ECOLOGY

Putting the Heat on Tropical Animals

Tropical animals may be particularly vulnerable to climate warming.

Joshua J. Tewksbury,[1] Raymond B. Huey,[1] Curtis A. Deutsch[2]

Impacts of climate warming in the tropics— the cradle of biodiversity—are often predicted to be small relative to those in temperate regions (*1*, *2*), because the rate of climate warming in the tropics is lower than at higher latitudes (*3*). Yet, predictions based only on the magnitude of climate change may be misleading. Models that include organismal physiology suggest that impacts of climate warming may be more severe in the tropics than in temperate regions.

The impacts of climate warming on organisms depend not only on the magnitude of the environmental temperature shift but also on the behavior, morphology, physiology, and ecology of the organisms in question (*4*–*6*). This added complexity is daunting, but some general principles are emerging from research focused mainly on ectothermal animals (such as insects, fish, reptiles, and amphibians), which cannot maintain a constant internal body temperature. Negative impacts should be greatest on animals that are physiologically specialized with respect to temperature (*7*) and have limited acclimation capacity (*8*). Further, species living in warm climates are likely to suffer disproportionately from small increases in temperature (*9*), and species that live in aseasonal environments may be particularly vulnerable to increases in temperature, because changes in behavior and physiology are less likely to provide relief from rising temperatures (*10*).

Terrestrial ectotherms with these vulnerability traits are typically tropical (*7*, *11*, *12*). In the 1960s, Janzen (*13*) noted that tropical ectotherms should be thermal specialists (see the figure, top) and have limited acclimation capacities, relative to higher-latitude species, because they have evolved in relatively constant, aseasonal environments. These predictions have been largely validated for various terrestrial and aquatic ectotherms (*7*, *11*, *12*, *14*–*17*), yet the implications of this pattern for species vulnerabilities to climate change have rarely been investigated (*15*, *17*–*19*).

Tropical ectotherms have other traits that

[1]Department of Biology, University of Washington, Seattle, WA 98195, USA. [2]Department of Atmospheric and Oceanic Sciences, University of California at Los Angeles, Los Angeles, CA 90095, USA. E-mail: tewksjj@u.washington.edu
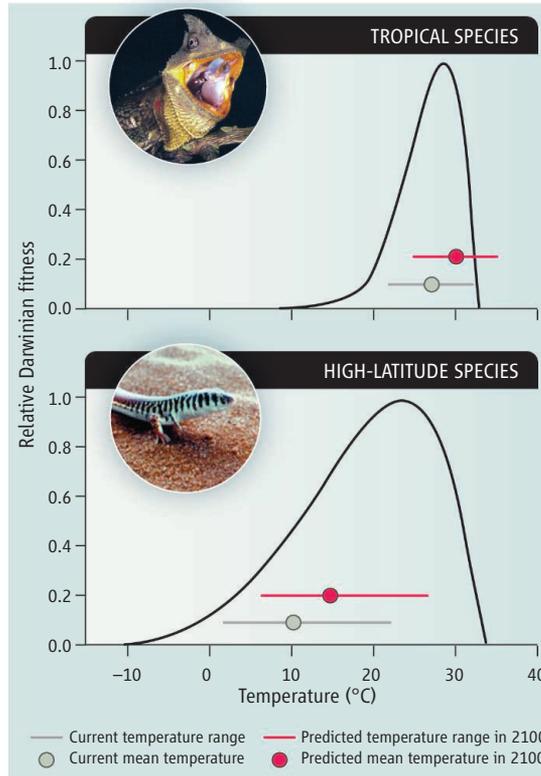
Survival in a warmer climate. Data from diverse terrestrial ectotherms suggest that tropical species living in stable aseasonal climates, such as the Amazonian lizard *Enyalioides palpebralis* (**top inset**), have narrower thermal tolerances than do higher-latitude species such as the temperate lizard *Nucras tessellata* (**bottom inset**), and also live in climates that are closer to their physiological optima. The former may thus be highly vulnerable even to modest climate warming.

increase vulnerability. Because tropical organisms experience far more warm weather throughout the year than do temperate organisms, tropical animals might be expected to have greater heat tolerance. Surprisingly, that is often not the case: Heat tolerance typically varies very little across latitude in terrestrial ectotherms (*7*, *12*, *15*). Thus, many tropical ectotherms live much of the year in environments where equilibrium body ("operative") temperatures are near or above optimal temperatures for performance (*15*). Tropical forest species may be particularly vulnerable, because they live in constant shade, are not generally adapted to the high operative temperatures found in warmer open habitats, and have few behavioral options available to evade rising tem-

peratures (*10*, *15*). Any climate-induced increase in operative temperature could cause steep declines in thermal performance and Darwinian fitness (see the figure, top).

