Phenotypic evolution in the Anthropocene

Priyanga Amarasekare
Department of Ecology and Evolutionary Biology
University of California Los Angeles

1. **Phenotypic traits constitute the interface between the organism and the environment**

Macroscopic patterns (community properties, biogeographic patterns) arise from phenotypic trait responses to environmental variation

Environment: biotic (competition, predation), abiotic (temperature, rainfall)

2. Evolution of phenotypic traits results from the interplay between selection and constraints

3. **Irreversible evolutionary end points result from constraints on phenotypic evolution**

Challenge: incorporate mechanistic descriptions of constraints into models of eco-evolutionary dynamics

Motivation: predict whether species can adapt to perturbations in their biotic and abiotic environment (e.g., climate warming, species invasions)

Phenotypic evolution: interplay between selection and constraints

Selection: biotic and abiotic factors generate variance in fitness

Evolution: heritable variation

Variation: **genetic constraint** on phenotypic evolution

Energetic constraints

Trade-offs (negative correlations between traits)

Only certain evolutionary outcomes are possible (e.g., fecundity-longevity, fecundity-body size, semelparity-iteroparity)

Transitions between outcomes are difficult

Morphological constraints

Irreversible evolutionary endpoints

Morphological constraints

Upper limit to evolutionary trajectories (e.g., body size in insects)

Biochemical constraints

DNA replication, protein folding, metabolic pathways

Constraints on selection

Irreversible evolutionary end points

Upper limit to evolutionary trajectories

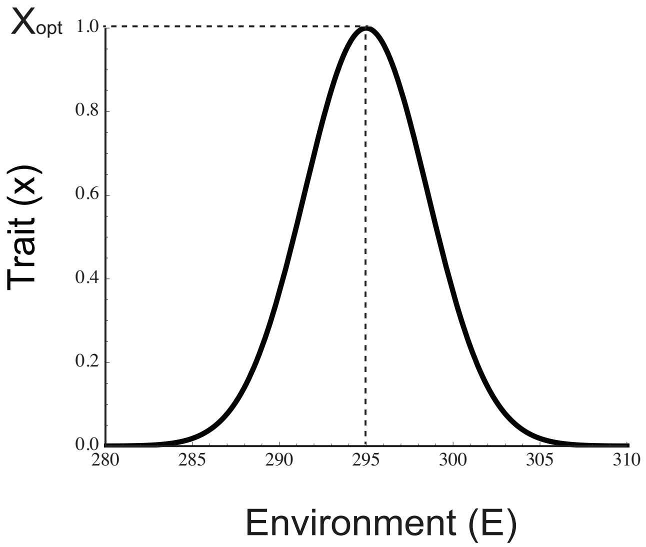
Phenotypic evolution in response to environmental perturbations

Data:

Rapid evolution in response to perturbations ==> species respond to novel selection pressures unimpeded by constraints

Failure to adapt to perturbations ==> constraints impede adaptation to new selection regimes

Phenotypic plasticity as a strategy to maximize fitness in variable environments



Reaction norm: range of phenotypic responses exhibited by a genotype in response to environmental variation

Evolution of phenotypic plasticity

Selection and constraints

Constraints: genetic

energetic

biochemical

Temperature variation and thermal reaction norms

Do organisms have sufficient plasticity to respond to changing thermal environments (climate warming)?

Can plasticity evolve fast enough to keep pace with warming?

Role of biochemical constraints

Thermal reaction norms

Framework for characterizing thermal reaction norms

Data: qualitative nature of reaction norms conserved across taxa

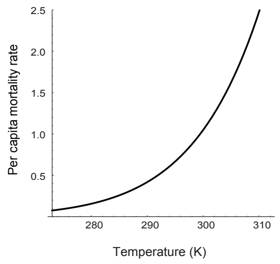
Mechanistic descriptions of thermal reaction norms

Mechanism at biochemical level

Trait response at phenotypic level

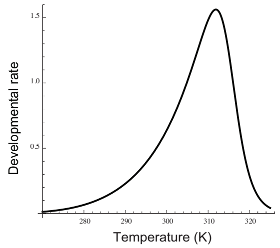
Rate-controlled
(reaction kinetics and enzyme inactivation)

Monotonic



Mortality

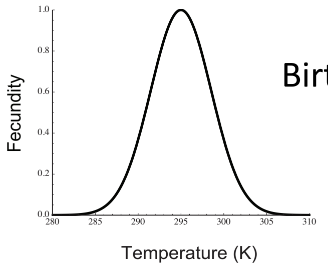
Left-skewed



Maturation

Regulatory
(neural and hormonal regulation)

