This remarkable E2 ubiquitin-conjugating enzyme appeared to be the specificity-promoting E3 ligase as well. Further in vitro studies showed that conserved domains of UBE2O display a broad ability to recognize hydrophobic patches in proteins, thus leading to their multi-monoubiquitylation. Like Nguyen *et al.*, they found that orphan α-globin is ubiquitylated by UBE2O. They also demonstrate that newly generated ribosomal proteins either are imported in the nucleus to be incorporated into ribosomal subunits, or are recognized and ubiquitylated by UBE2O for degradation.

Both studies show that UBE2O is a uniquely talented E2 enzyme that is capable of autonomously ubiquitylating a wide range of substrates to promote their degradation by the proteasome. The widely found "signal" in target proteins for UBE2O-mediated multi-monoubiquitylation consists of adjacent sequences of basic and hydrophobic amino acids, which are overrepresented in unassociated interaction surfaces that are typical of orphan subunits. Interestingly, such orphans are unstable in the first hours of their life and are stabilized with age (*6*). In this respect, UBE2O, despite its clear homology to E2 ubiquitin-conjugating enzymes, belongs to a group of quality control ubiquitin E3 ligases that function without adaptor or chaperone proteins to select their targets (*7*). In fact, physiological or artificial overexpression of UBE2O led to vast proteome remodeling. Whether such a property is shared by other quality control factors, and whether quality control is more generally used in proteome remodeling and differentiation pathways, are important avenues of future investigation.

Further understanding of UBE2O and other quality control pathways might open new therapeutic avenues to alter proteomes to improve cellular health, such as removal of α-globin aggregates that are observed in the blood disorder β-thalassemia, which features reduced hemoglobin expression. Learning how the cell alters these pathways, and possibly how we can do the same, could have remarkable basic and translational potential (*8*, *9*). ■


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An unusual cold event led to evolutionary change in anole lizards.



EVOLUTION

# Evolution, climate change, and extreme events

## Cold tolerance allows a selected few anole lizards to survive a cold snap

*By* **Peter R. Grant**

Climatic extremes such as unusual heat waves, droughts, or exceptional rainfall have been tied directly or indirectly to the rapid increase in global atmospheric carbon dioxide concentrations and resulting rise in temperature and are expected to become more frequent as the climate warms further (*1*). Ecologists have studied their effects on biological communities, warning of changes in the distribution of species, altered composition of communities, and impending extinctions (*2*). Extreme events can also bring about evolutionary changes (*3*), but these changes have been rarely studied because such events are cryptic, rare, and unpredictable. On page 495 of this issue, Campbell-Staton *et al.* (*4*) report an unusually detailed example of natural selection caused by an extreme event. The study shows what needs to be done to detect the evolutionary effects of rare events and offers insights into biological consequences of global warming.

In 2013, 16 extreme events occurred on four continents: heat waves, heavy rain events, and storms (*5*). During the following winter, a weakening of the arctic low-pressure zone (the polar vortex) resulted in weeks of extreme cold weather in the southern United States. Campbell-Staton *et al.* were studying populations of anole lizards (*Anolis carolinensis*, see the photo) before the extreme weather event and were thus well placed to investigate how the lizards responded to this major perturbation of their climatic environment.

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Before the winter, the authors had measured the critical thermal minimum temperature at which anole lizards lose coordination under cold challenge, at five sites along a latitudinal transect. They repeated the measurements on a different set of anole lizards at all five sites in the following spring. Lizards from the southernmost population in Texas, which experienced the greatest number of days below the critical minimum temperature during the 2013 to 2014 winter, had higher cold tolerance in the following spring. This shift could have been due entirely to a plastic response to extremely cold conditions, but this seems unlikely because the lower critical minimum was maintained throughout the following summer. Thus, it is reasonable to suggest, as the authors did, that natural selection on variation in cold tolerance had occurred. If cold tolerance is a heritable trait, which seems likely but has not been demonstrated (*6*, *7*), then natural selection probably gave rise to an evolutionary change in the next generation.

To investigate this possibility at the genetic level, the investigators sequenced 48 liver transcriptomes of lizards collected before and after the storms. They acclimatized lizards from different points along a latitudinal gradient to a common temperature (30°C) for 14 days and then compared genomic profiles of 57 coexpressed gene modules before and after the event and at different sites. The comparisons yielded two main findings. First, a large change in 14 genomic regions occurred across the winter, but only at the southern and most severely affected site. Second, three of the coexpressed gene modules varied with latitude. Winter survivors at the southern site displayed a shift toward the more northerly populations, whereas the northern populations themselves showed no change, presumably because winter conditions there were less severe.

