). Typically, higher temperature shortens time to death. But predicting heat death in nature is challenging because an animal's temperature and stress level—especially for small species—can fluctuate markedly within days and across seasons. Can risk of heat death in fluctuating environments be understood only by brute-force experiments involving all possible temperature sequences, or can exposure to a few fixed temperatures capture key dynamics of heat death? On page 1242 of this issue, Rezende *et al.* (*2*) extend a recently developed mathematical model (*3*) and show that fixed-temperature experiments can be generalized to dynamic patterns and can predict mortality of a fly (*Drosophila subobscura*) in nature across seasons and climate shifts.

Ecologists have long known that heat stress constrains the distributions and abundances of organisms as well as the spread of pests, diseases, and invasive species (*4*). However, the increased intensity and duration of heat waves with contemporary climate change have stoked renewed interest in these issues from conservation and health perspectives. With human data, nonlinear statistical models can evaluate the impact of environmental temperatures on observed mortality rates and causes of death (*5*). But with animals in nature, mortality rates are usually unknown, and biologists must develop other approaches to evaluate risks of heat mortality (*6*, *7*).

One simple but widely used approximation of risk is the thermal safety margin (TSM), which quantifies the temperature difference between a threshold measure of an organism's heat tolerance and maximum environmental temperatures (*6*). Organisms with small or especially negative TSMs are judged at risk of heat stress (*8*).

Critical maximum temperature (CT_{max}) is a common and nonlethal index of heat tolerance: An animal is heated until it loses its righting response when placed on its back.

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CT_{max} has been measured for thousands of species, but its sensitivity to measurement protocols (e.g., fast versus slow heating) has sparked debates about its ecological and evolutionary relevance (*3*, *9*). Ironically, the study highlighted here (*2*) evolved from an attempt to resolve this debate. In a previous paper, Rezende and colleagues (*3*) developed the concept of a "thermal tolerance landscape," which is a three-dimensional portrayal of survival time as a function of constant temperature plus exposure duration. As Rezende *et al.* show here (*2*), this landscape can even help to predict survival in dynamic environments.

The mathematical extension from static to dynamic begins by relating survival probabilities to exposure time, temperature, and a functional constant (z) describing sensitivity to temperature change. Then survival rate can be estimated by summing instantaneous survival rates across a temperature

> ## "A single survival function successfully describes empirical survival probabilities..."

series. A single survival function successfully describes empirical survival probabilities in both static and dynamic (at least monotonically increasing) thermal exposures. Next, Rezende *et al.* use heat tolerance data for *D. subobscura* and predict that daily mortality rates should start rising in spring for cold-acclimated flies but not until midsummer in warm-acclimated ones. However, their empirical estimates of relative abundance in central Chile show population crashes in late spring through early summer. The crash occurs somewhat earlier than predicted, which might reflect insufficiently warm acclimation temperatures. When recent climate warming is considered, predicted population crashes are accelerated by 1 or 2 months and the summer low is protracted.

Despite the success and power of the model, it remains a black box with respect to mechanisms of heat death. High heat denatures enzymes and disrupts cell membranes, which likely knock out cellular processes that vary idiosyncratically among species (*10*). Even so, Rezende *et al.* show that their simple model adequately captures the dynamic accumulation of damage and its net

effect on mortality, at least in *Drosophila*.

Cellular repair processes may reduce or stall heat-related damage (*10*). Rezende *et al.* do not explicitly model repair dynamics but assume that flies heat-stressed by day fully recover overnight. Thus, recent "thermal history" (other than acclimation state) is assumed to be unimportant. But heat tolerance in flies varies with thermal history and prior stress exposure (*11*). Whether organisms recover overnight depends on the stress's magnitude, nighttime temperatures, and whether heat stress occurs on sequential days, as in a heat wave (*12*, *13*). Such effects need to be studied experimentally and modeled dynamically (*14*).

The model's implementations (*2*) did not explicitly account for effects of ontogeny, sex, and condition on heat stress or for the possibility of behavioral evasion in heterogeneous thermal environments. Nor did it consider correlates of heat stress such as desiccation and the energetic consequences of activity restriction (*7*). But the approach here can be integrated with existing models of these indirect consequences (*15*).

The correspondence of mortality predictions with field observations suggests that this model captures real-world phenomena. And, perhaps most important, the model suggests that relatively low field temperatures—that is, even those well below CT_{max}—can cause substantial mortality and population collapse. Thus, CT_{max}-based inferences may underestimate the population consequences of climate change but overestimate potential ranges of invasive species. In addition, Rezende *et al.* help to highlight open challenges, both theoretical and empirical, to our ability to understand and predict population mortality and reproduction in fluctuating environments. ∎

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