To assess whether independent data support these assertions, long-term demographic data on tropical species are required. Such data are rare, but in the study of frogs and lizards in lowland Costa Rica, densities have declined by ~4% per year between 1970 and 2005 (*20*). These declines are explained by climate-driven declines in leaf litter on the forest floor over the study period.

Theoretically, these patterns can cut both ways: The same factors that make tropical ectotherms vulnerable to changing climate may benefit some temperate ectotherms (*15*) (see the figure, bottom). Empirical data tell a more complex story. During the last rapid warming event, 50 million years ago, insect damage on temperate plants did increase sharply (*21*), but data on contemporary temperate-zone insects are mixed: Some species are expanding rapidly (*22*), occasionally causing large changes to ecosystems and economies (*23*), whereas others—often specialists relying on day-length cues and species living in disappearing high-elevation habitats—are predicted to decline (*6*).

All these predictions are for terrestrial habitats, and patterns may differ elsewhere. In marine habitats, for example, thermal specialists occur both at low and high latitudes, and thermal generalists appear most common at mid-latitudes (*9*, *24*). Yet this pattern tracks the seasonality of ocean surface temperatures—polar oceans are cold but show little temperature variation throughout the year, and the largest seasonality in ocean surface temperatures are seen at mid-latitudes. Therefore, both tropical and high-latitude species live at near-stressful temperatures and could be vulnerable to warming (*24*). In intertidal habitats, which

have very sharp temperature gradients, an organism's vulnerability to warming depends on vertical position, latitude, daily time of exposure, and interactions with predators and competitors (*4*). Despite this complexity, thermal tolerance and acclimation capacity are still governed by temperature variability (*4*, *8*, *16*).

The strong association between the physiological flexibility of ectotherms and the temperature variations they experience will create serious problems in the tropics, compounding threats from habitat loss and fragmentation. We have focused on the direct impacts of changing temperature on ectotherm physiology. Equally important is the integration of these effects into a framework that includes the impacts of changing climate on species interactions, community structure, and ecosystem function. Such an integration is critical if we hope to predict the impacts of global warming on biodiversity.

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SYSTEMS BIOLOGY

The Scale of Prediction

Nitin S. Baliga

A predictive model for a biological system requires capturing the network of environmental factors that affect system responses.

The predictability of cellular responses is the basis for applications as diverse as preventive medicine and the reengineering of microbes for biotechnology. At first glance, the diversity of biological systems suggests that they can adopt a seemingly infinite number of behaviors or states. If this were true, it would severely hinder our ability to predict the responses of biological systems to new environmental changes. Fortunately, this is not the case (*1*). An individual biological system functions optimally within an environmental space (defined by the ranges in any given parameter) in which it has evolved. Furthermore, within this defined space, changes in individual factors (temperature, pH, O_2, etc.) do not occur in isolation but in a temporally coupled and nonrandom manner for physicochemical reasons. On page 1313 of this issue, Tagkopoulos *et al.* (*2*) offer theoretical simulations and experimental validation to show that even simple microbes can learn temporal interrelationships among changes in environmental factors, and thus can predict and prepare for future environmental changes, a behavior attributed to metazoans. This work not only demonstrates how biological networks (gene, protein, and metabolic) have assembled during evolution, but also explains why decoding these networks into predictive models is a tractable problem.

Interlocking architectures. The associations between environmental and biological networks facilitate predictive modeling of cellular responses. The interlocked gears within a microbial cell represent coupled biochemical processes that operate in sync with similarly coupled changes in environmental factors, also represented by interlocked gears.

The progression of naturally coupled environmental changes over billions of years has been the primary selection pressure in evolution. Because these natural environmental changes occur in a coordinated manner, from the perspective of an organism they are routine and predictable. Not surprisingly, biological systems have used this to their advantage and evolved anticipatory behavior. Tagkopoulos *et al.* show that this ability to predict environmental changes lends a competitive advantage to the organism. In fact, they demonstrate that decoupling environmental changes reduces the fitness of an organism and that this fitness can be regained through evolution of new network architectures from the same original parts list. This is especially exciting because relationships among environmental factors can change markedly from one niche to another (for example, the relationship among temperature, light, and nutrient availability across the ocean surface, hypersaline lake, and hydrothermal vent environments). Given sufficient separation on evolutionary time scales, this can result in different regulatory logic in related organisms that share similar genes but have gone on to inhabit different niches (*3*) [e.g., different ecotypes of the cyanobacterium *Prochlorococcus marinus* (*4*)].

Tagkopoulos *et al.* provide insight into the process by which the architecture of an environmental network is imprinted onto the

Institute for Systems Biology, 1441 N. 34th Street, Seattle, WA 98103, USA. E-mail: nbaliga@systemsbiology.org