***"Will evolutionary change be short-lived and transitory, or will it substantially contribute to the persistence of species?"***

What are the genes in these modules, and what are their functions? Some of the differentially expressed genes are known to participate in the maintenance of synaptic function and neurotransmission, as well as the neurotransmitter inhibition that is crucial to the maintenance of muscle tone (*4*). These functions are plausibly linked to increased cold tolerance.

Thus, Campbell-Staton *et al.* establish a strong case for the most likely target of natural selection by performing physiological research on a fitness-related trait combined with molecular sleuthing (*4*). A follow-up study is needed to investigate the multiple functions of these genes in anole lizards in Texas.

The study is restricted to a single generation; like the pioneering (*8*) but controversial (*9*) study of house sparrows (*Passer domesticus*) in Rhode Island that survived or died in a severe snowstorm in 1898, it does not document evolution directly. This can be accomplished, however, by following the fates of measured and individually marked adults through a period of stress, together with the offspring produced by the survivors, in order to quantify both natural selection on ecologically important traits and the evolutionary consequence in the next generation (*3*). Large animals such as lizards are suitable for this kind of study, and so are plants. An alternative approach is to use genome-wide sequencing of a population before and after an extreme stress, and then in the descendant population (*10*).

On the face of it, selection for increased cold tolerance has nothing to do with global warming. Yet, there is a connection. A geophysical perturbation in one region can have contrasting effects in other regions owing to the teleconnections that link them in a geospatial network. For example, El Niño warming of the eastern Pacific brings heavy rains to Peru and Ecuador but drought conditions to Panama.

A straightforward prediction of gradual warming is a shift in the distribution of animals and plants to higher latitudes and elevations, either by differential dispersal or through local adaptation (*2*, *7*, *11*). By contrast, there is limited theory to guide expectations of how climatic extremes will affect evolution (*7*, *12*). As the study by Campbell-Staton *et al.* brings home, episodic extremes are unpredictable in occurrence; moreover, their effects are heterogeneous. Will evolutionary change be short-lived and transitory, or will it substantially contribute to the persistence of species?

Answers will depend on the magnitude of deviations from average environmental conditions, how long extreme conditions persist, and on the pattern of intervals between successive events. They will also depend on many biological factors, including prior exposure of the organisms to extremes, their behavior, how phenotypically plastic they are, the degree to which they are genetically variable in fitness-related traits, demographic factors such as lifespan and dispersal (gene flow), and the ramifying effects on other members of their food webs (*3*). All of this means that linking extreme events and evolutionary responses presents investigators with substantial challenges. Yet, the importance of doing so can only grow as extreme events become more frequent and extreme. ■


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PLASMONICS

# A low-loss origami plasmonic waveguide

## DNA assembles silver and gold nanoparticles for fast and efficient energy transfer

By **Fiorenzo Vetrone** *and* **Federico Rosei**

Computers consume large amounts of energy because the electrons that carry information dissipate heat as they move through chips. Optical computing platforms, which transfer information using photons, would mitigate the losses incurred through heat generation. Glass fibers can transport light across large distances with virtually no loss, but they are unsuitable for length scales below 1 μm because propagation is based on classical optics, which requires the size of the medium to be larger than the photon wavelength. Roller *et al.* (*1*) have now addressed this size challenge by demonstrating a low-loss nanoscale plasmonic waveguide based on a heterogeneous trimer composed of gold-silver-gold nanoparticles (Au-Ag-Au NPs). This concept validates the possibility of using such heterogeneous assemblies as energy-transfer elements through near-field interactions, while avoiding the typically high dissipation associated with plasmonics.

The reported low-loss waveguide may be relevant to both optical information processing and energy harvesting. In photosynthesis, chloroplasts convert the energy of sunlight into chemical energy through dipole interactions (Förster resonance energy transfer, or FRET) (*2*). Although FRET in nature is very efficient, it is incoherent and therefore dissipative. "Plasmonic" waveguides in theory could transfer energy through the linear arrangement of metal NPs forming a homogeneous wirelike architecture (*3*). Plasmons—collective oscillations of charge density that occur, for example, in Au and Ag

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