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Fluctuating Thermal Histories Produce Nonlinear Effects on Developmental Rate, Growth, and Adult Performance in Insects

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ABSTRACT

Thermal biology commonly represents insect environments by mean temperature, yet insects develop within sequences of temperatures whose amplitude, duration, order, and recovery intervals can alter biological responses even when means are identical. This theoretical framework evaluates why thermal history should be treated as an ordered biological exposure rather than as variance surrounding a mean. Evidence across insects indicates that fluctuating regimes can accelerate, retard, improve, impair, or leave unchanged different components of performance depending on the thermal region occupied, fluctuation amplitude, developmental stage, exposure duration, trait measured, and subsequent environment. Developmental rate is particularly sensitive to nonlinear temperature–response relationships, whereas growth, energetic reserves, body composition, and reproduction can respond discordantly. Thermal effects may also persist across stages, decay after transfer to new conditions, or be modified by acclimation and environmental recovery. The article therefore develops a proposed thermal-history framework in which current performance emerges from interaction among instantaneous temperature, nonlinear trait sensitivity, accumulated exposure, developmental timing, recovery opportunity, and state carried from earlier conditions. The framework does not assume that variability is intrinsically detrimental or beneficial, nor that laboratory thermal responses transfer directly to field performance. Instead, it identifies conditions under which constant and fluctuating regimes with similar means are expected to diverge and specifies boundaries requiring direct validation. This history-based interpretation offers a more precise basis for linking experimental thermal physiology with development, life-history performance, and environmentally realistic insect responses.

Keywords: Thermal variability, Developmental rate, Thermal performance curves, Acclimation, Carry-over effects, Insect energetics

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Introduction

Temperature structures insect development, physiology, and life history, but a thermal environment is not fully represented by its arithmetic mean. Across experimental biology, manipulated thermal variability produces effects whose magnitude and direction depend on the underlying thermal context rather than following a universal response to variance [1]. Within insects, acclimatory plasticity in critical thermal limits is widespread but generally modest, and its magnitude differs among developmental stages and taxa [2]. These observations already

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caution against treating a temperature mean, or even a single tolerance endpoint, as a sufficient description of thermal exposure.

A second complication is that different components of performance need not share the same thermal optimum. Comparative arthropod evidence indicates that temperatures associated with peak performance can differ among life-history traits, so an environment favorable for one component of performance may simultaneously move another away from its optimum [3]. Developmental rate, growth, energetic state, survival, and later reproduction should therefore not be collapsed into a single thermal-performance quantity.

This article develops a proposed thermal-history framework for interpreting that multidimensional response. Its central premise is that insects encounter ordered exposures: temperature changes through time, stages differ in sensitivity, damaging episodes can be separated by recovery opportunities, and physiological states generated early in development may persist or disappear later. The framework consequently separates instantaneous nonlinear thermal effects from accumulated history, and separates developmental rate from growth, energetic condition, acclimatory state, and adult performance. It is intended as an evidence-bounded theoretical organization of existing findings, not as an empirically validated universal mechanism.

Why mean temperature is insufficient

The inadequacy of mean temperature follows first from nonlinear thermal-response geometry. When biological performance is a curved function of temperature, averaging performance across a fluctuating regime does not necessarily recover performance at the regime's mean. More importantly, the direction of that difference is not fixed. Experimental work testing Jensen-type expectations shows that moderate and large fluctuations can produce opposite deviations at high mean temperature, demonstrating that fluctuation amplitude and the region of the response curve must be considered jointly [4]. Variability therefore cannot be assigned an invariant beneficial or detrimental sign.

Matched constant and fluctuating treatments reinforce this conditionality. In *Spodoptera littoralis*, incorporating daily fluctuation altered multiple life-history outcomes, with particularly consequential effects under the highest tested mean temperature [5]. A whole-life-cycle study of *Spodoptera frugiperda* similarly found that mean temperature, fluctuation magnitude, developmental stage, and trait identity interacted, rather than producing a single consistent response to increased variability [6]. These noctuid results support concern about extrapolation from constant warm treatments, but they do not justify assuming that fluctuation is generally harmful.

Contrasting taxa demonstrate why such restraint is necessary. In the ladybird *Menochilus sexmaculatus*, some variable thermal regimes supported rapid development and substantial reproductive output [7]. In *Rhodnius prolixus*, daily fluctuation imposed costs on fecundity and survival while development and fertility were comparatively less responsive, revealing discordance among traits exposed to the same thermal environment [8]. In *Onthophagus taurus*, developmental thermal mean and variance altered metabolic phenotype and later adult body size, again showing that thermal variation can be expressed through particular physiological and morphological channels rather than through uniform whole-organism decline [9].