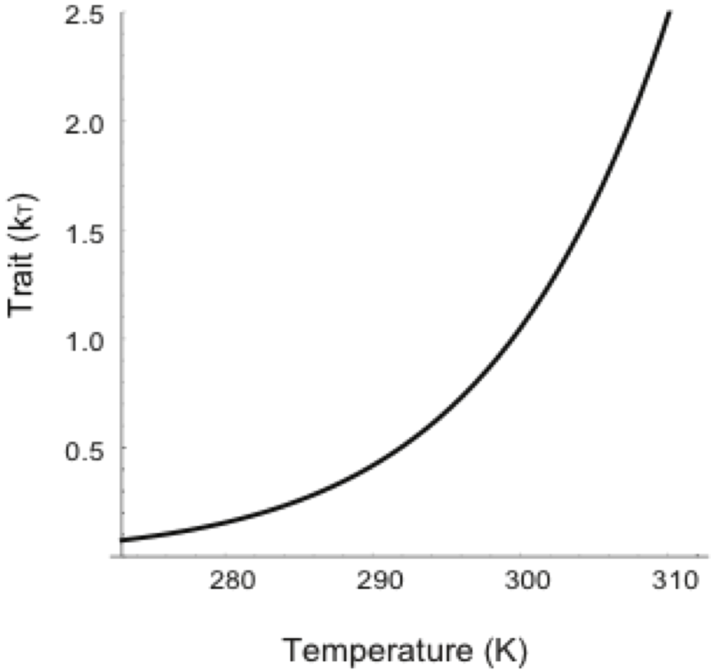
Unimodal, symmetric



Birth, attack

Rate-controlled temperature responses

Monotonic

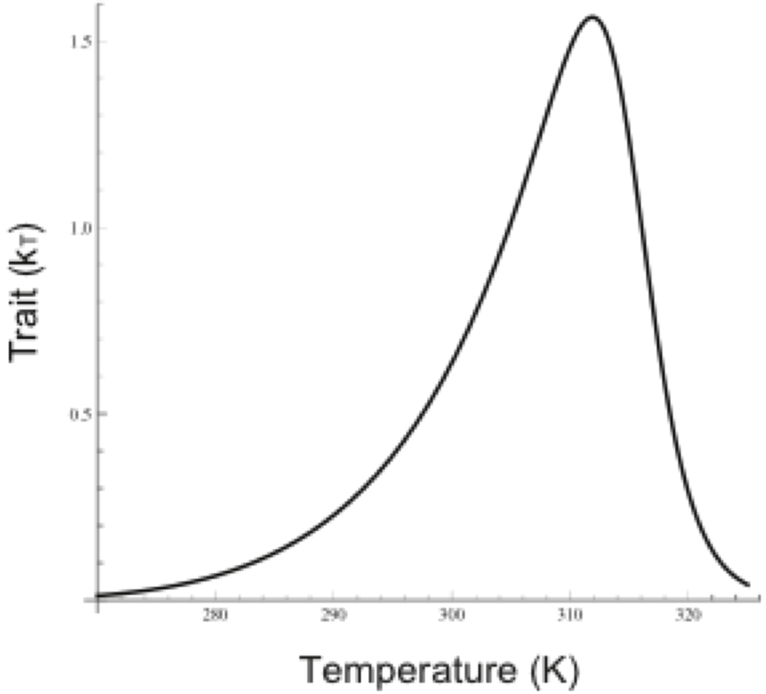


$$k_T = k_{T_R} e^{A_k \left(\frac{1}{T_R} - \frac{1}{T} \right)}$$

Boltzmann-Arrhenius function

Rate-controlled temperature responses

Left-skewed

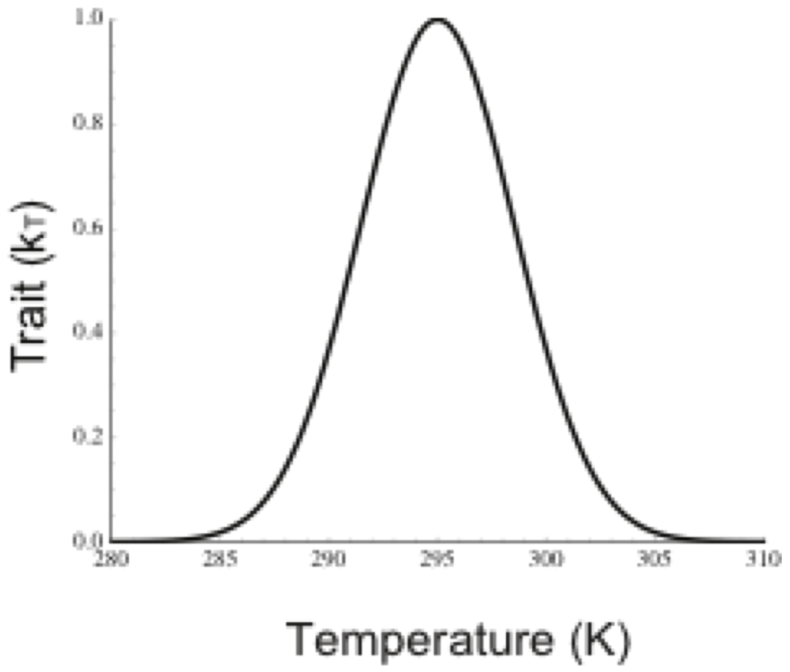


$$k_T = \frac{\frac{k_{T_R} T}{T_R} e^{A\left(\frac{1}{T_R} - \frac{1}{T}\right)}}{1 + e^{A_L\left(\frac{1}{T_{L/2}} - \frac{1}{T}\right)} + e^{A_H\left(\frac{1}{T_{H/2}} - \frac{1}{T}\right)}}$$

Sharpe and DeMichele (1977), Schoolfield et al. (1981)

Regulatory responses

Symmetric, unimodal



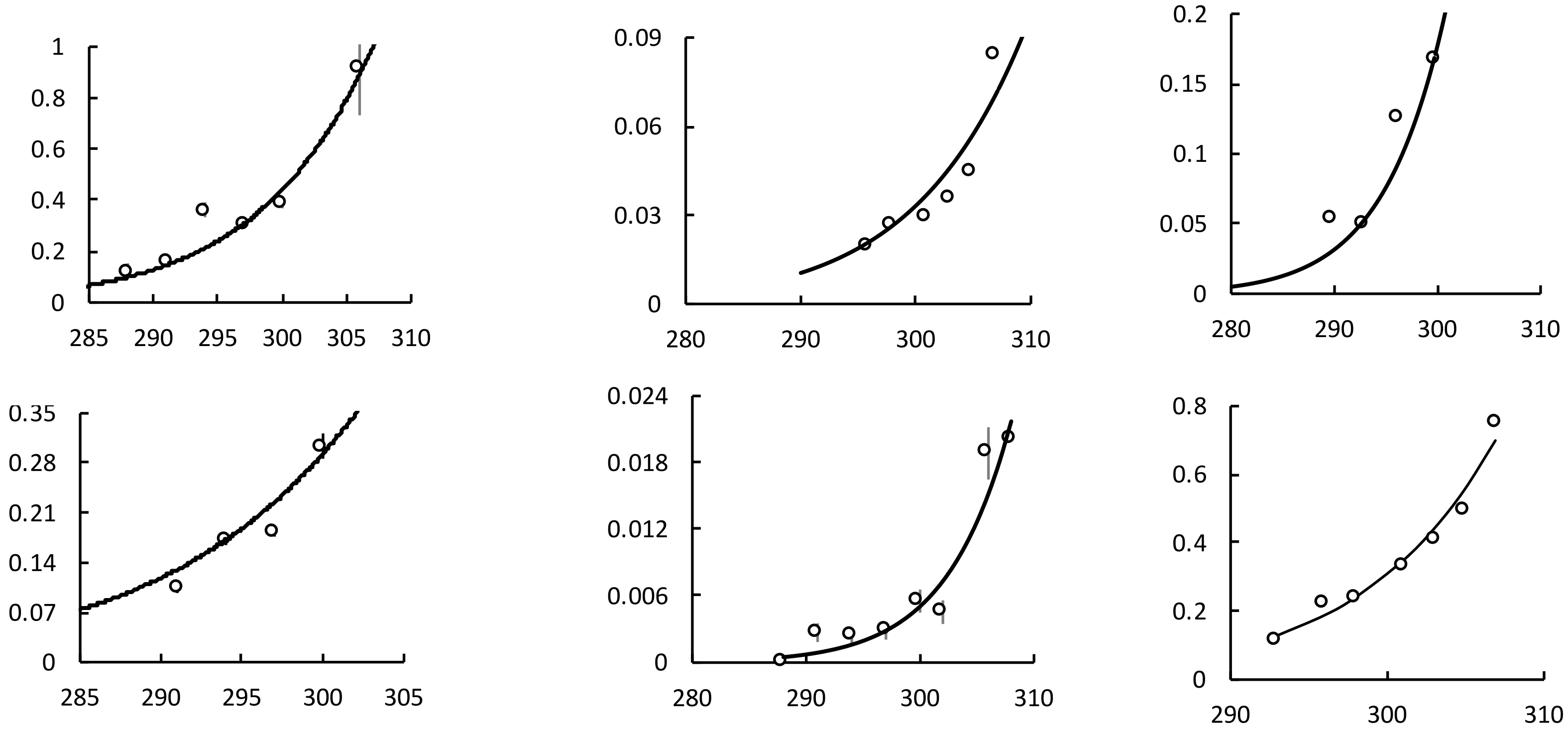
$$k_T = k_{T_{\mathrm{opt}}} e^{-\frac{\left(T - T_{\mathrm{opt}}\right)^2}{2s^2}}$$

Gaussian function

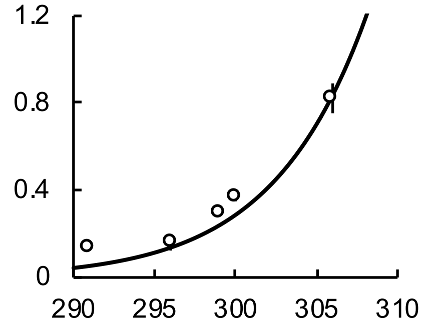
Framework: characterize reaction norms based on temperature effects on biochemical processes

