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Perspective

Plasticity and local adaptation explain lizard cold tolerance

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How does climate variation limit the range of species and what does it take for species to colonize new regions? In this issue of *Molecular Ecology*, Campbell-Staton et al. (2018) address these broad questions by investigating cold tolerance adaptation in the green anole lizard (*Anolis carolinensis*) across a latitudinal transect. By integrating physiological data, gene expression data and acclimation experiments, the authors disentangle the mechanisms underlying cold adaptation. They first establish that cold tolerance adaptation in *Anolis* lizards follows the predictions of the oxygen- and capacity-limited thermal tolerance hypothesis, which states that organisms are limited by temperature thresholds at which oxygen supply cannot meet demand. They then explore the drivers of cold tolerance at a finer scale, finding evidence that northern populations are adapted to cooler thermal regimes and that both phenotypic plasticity and heritable genetic variation contribute to cold tolerance. The integration of physiological and gene expression data further highlights the varied mechanisms that drive cold tolerance adaptation in *Anolis* lizards, including both supply-side and demand-side adaptations that improve oxygen economy. Altogether, their work provides new insight into the physiological and genetic mechanisms underlying adaptation to new climatic niches and demonstrates that cold tolerance in northern lizard populations is achieved through the synergy of physiological plasticity and local genetic adaptation for thermal performance.

KEYWORDS
local adaptation, physiology, thermal tolerance, transcriptomics

There is a long history of research that aims to understand the biotic and abiotic factors that limit the distribution of species, and the mechanisms that enable particular species to overcome these limitations to expand their ranges. For example, Janzen's 1967 paper, "Why mountain passes are higher in the tropics," presented a detailed theoretical answer to the related question of why species diversity decreases as latitude increases (Janzen, 1967). Focusing on tropical regions, Janzen postulated that temperature uniformity selects for organisms with a relatively narrow, specifically adapted physiological tolerance. Adaptation to specific temperatures in tropical organisms, therefore, leads to highly stratified thermal niches across microclimates and altitudes, which drives higher species diversity in the tropics. Importantly, his work suggested that the narrow physiological tolerances of tropical organisms limit colonization of even marginally different thermal regimes. Therefore, when the ranges of tropical organisms expand into temperate regions, these organisms are subjected to higher temperature variability, including lower temperatures, and must adapt to this temperature variability to persist, which can pose major challenges for ectotherms in particular. In the 50 years since Janzen's work, various models have been proposed to explain how natural selection may act on physiological traits that limit the climatic tolerance and related geographic ranges of species. A widely applied model for ectotherms is the oxygen- and capacity-limited thermal tolerance (OCLTT) model (recently reviewed in Pörtner, Bock, & Mark, 2017), which is based on the mismatch between the rates of decline in oxygen supply and demand. At a temperature threshold known as the critical thermal minimum (CT_{min}), the demand for oxygen becomes higher than the oxygen supply, resulting in reduced fitness in colder environments. Organisms expanding into more temperate regions must, therefore, respond to cooler climates by lowering their CT_{min}.

In this issue of *Molecular Ecology*, Campbell-Staton, Bare, Losos, Edwards, and Cheviron (2018) use the green anole lizard (*Anolis carolinensis*; Figure 1) as a model system to identify mechanisms that enable ectothermic lineages with tropical origins to colonize more temperate climatic niches. By sampling anole populations across a latitudinal transect, they tested the broad question of whether success in higher latitudes, with lower temperatures, occurs through phenotypic plasticity or the evolution of heritable genetic variation.

FIGURE 1 In situ photograph of *Anolis carolinensis* (courtesy of Alexander Jaffe)

They then tested how genetic, cellular and physiological changes contribute to increased oxygen supply or decreased oxygen demand during expansion into a novel temperate environment, thus, searching for the specific mechanisms by which the OCLTT model may explain cold tolerance in northern latitude populations.

The authors first demonstrate that physiological patterns in *Anolis* lizards follow expectations of the OCLTT model, which was verified by the presence of latitudinal clines in metabolic rate, CT_{min}, and blood lactate concentration (a measure of oxygen limitation; Figure 2). Next, the authors evaluate the contributions of two broad modes of cold tolerance adaptation: phenotypic plasticity and heritable genetic variation. To address this, the authors measure CT_{min} between control and cold-acclimated lizards from each population and find that while CT_{min} does decrease following cold acclimation (supporting a plastic response), CT_{min} in both the control and cold acclimation treatments negatively correlates with population latitude (supporting a heritable genetic response). These results, therefore, provide exciting evidence that both plasticity and heritable genetic variations underlie adaptation to cold in *Anolis* lizards (Figure 2). Interestingly, the magnitude of the plastic response is remarkably consistent across latitude, indicating that even southern populations have great potential to rapidly acclimate to colder temperatures. The authors also specifically address whether adaptation is a product of an increase in oxygen supply (supply-side adaptation) or a decrease in oxygen demand (demand-side adaptation). Comparisons of heart size and haemoglobin concentration, both proxies for oxygen supply, indicate no correlation with latitude of population origin and do not change with acclimation. The authors find, however, that estimates of oxygen consumption respond to acclimation and correlate significantly with thermal variability, which is tightly associated with latitude across the species' range. Collectively, these physiological experiments suggest that *Anolis* lizards may adapt to acute and chronic exposure to cold temperatures primarily by reducing oxygen demand, begging the question of what molecular mechanisms underlie these differences in physiological tolerance and performance.