Developmental responses also change according to where fluctuations occur on the thermal-response curve. In *Ips typographus*, diurnal fluctuations accelerated development under cooler conditions but slowed it under warmer conditions, altering phenological estimates [10]. For *Drosophila suzukii*, reaction norms obtained under constant and fluctuating regimes differed, and transfer to field conditions became less reliable where environmental temperatures extended beyond well-characterized laboratory domains [11]. A multispecies analysis of sepsid flies likewise showed that thermal-performance curves can predict development reasonably under some circumstances while losing accuracy under more complex field trajectories [12]. Mean temperature is therefore insufficient not because constant-temperature experiments are intrinsically invalid, but because their interpretation depends on curvature, exposure range, fluctuation magnitude, and environmental transfer.

Thermal sequence and exposure duration

Two environments can share a mean and even a similar temperature distribution while differing biologically because exposure is ordered in time. Thermal stress depends on both intensity and duration. In *Drosophila suzukii*, progressively stronger heat shortened tolerated exposure times, and reproductive performance could be impaired at thermal doses below those associated with more extreme failure endpoints [13]. Consequently, a brief temperature excursion and a prolonged exposure to the same temperature cannot be assumed to be equivalent components of thermal history.

Developmental timing further modifies this relationship. Experiments involving *Myzus persicae* and its parasitoid *Aphidius gifuensis* showed that heat level, duration, and developmental stage jointly influence subsequent performance, with sensitivity differing across biological contexts [14]. The appropriate unit of comparison is therefore not simply "temperature experienced" but temperature experienced when, for how long, and by which stage.

Recent thermal-history modeling provides a mechanistic reason why order may matter. Damage can accumulate during stressful intervals and decline during conditions that permit recovery or repair, meaning that the effect of a current temperature may depend partly on what preceded it [15]. The present framework extends this principle cautiously: it treats accumulated damage and recovery opportunity as possible history-bearing processes without assuming that one universal damage–repair function applies across taxa or traits.

Recovery is also environmentally conditional. In *Lobesia botrana*, responses following a heat wave varied with developmental stage and post-stress nutritional conditions, showing that later resource environments can alter realized thermal costs [16]. At the molecular level, pupae of the solitary bee *Megachile rotundata* exposed to fluctuating versus constant cold exhibited distinguishable transcriptional profiles [17]. Such expression differences indicate physiological differentiation between thermal schedules but do not establish that particular transcripts causally generate improved survival or later performance. Mechanistic synthesis of fluctuating cold regimes further suggests that benign thermal intervals can permit restoration of ion balance, metabolism, and other homeostatic processes [18]. These cold-focused mechanisms should not be transferred automatically to heat stress, but they demonstrate why the temporal placement of recovery intervals can matter biologically.

Together, the evidence supports a distinction between an unordered thermal distribution and an ordered thermal history. The proposed framework therefore treats duration, developmental timing, and recovery opportunity as independent descriptors of exposure rather than as details reducible to a mean and variance.

Nonlinear developmental rate

Developmental rate provides one of the clearest cases in which thermal averaging becomes biologically misleading. Across the viable thermal range, development commonly accelerates with temperature only over part of the response and then departs from linearity as temperatures approach stressful regions. In the small brown planthopper *Laodelphax striatellus*, developmental and associated life-history responses changed nonlinearly across temperature treatments, with additional heterogeneity among biological states [19]. Such responses make linear accumulation of thermal time increasingly fragile when daily temperatures repeatedly traverse different parts of the curve.

Realistic fluctuating profiles illustrate the practical consequence. For the avocado lace bug *Pseudacysta perseae*, development and reproduction were characterized across six fluctuating temperature profiles using nonlinear models [20]. These data demonstrate substantial profile-specific variation and the utility of nonlinear developmental functions, but because the study did not include a matched series of constant-temperature means, it should not be used to claim that fluctuation itself caused every observed difference.

Taxonomic transfer adds another boundary. Five *Drosophila* species exposed to developmental temperature fluctuation differed in life-history and morphological responses, and some traits showed comparatively weak responses even when development changed [21]. Thus, neither the sign nor the magnitude of a fluctuating-temperature effect should be assumed to transfer reliably among congeners.