Prediction: if temperature effects on biochemical processes conserved across taxa, qualitatively similar reaction norms

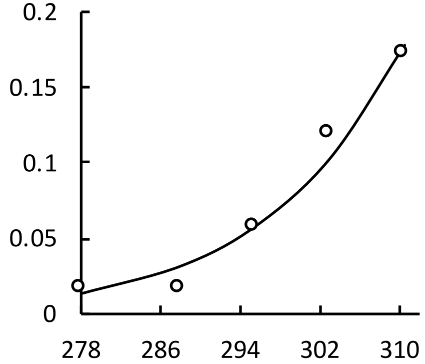
Monotonic temperature responses: mortality



Hemipteran herbivores

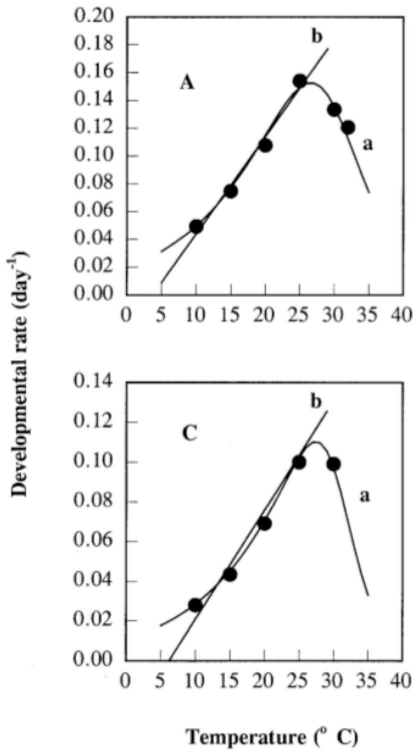


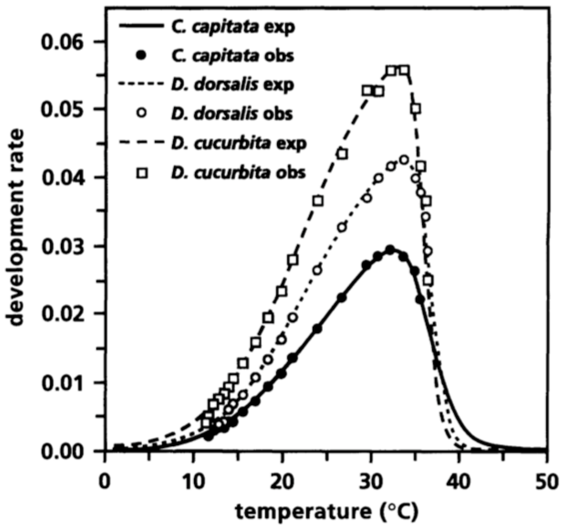
Insect parasitoids



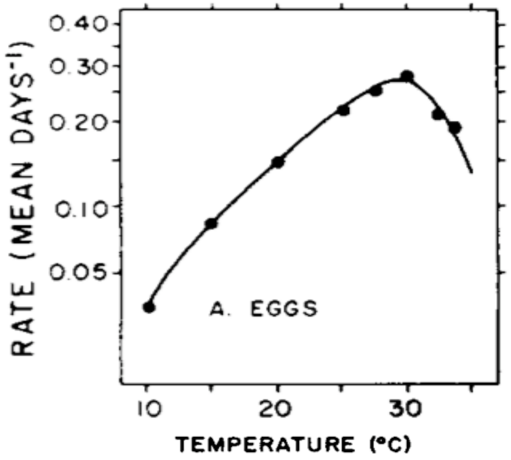
Beetles

Left-skewed temperature responses: maturation

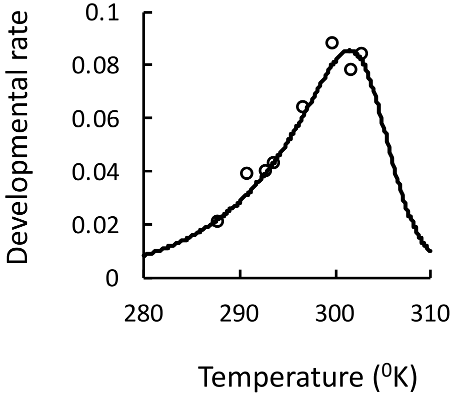


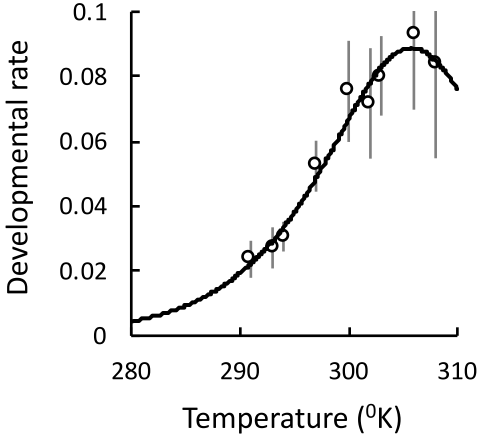


Drosophila species

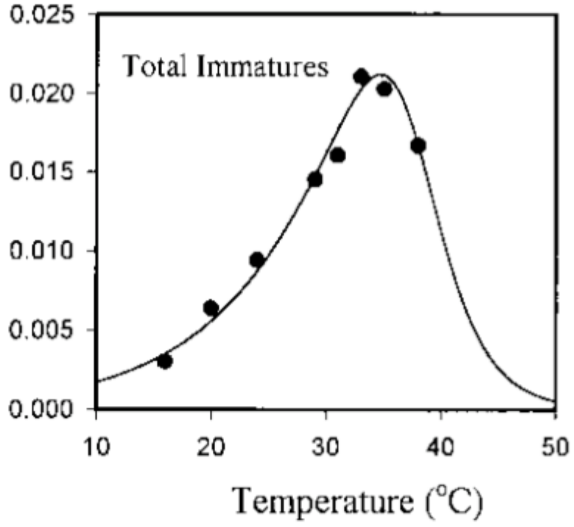


Pine beetle



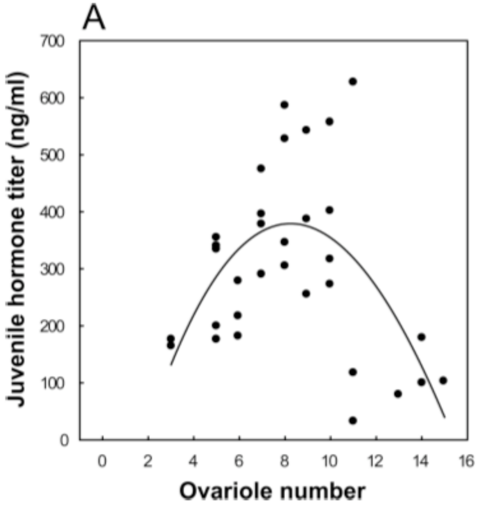


Insect parasitoids

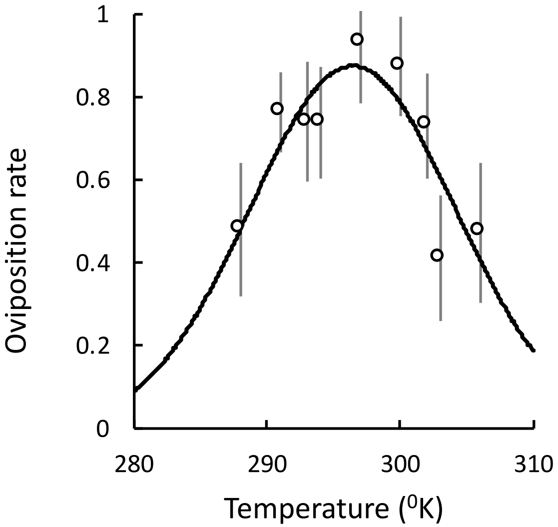


Mite

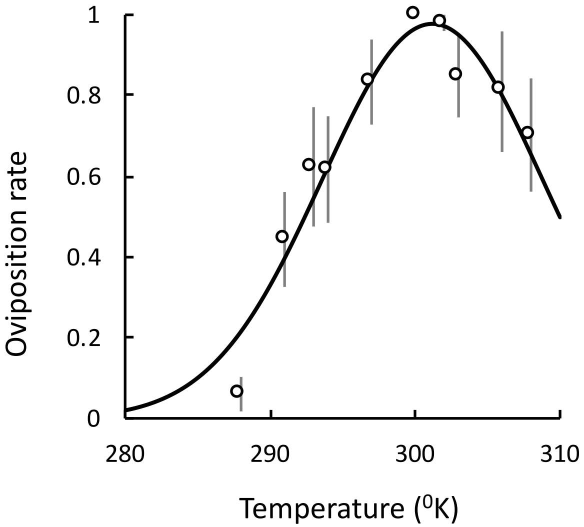
Unimodal temperature responses: reproduction

