

# Realized thermal performance predicts range limits of fishes

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Exploring the role of temperature in setting species' range boundaries has been a key goal of ecologists for many decades. Traditionally, physiological thermal thresholds (such as the temperatures coinciding with maximum physiological performance [ $T_{opt}$ ], or that lead to a loss of motor function or death [ $CT_{min}$  and  $CT_{max}$  for low and high temperatures, respectively]) are compared to species' range boundaries, and such comparisons have proved highly informative. However, these physiological thresholds often fail to explain the range limits of animals; probably because wild animals balance physiological constraints with the need to feed, avoid predators and competition, and reproduce. Therefore, it seems intuitive that thermal performance data collected from wild animals ("realized thermal performance") may be better predictors of range limits than physiological data alone, yet this prediction is relatively unexplored.

We collected realized thermal performance data (relative rates of locomotion *via* biologging and reproductive growth *via* analyses of gonadosomatic indices [GSI]) from several species of wild fishes, and compared these to temperatures at their latitudinal range boundaries. We found that optimal temperatures for realized locomotion, GSI and somatic growth (collected from wild fishes in previous studies) predicted the maximum warm range boundaries of fishes extremely well (top panel of figure;  $R^2 = 0.97$ ), and the type of performance measure (locomotion, GSI or somatic growth) did not contribute to the best model of range boundary temperatures. To explore why the slope of this relationship was  $\sim 0.75$ , we compiled estimates of physiological  $T_{opt}$  and  $CT_{max}$  (the "upper critical temperature") from laboratory studies of two major ectothermic groups: fishes and lizards (performance was reported as the scope for aerobic metabolism in fishes, and sprinting capacity in lizards). Given most biological rates (including metabolism and enzyme reactive rates) increase exponentially with temperature, we converted all  $T_{opt}$  (realized and physiological), physiological  $CT_{max}$  and warm boundary temperatures to an equivalent "biological rate" using the temperature coefficient ( $Q_{10}$ ) generally found to describe the temperature dependence of most biological rates in ectotherms ( $\sim 2.0$ ). We found that slopes for all three relationships (realized  $T_{opt}$  – boundary temperatures of fishes, and

physiological  $T_{opt}$  – physiological  $CT_{max}$  in fishes and lizards) were similar to one another, and close to 1 (bottom panel of figure). This finding suggests two things. First, the warm range boundaries of fishes are largely driven by a universal physiological relationship between optimal and upper critical temperatures that holds across ectotherms. Second, since optimal and critical temperatures approach one-another on an increasing empirical temperature scale (the slope of all three relationships are  $\sim 0.75$  when temperature is reported in degrees Celsius or Kelvin), but do not on a thermodynamic scale (e.g. when accounting for the temperature dependence of biological rates all slopes  $\sim 1.0$ ) the universal  $T_{opt}$ - $CT_{max}$  relationship appears to be well-explained by the temperature dependence of biological rates.

While physiological thermal performance data are unreliable estimators of animal range boundaries, results from this study suggest realized thermal performance measurements may strongly predict the distribution of ectotherms. Improving our ability to explain the temperature dependence of species' range boundaries is particularly important given the likelihood of future climate change.

Top panel: Realized  $T_{opt}$  versus maximum summer temperatures at equatorward range boundaries in wild fishes. Bottom panel: transformed estimates of realized  $T_{opt}$  and warm boundary temperatures for wild fishes (blue data and left y-axis), and physiological  $T_{opt}$  and  $CT_{max}$  for laboratory-measured fishes (pink data and right y-axis) and lizards (green data and right y-axis).