The proposed interpretation is consequently narrower than a universal degree-day correction. Developmental rate at time t may depend on current temperature through a nonlinear response, but cumulative development also reflects how much time is spent in different regions of that response and whether prior exposure changes subsequent physiological state. This distinction becomes especially important when daily oscillations cross from favorable into stressful temperature ranges.

Growth and energetic consequences

Developmental timing and somatic growth are related but not interchangeable. In *Onthophagus taurus*, developmental temperature mean and variance modified metabolic phenotype and adult body size, indicating that altered thermal histories can be expressed through energetic and morphological consequences even when the principal experimental contrast concerns development [9]. A faster developmental trajectory therefore cannot automatically be interpreted as greater growth efficiency or improved adult condition.

Evidence from adult dung beetles makes this separation clearer. Diurnal thermal variation affected energetic reserves, yet reproductive effort did not show a corresponding response to variation; reproductive patterns were more closely associated with other thermal features [22]. This discordance is important because energetic depletion is biologically meaningful without being equivalent to immediate reproductive failure. Conversely, unchanged reproduction during a particular observation window does not demonstrate absence of physiological cost.

Adult state also continues to change after development. In female mosquitoes, developmental temperature and adult age jointly shaped body size, mass, and components of body composition, while some measurements were influenced more strongly by age than by thermal treatment [23]. Because these experiments used constant developmental temperatures, they support temperature-history and age dependence but do not constitute direct evidence for a fluctuation-specific mechanism.

The resulting analytical problem is not simply whether variable temperature changes "growth." It is whether a thermal history produces concordant or discordant effects among metabolic demand, stored energetic reserves, somatic size or composition, and later reproductive allocation. **Table 1** is needed because these outcomes cannot be ranked on one common scale without erasing their different biological meanings and evidential limits.

Table 1. When thermal-history effects on growth, energetic state, and reproduction should be interpreted as concordant, discordant, or unresolved

Growth–energetic state	Organismal setting	Observed trait configuration	Thermal-history reading	Source of uncertainty	Decisive test with evidence state
Developmental remodeling					
Developmental metabolic remodeling with altered adult size	Pupal development under different thermal means and variances	Metabolic phenotype and adult body-size responses	Thermal history can alter energetic processing and somatic outcome together	Adult size is not a direct measure of lifetime fitness	Measure metabolic expenditure, development time, adult condition, and later reproduction in the same individuals or cohorts Evidence-supported distinction
Reserve loss and adult composition ambiguity					
Energetic-reserve loss without matched reproductive decline	Adult beetles experiencing seasonally variable thermal conditions	Changes in stored energetic reserves with comparatively unchanged reproductive effort	Energetic cost and reproductive allocation can be temporarily discordant	Reproductive effects may emerge later or under different resource conditions	Extend measurements across time and resource environments rather than treating reproduction as an immediate proxy for energetic state Evidence-supported distinction
Temperature-associated adult body-composition shift	Mosquitoes differing in developmental temperature and adult age	Mass, size, and biochemical body-composition measurements	Adult energetic phenotype reflects both prior temperature and current age	Constant-temperature design does not isolate fluctuation effects	Cross developmental regimes with adult age and fluctuating histories Evidence-supported distinction
Development-rate and opposing-trait discordance					
Faster development with uncertain somatic benefit	Developmental regimes that shorten time to adulthood	Developmental timing without complete energetic accounting	Reduced development time cannot by itself establish improved growth efficiency	Rate, final size, reserves, and reproduction may respond differently	Jointly measure rate, size, reserves, and adult performance **Proposed interpretive rule**

Multiple downstream traits move in opposing directions	Any history producing different signs among rate, reserves, size, or reproduction	Trait-specific response vector	A single "thermal performance" score would conceal biological discordance	Relative importance is species-, stage-, and environment-dependent	Preserve trait-specific response functions and test their demographic relevance separately **Proposed classification**

The growth evidence also motivates a visual distinction between biological discordance and simple measurement noise. A thermal history may produce a clear physiological shift without a parallel reproductive response, or alter adult size while leaving the fitness consequence unresolved. **Figure 1** therefore triages these discordant outcomes before they are combined into any broader claim about adult performance.