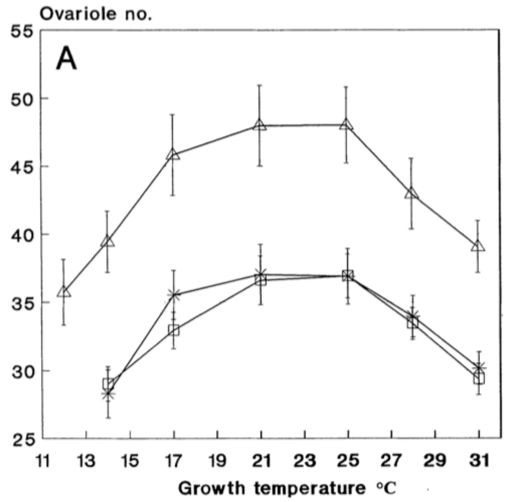


Honeybees

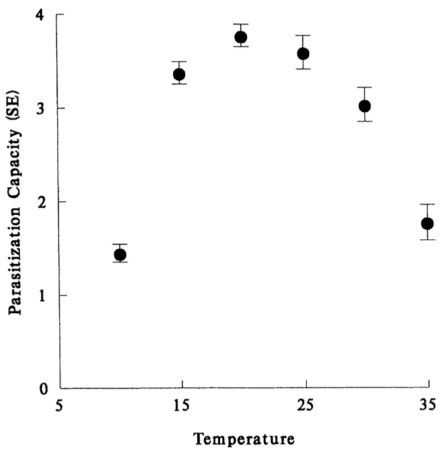


Trissolcus murgantiae

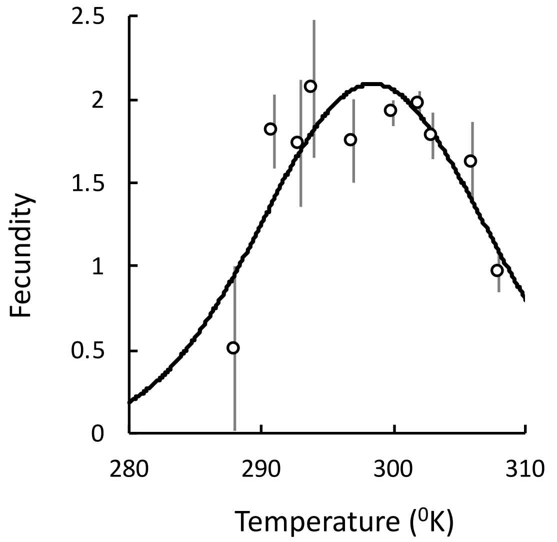




Drosophila species

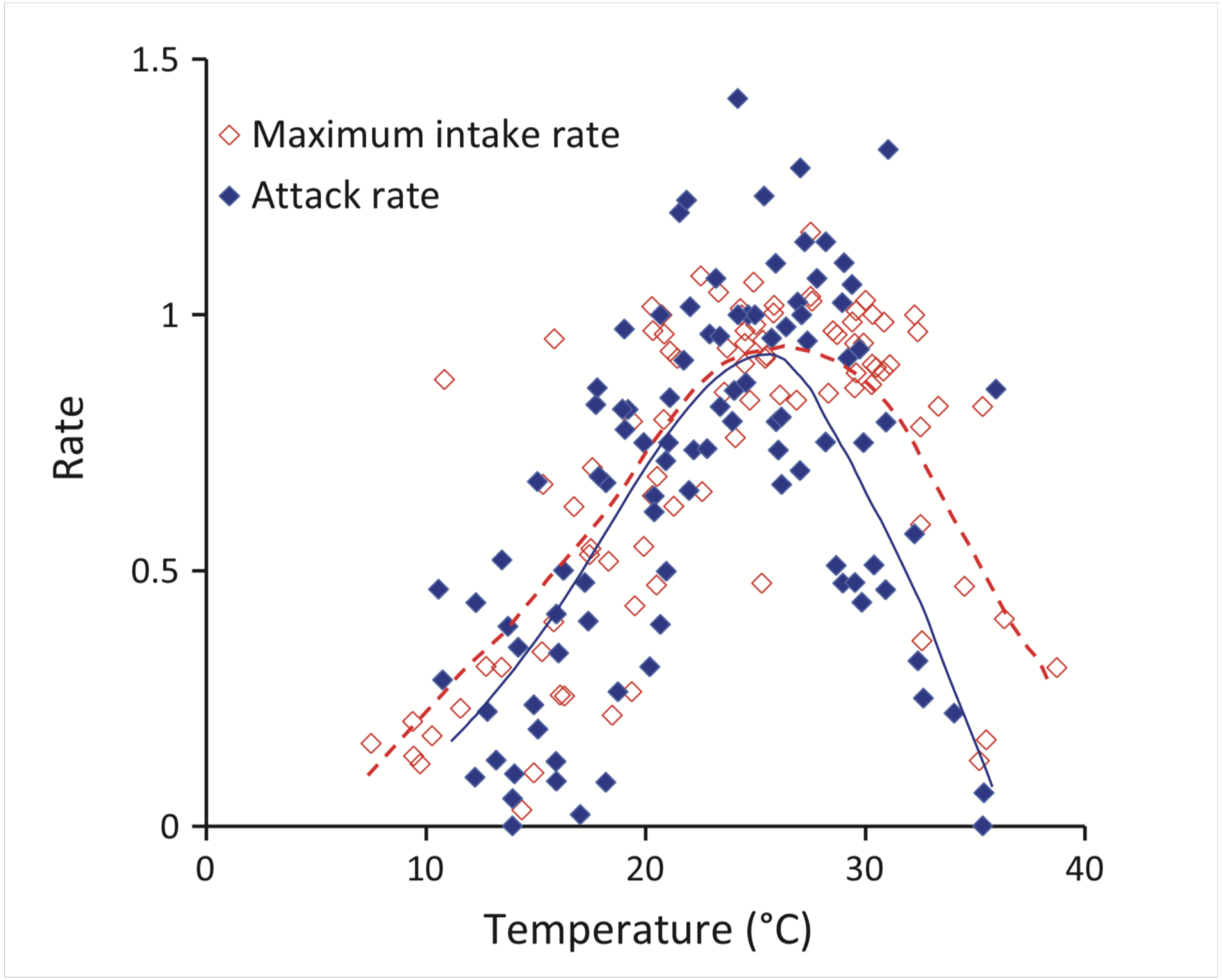


Trichogrammatidae



Ooencyrtus johnsonii

Unimodal temperature responses: attack and maximum uptake rates



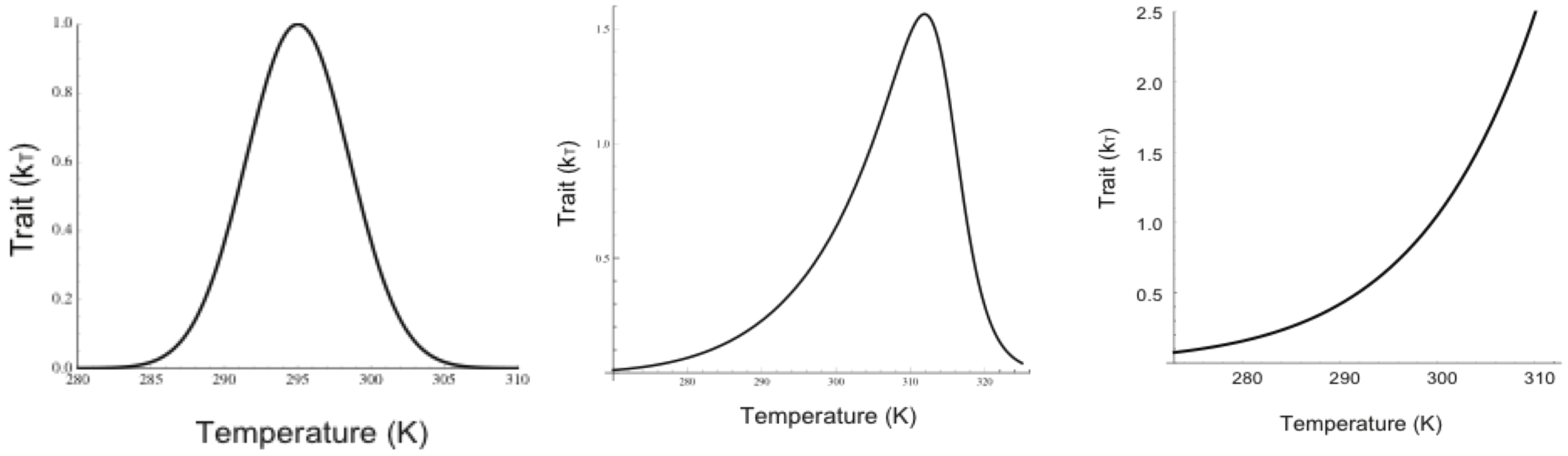
Thermal reaction norms

Framework for characterizing reaction norms

Data: qualitative nature of reaction norms conserved across taxa

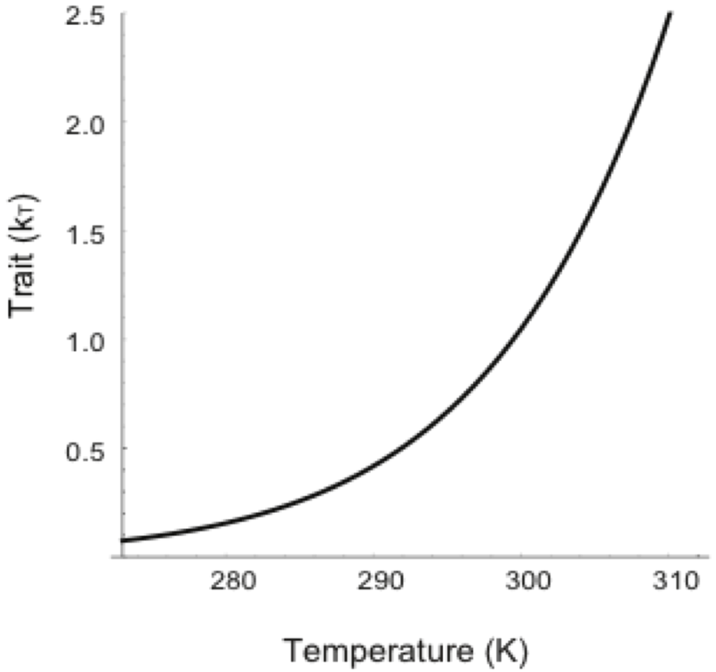