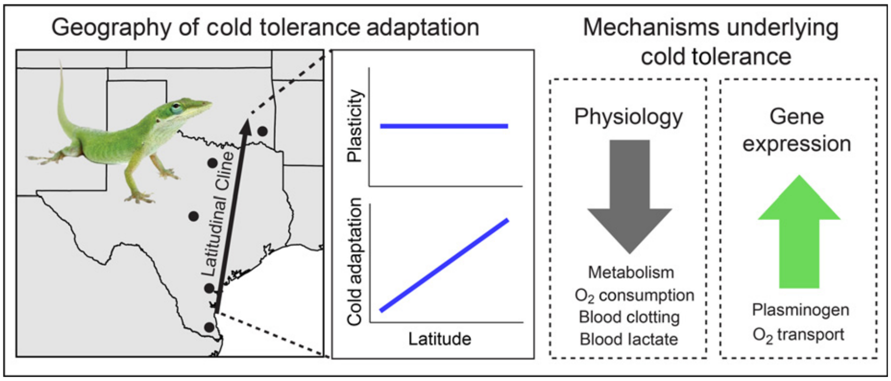

FIGURE 2 Schematic of *Anolis carolinensis* populations (black dots) analysed in Campbell-Staton et al. (2018), which were situated along a latitudinal transect through Texas and Oklahoma. Along this cline, cold tolerance increases with latitude, while phenotypic plasticity remains constant. Detailed investigations of physiological and gene expression data indicate that anoles follow the expectations of the OCLTT model and that CT_{min} is lower in northern latitude populations due to adaptations that both reduce oxygen demand (lower metabolism) and increase oxygen supply (activation of plasminogen, which reduces blood viscosity)

A major contribution of the work of Campbell-Staton et al. (2018) is providing one of the first illustrations of the molecular mechanisms that may enable adaptation of lower CT_{min} and, thus, the expansion of tropical vertebrates into more temperate climates. Using liver gene expression data from control and acclimation treatment samples from various latitudes, the authors identify 15 clustered sets of co-expressed genes that were significantly associated with oxygen demand, including functions such as oxygen transport and aerobic respiration. The authors further examine multiple genes involved in a key blood-clotting pathway (plasminogen/plasmin pathway) whose expression is associated with blood lactate concentration—a proxy for oxygen limitation that increases under cold stress. Together, these findings suggest that anoles have adapted to cold temperatures through changes in pathways that mediate blood coagulation, which aligns with previous observations of decreased circulatory performance (Pörtner, 2001) and increased blood viscosity (Snyder, 1971) in cold-stressed ectotherms. The integration of multiple data types also further reveals idiosyncrasies regarding the evolution of cold tolerance. For example, while physiological measurements suggest that oxygen demand may drive cold tolerance adaptation, gene expression results indicate instead that oxygen supply (through reduced blood viscosity) may be a more important target for selection in cold environments.

A hallmark of science that drives the field forward is that it tends to pose as many questions as it answers, and the work of Campbell-Staton et al. (2018) accomplishes both. This study elegantly demonstrates the synergy between plasticity and local genetic adaptations during species expansions into new climatic niches and also provides insight into the molecular mechanisms that explain how adaptation and plasticity might manifest in shifts of physiological tolerances. Despite the finding that plastic responses are consistently high across both cold-adapted and noncold-adapted populations, this study argues for the importance of locally adapted allelic combinations that may enable certain species to persist and potentially respond to climate change. Combined with other recent studies in this system, which demonstrate the ability of acute climatic variation to drive rapid adaptation in cold tolerance (Campbell-Staton et al., 2017), the results of this work invoke additional interesting and important questions. For instance, what is the relative importance of long-term selection pressures versus acute or extreme climatic events in shaping local signatures of cold tolerance, variation in tolerance and population-level patterns of evolution? Ongoing patterns of global climate change (e.g. global warming) are not only associated with gradual trends but also with an increased frequency of extreme climatic events, and studies that emulate the work of Campbell-Staton et al. (2018) and illustrate how organisms adapt to climatic variation are valuable for understanding and predicting species responses to climate change. This study also provides valuable testable hypotheses for how acute and chronic cold temperature exposure may drive adaptation of sets of co-adapted gene complexes in ectotherms. Future studies that test the generality of these patterns in other species would provide important insight into the spectrum of mechanisms underlying cold adaptation, and the degree to which mechanisms are shared across diverse taxonomic groups.

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