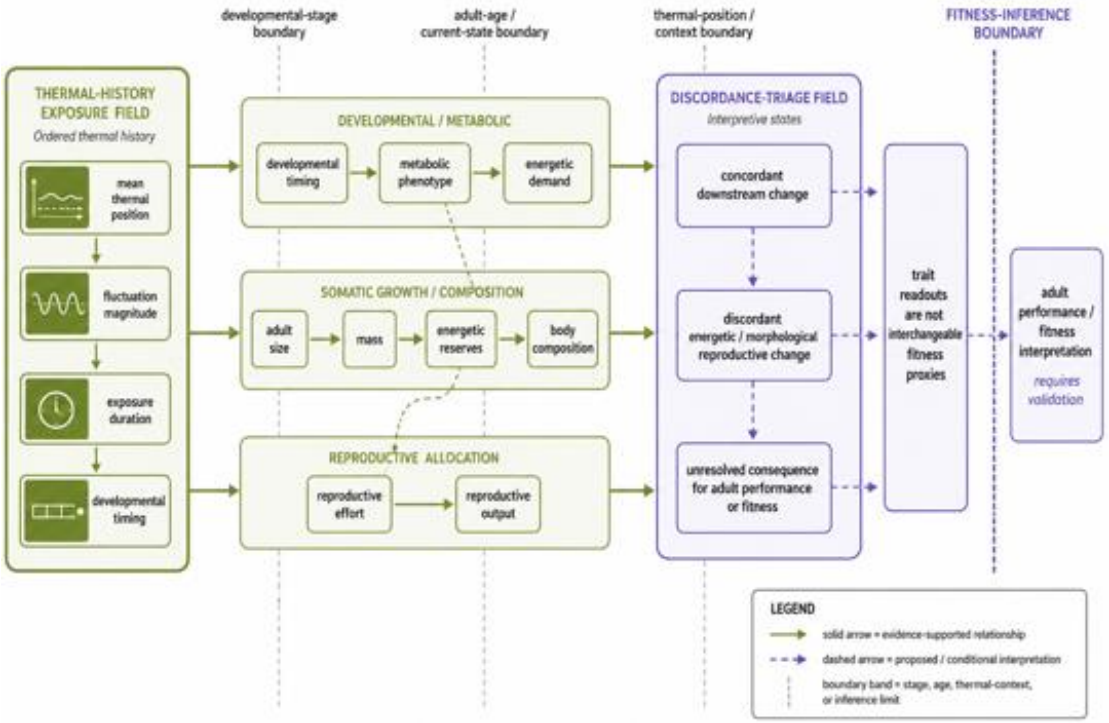


Figure 1. Discordant growth and energetic readouts prevent a single thermal-history performance score

Thermal memory and acclimation

Thermal history becomes biologically consequential only if some influence of prior exposure persists long enough to modify a later response. Such persistence is not synonymous with permanent memory. In *Drosophila melanogaster*, developmental and adult thermal fluctuations affected critical thermal limits differently, and some acquired effects changed after transfer to another adult thermal environment [24]. This demonstrates that the stage at which a thermal regime is experienced can influence both the direction and durability of acclimatory responses. Population background adds another scale of conditionality. Among Mediterranean water beetles, thermal-tolerance and acclimation patterns differed among species and populations associated with different climatic variability [25]. These observations are compatible with population-specific thermal histories and differing plastic responses, but they do not by themselves establish a universal relationship between environmental variability and genetically based local adaptation.

Field transfer can further shorten the apparent lifetime of acclimation. In sterile *Bactrocera dorsalis*, pre-release thermal acclimation influenced early recapture patterns, but the effect was transient and later environmental conditions became increasingly important [26]. Recapture is not equivalent to lifetime fitness, yet the result is valuable because it shows that a laboratory-imposed physiological state can be overwritten or diluted after release. The framework therefore uses thermal memory in a deliberately operational sense: a detectable dependence of current phenotype or performance on prior thermal conditions after accounting conceptually for current exposure. It does not require a particular molecular mechanism, permanence, or adaptive value. Memory may arise from

physiological state, accumulated damage, altered reserves, acclimatory adjustment, or developmental carry-over, and those possibilities should remain separate until directly tested.

Three properties are especially important for later synthesis. First, persistence can be trait-specific: a history affecting a thermal limit need not affect growth or reproduction similarly. Second, persistence can be stage-gated: developmental and adult exposures may leave different signatures. Third, persistence can be erasable or overwritable when subsequent conditions induce recovery or a new acclimatory state. The integrated model developed later therefore cannot treat thermal history as an indefinitely accumulating scalar. It must allow prior exposures to be weighted differently according to timing, biological state, and subsequent environmental experience.