Constraints on thermal reaction norms

Regulatory | Rate-controlled



Regulatory responses: symmetric at extremes ==> similar constraints

Rate-controlled responses: asymmetric ==> different constraints

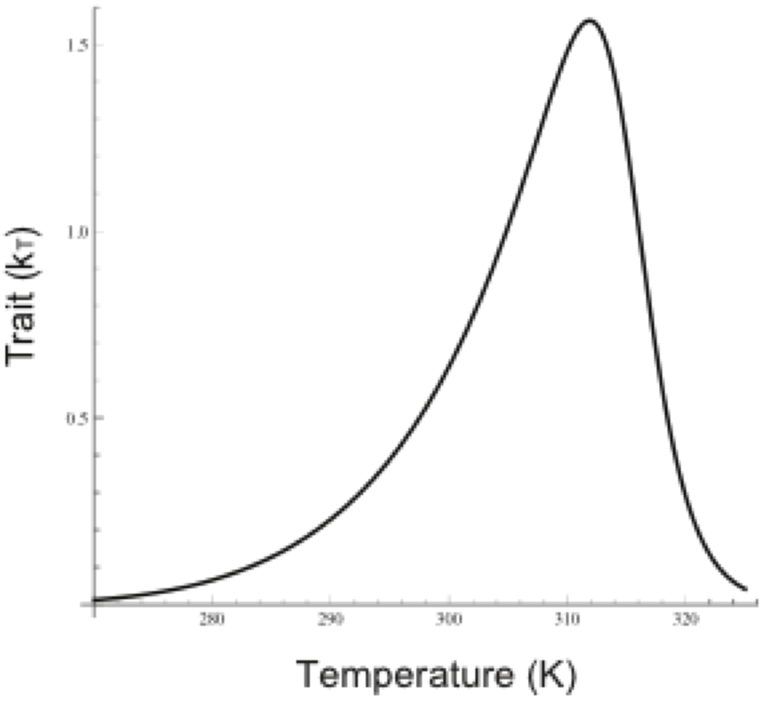


$$k_T = k_{T_R} e^{A_k \left(\frac{1}{T_R} - \frac{1}{T} \right)}$$

Monotonic reaction norms

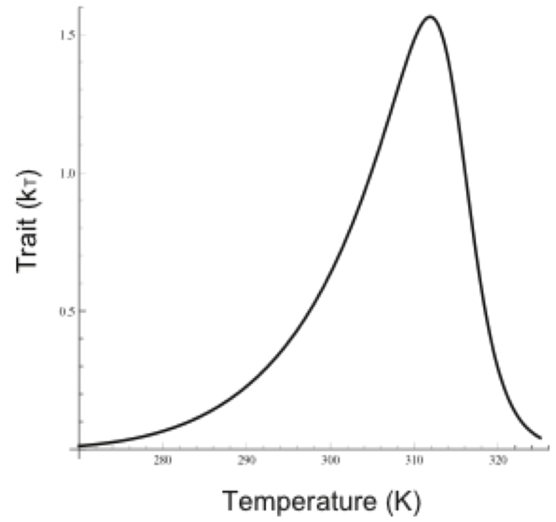
Reaction rates (e.g., metabolic, mortality) increase with temperature ==> biochemistry imposes fundamental constraint on longevity