Adult carry-over

Developmental temperature can remain biologically relevant after metamorphosis, but persistence is selective rather than uniform. In *Aedes albopictus*, developmental temperature altered several adult phenotypes, with responses differing between populations and among measured traits [27]. Developmental history therefore cannot be represented as a simple permanent adjustment applied equally to all later traits.

Later performance is also conditioned by sex and species. Comparative thermal-stress experiments in *Drosophila melanogaster* and *Drosophila pseudoobscura* revealed differences between species, sexes, and response variables [28]. Because these experiments did not manipulate fluctuating developmental histories directly, they define important transfer boundaries rather than demonstrating a fluctuation-specific carry-over mechanism.

Carry-over can additionally generate opposing life-history consequences. In *Enchenopa binotata*, elevated developmental temperature reduced juvenile survival while later reproductive effects could partly offset mortality-driven demographic decline in a population model [29]. Such compensation demonstrates that adult performance cannot be inferred from juvenile survival alone, although modeled buffering should not be interpreted as demonstrated persistence under natural population conditions.

Timing and later recovery can determine whether a thermal effect persists at all. Experiments with *Tribolium castaneum* showed that consequences of fluctuating temperatures differed with parental or offspring exposure, exposure duration, and subsequent benign conditions; some effects weakened when stressful histories occurred later or were followed by recovery [30]. The proposed framework therefore treats adult carry-over as a selective history-transfer process: earlier conditions may influence later phenotype, but retention depends on trait, developmental stage, intervening environment, and current physiological state.

Integrated thermal-history model

The preceding evidence supports a model in which thermal exposure is represented as a temporally ordered history rather than an average environment. The model proposed here contains four analytically distinct filters. The nonlinearity filter determines how each instantaneous temperature maps onto a trait-specific response. The dose-and-sequence filter represents exposure duration, ordering, and opportunities for damage accumulation or repair. The state-retention filter represents persistence, decay, or overwriting of physiological and energetic states. Finally, the cross-stage filter determines whether developmental effects are transmitted into adult traits.

These filters should not be collapsed into one latent measure of “thermal quality.” Trait-specific thermal optima can differ [3], energetic responses may occur without parallel reproductive change [22], and developmental temperature can produce selective adult carry-over [27]. Even compensatory downstream responses need not restore every earlier loss [29]. The proposed model therefore represents developmental rate, energetic condition, acclimatory state, and adult performance as parallel but interacting channels.

A further boundary concerns environmental transfer. Laboratory-derived thermal responses can depend on colony history and on whether experimental regimes reproduce the thermal structure experienced by field populations. Comparisons of laboratory-reared and field-derived aphids demonstrate that thermal-performance conclusions can shift with population and rearing background [31]. The model is therefore not presented as prospectively validated. Its intended function is to identify which historical dimensions should be measured and experimentally separated before equivalent mean temperatures are assumed to be biologically equivalent.

The model generates several distinct history states that prose alone cannot compare efficiently. **Table 2** separates those states according to what would have to be observed before a history-sensitive interpretation could be accepted or rejected.

Table 2. Thermal-history states that distinguish equal-mean exposure regimes and the tests required to resolve them

Thermal-history geometry	Biological setting and observation	Model meaning and boundary	Discriminating experiment and state
Curvature and duration effects			
Curvature-dominated history	Temperatures repeatedly traverse different regions of a nonlinear trait response Different developmental or performance outcomes despite similar means	Instantaneous nonlinear responses accumulate differently Depends on trait-specific response shape and tested thermal range	Compare equal-mean regimes with systematically altered amplitudes **Proposed model state**
Duration-dominated history	Similar thermal extremes occur for different lengths of time Outcome changes with exposure duration	Thermal dose cannot be represented by maximum temperature alone Damage and tolerance endpoints may differ among stages	Manipulate duration while holding peak temperature and stage constant **Proposed model state**
Recovery and stage-gated memory			
Recovery-sensitive history	Stressful intervals are separated by benign periods Performance differs according to recovery opportunity	Repair or physiological restoration changes subsequent response Recovery process may differ between heat and cold stress	Exchange the order and spacing of stressful and benign intervals **Proposed model state**
Stage-gated retained history	Developmental exposure influences selected adult traits Persistent adult phenotype after developmental treatment	Earlier state crosses a developmental boundary selectively Persistence may be trait-, sex-, population-, or species-specific	Follow multiple traits through development and adulthood **Proposed model state**
Overwrite and transfer limits			
Overwritten history	Early acclimatory or stress effect weakens after transfer Initial difference disappears or changes under later conditions	Recent environment receives greater effective weight Loss of difference may reflect recovery, acclimation, or measurement timing	Reassess repeatedly after controlled environmental transfer **Proposed model state**
Transfer-limited history	Laboratory response differs among field-derived or laboratory populations Performance ranking changes with rearing or environmental background	Experimental history is itself part of model context External validity remains taxon- and environment-specific	Replicate matched regimes across laboratory and field-origin populations Evidence-supported boundary