Left-skewed reaction norms



$$k_T = \frac{\frac{k_{T_R} T}{T_R} e^{A\left(\frac{1}{T_R} - \frac{1}{T}\right)}}{1 + e^{A_L\left(\frac{1}{T_{L/2}} - \frac{1}{T}\right)} + e^{A_H\left(\frac{1}{T_{H/2}} - \frac{1}{T}\right)}}$$

Rate-controlled responses: faster decline at high temperatures than at low temperatures ==> different constraints



$$k_T = \frac{\frac{k_{T_R} T}{T_R} e^{A\left(\frac{1}{T_R} - \frac{1}{T}\right)}}{1+e^{A_L\left(\frac{1}{T_{L/2}} - \frac{1}{T}\right)} + e^{A_H\left(\frac{1}{T_{H/2}} - \frac{1}{T}\right)}}$$

Left-skewed responses

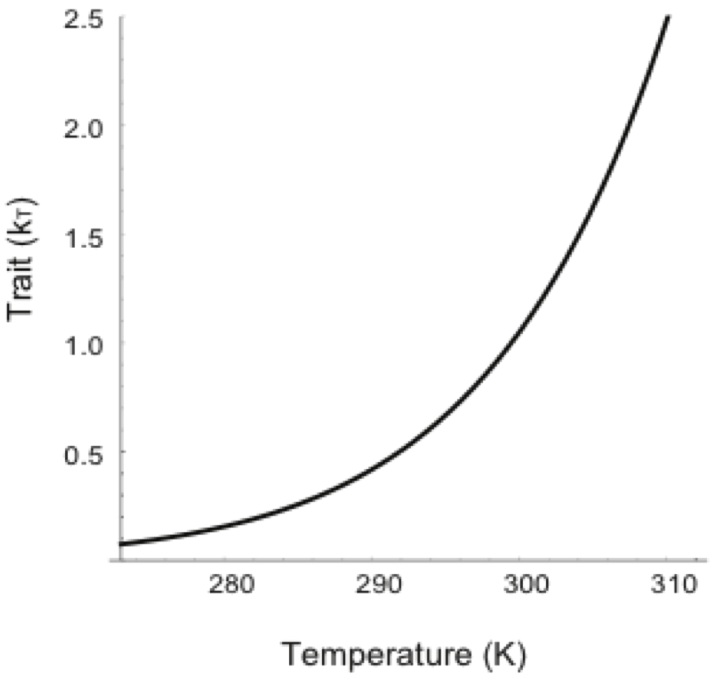
Low-temperature decline: freezing of body fluids, slower response

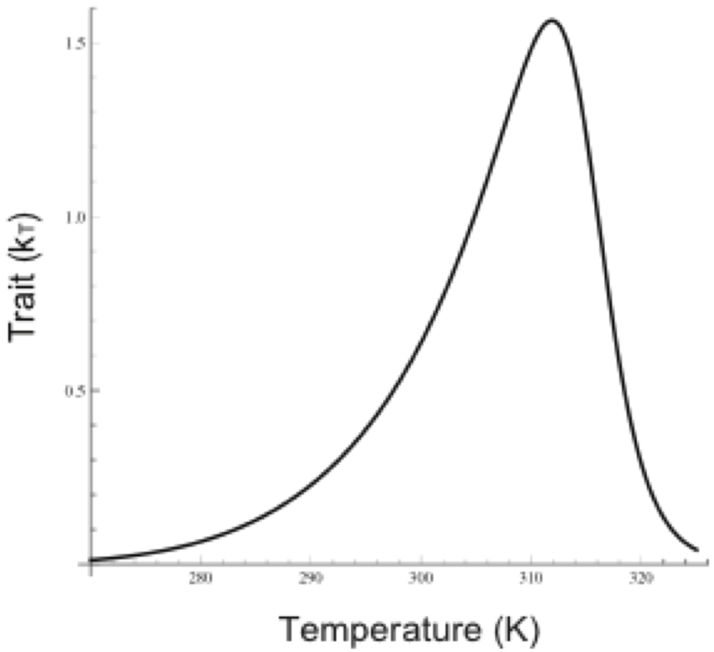
High-temperature decline: protein denaturation, faster response

Hard limit at high temperatures: protein denaturation (irreversible process)

Softer limit at low temperatures: freezing of body fluids

Adaptations to avoid/minimize freezing of body fluids, not so for heat-induced protein denaturation





Biochemical constraints on thermal adaptation: **slow down at low temperatures, drop dead at high temperatures**

Climate warming ==> exposure to warmer thermal regimes ==> organisms more likely to encounter upper limit of phenotypic plasticity

Traits under strong biochemical control (e.g., development, mortality) more adversely affected

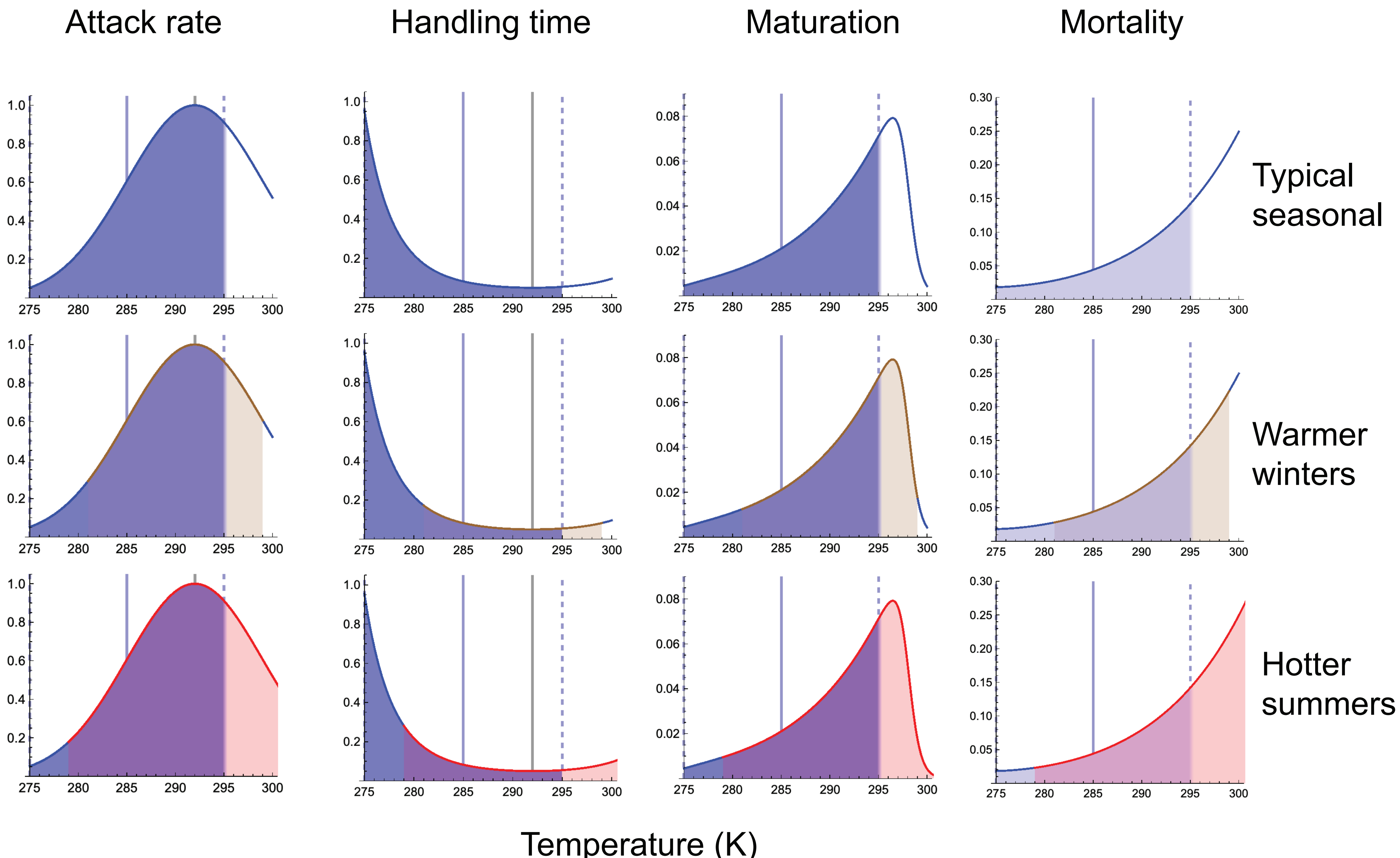
Thermal reaction norms of life history and interaction traits

Attack rate

Handling time

Mortality

Maturation



Attack rate
Handling time
Maturation
Mortality
Typical seasonal
Warmer winters
Hotter summers
Temperature (K)

Warming effects on trait responses

Rate-controlled responses (maturation and mortality) more adversely affected by warming than regulatory responses (attack rate, handling time)

Trait-level constraints and population/community-level consequences

Biochemical constraints --> demographic constraints prevent adaptation to novel thermal environments --> irreversible biogeographic pattern

Latitudinal directionality in invasion success

Tropical ectotherms more successful in invading temperate communities than *vice versa*

Evidence

1. Paleontological and biogeographic data

Diversity at higher latitudes

Geographic expansion of taxa originating in tropics (**common**)

Taxa originating at higher latitudes expanding to tropics (**rare**)

Re-invasion of tropics by higher-latitude taxa (**rare**)

Evidence

2. Contemporary invasion data

Most successful invaders of temperate habitats

Ectotherms of tropical origin

Cane toad, Asian tiger mosquito, Fire ant, scale insects, marine invertebrates

Most successful temperate invaders of tropical habitats

Endotherms

Passerine birds, rodents

Goal

Mechanistic underpinnings of directionality in invasion success

Latitudinal directionality in invasion success

Adaptation to novel environments

Tropical species better able to adapt to temperate habitats but not *vice versa*

Eco-evolutionary dynamics: quantitative genetic model of trait evolution, stage-structured model of population dynamics

Evolution of thermal reaction norm for reproduction

Amarasekare and Johnson (2017)

Tropical ectotherms invading temperate habitats (warmer to colder): reaction norm rapidly adapts to temperate thermal regime

Temperate ectotherms invading tropical habitats (colder to warmer): stochastic extinction during invasion phase precludes adaptation to tropical thermal regime

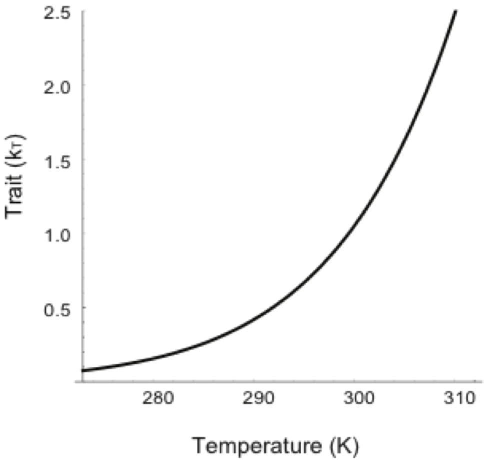
Temperate ectotherms invading tropical habitats

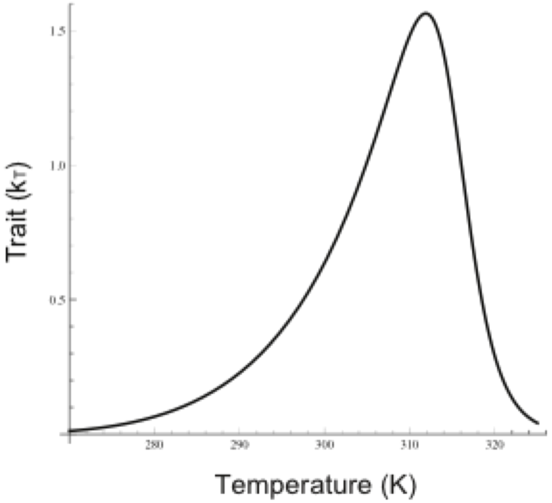
Thermal reaction norms for mortality and maturation reach upper limit of plasticity: increase in mortality and decrease in maturation --> low abundances during invasion phase --> extinction due to demographic stochasticity

Biochemical constraint imposes demographic constraint

Biochemical constraint on reaction norm evolution --> irreversible biogeographic pattern: latitudinal directionality in invasion success

Adaptation to climate warming





Evolution of upper thermal limit

Genetic variation in thermal reaction norms

Evolution of thermal reaction norms

Cryptic genetic variation: expressed in novel or extreme environments

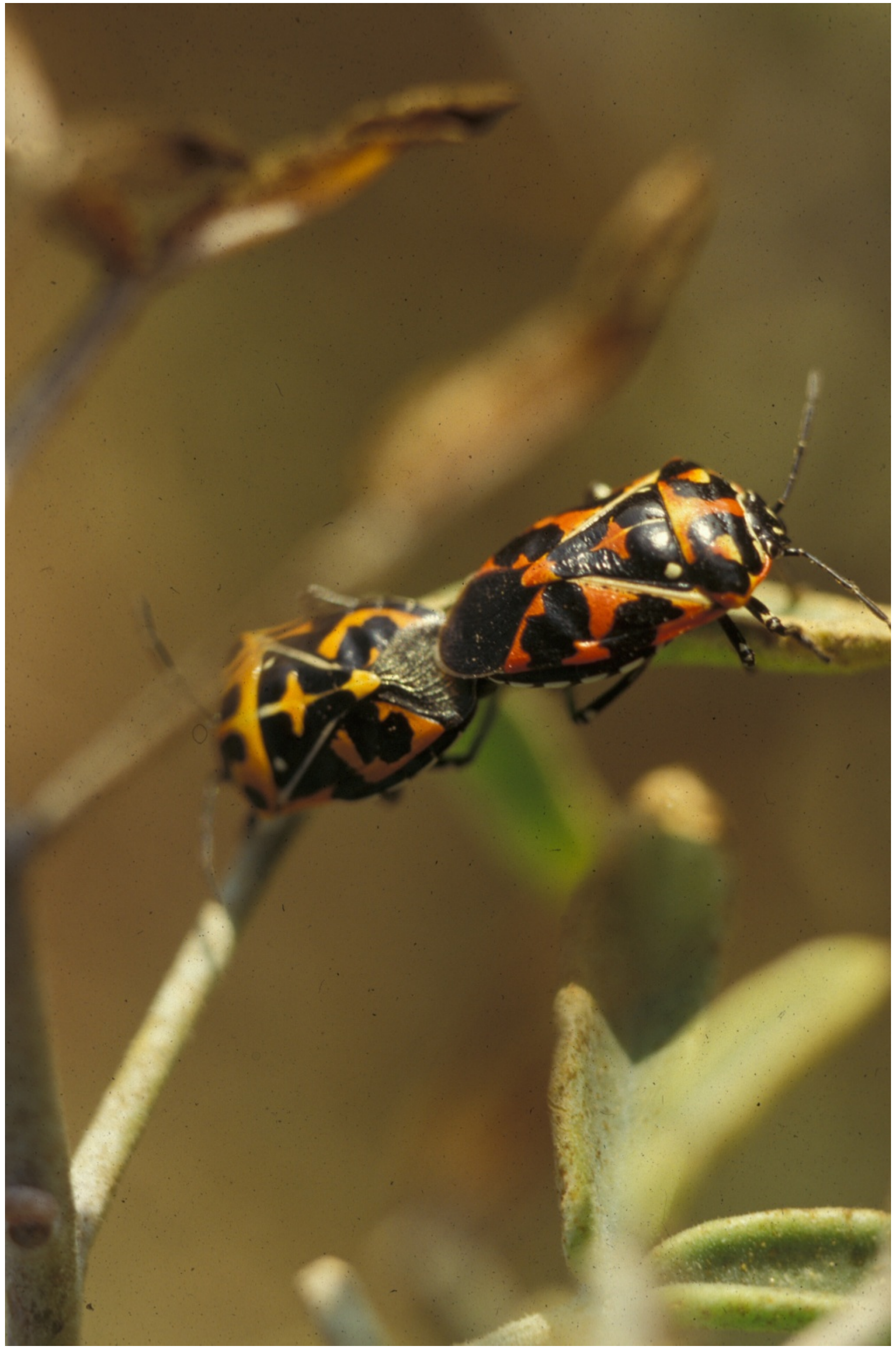
(Waddington 1957; Gibson 2009; Masel & Siegal 2009)

Allow organisms to adapt to perturbations in typical environment

Uncovering cryptic genetic variation

Prediction:

Greater genetic variability in reaction norms in perturbed environments compared to typical environments

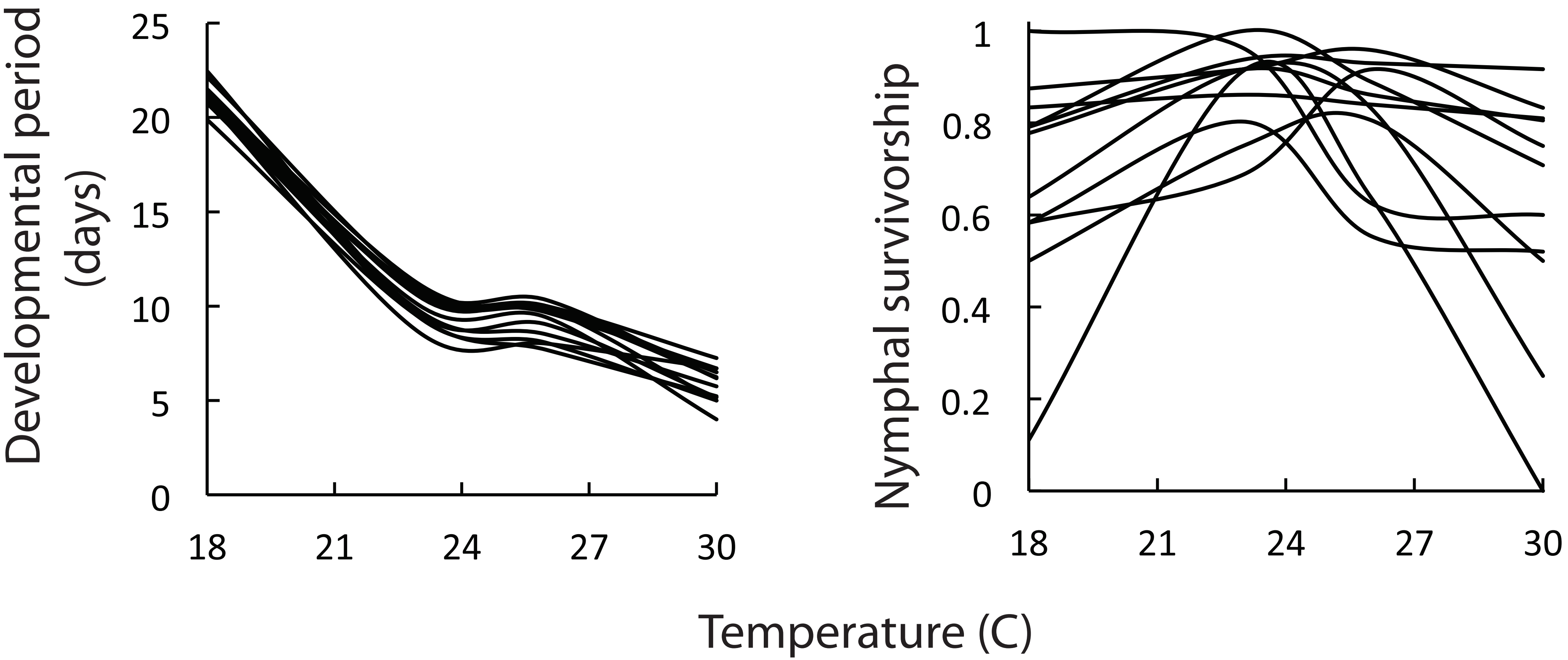


Harlequin bug

(*Murgantia histrionica*)

(Hemiptera: Pentatomidae)

Uncovering cryptic genetic variation



Other empirical evidence

Rapid adaptation of low temperature threshold, no evidence for high temperature threshold

Data:

Rapid evolution in response to perturbations ==> species respond to novel selection pressures unimpeded by constraints

Failure to adapt to perturbations ==> constraints impede adaptation to new selection regimes

Hypotheses

Rapid evolution in response to environmental perturbations:

Genetic variation in reaction norms
Weak biochemical/energetic constraints

Failure of evolution:

Genetic and biochemical constraints

Life is driven by biochemistry

Biochemical constraints constitute strong impediments to evolution in response to changing environments

Things I do not understand

1. Irreversible processes in evolution

2. Constraints that cause regulatory responses to be symmetric at extremes

3. How to incorporate constraints into models of eco-evolutionary dynamics