These model components require a visual architecture that preserves parallel trait channels while showing where history can be retained, modified, or lost. **Figure 2** therefore places the thermal sequence above separate developmental, energetic, acclimatory, and adult-performance lanes and makes the inference and validation boundaries explicit.

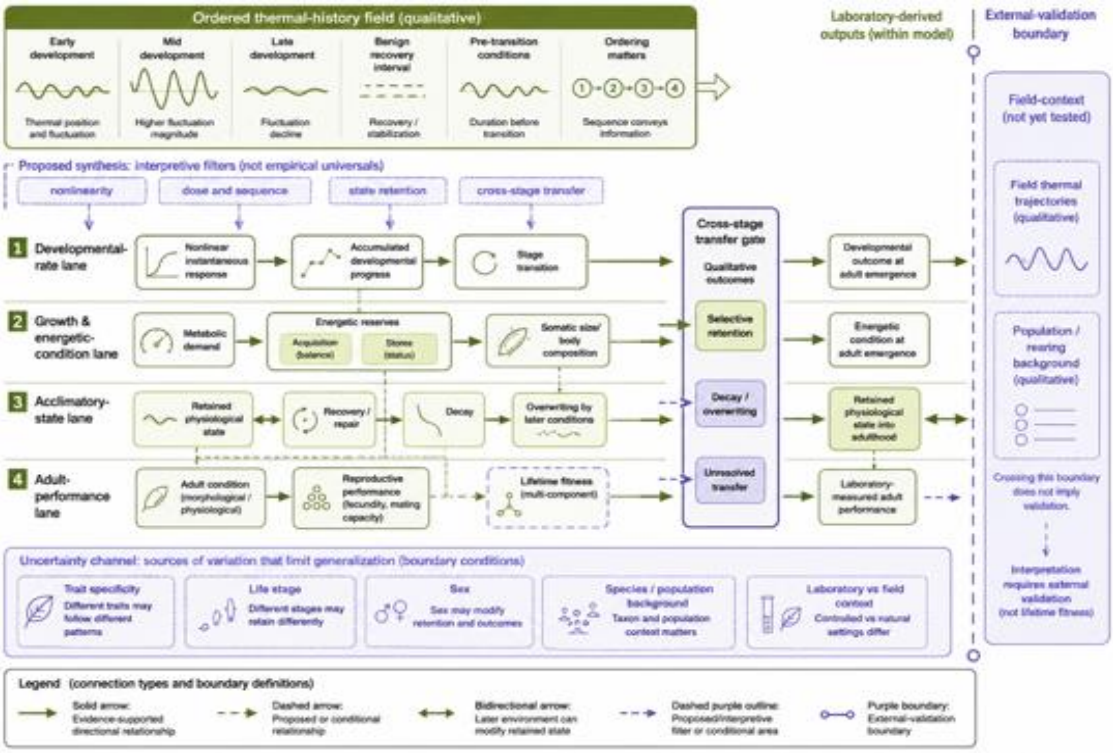


Figure 2. Where thermal history is retained, reweighted, or lost across insect performance channels

Predictions for constant versus fluctuating regimes

The model predicts that equal-mean thermal regimes will diverge most strongly when fluctuations span regions of substantial response-curve curvature. Experimental reversal of fluctuation effects across amplitudes supports this conditional expectation [4], while the cool-versus-hot developmental responses of *Ips typographus* illustrate how the sign of divergence can change with thermal position [10]. The prediction is therefore not that variability itself reduces performance, but that variance becomes increasingly consequential where the underlying response is strongly nonlinear.

A second prediction concerns temporal ordering. If accumulated injury and recovery contribute to current state, histories containing the same thermal extremes should yield different outcomes when exposure duration or intervening benign intervals are rearranged. Duration-sensitive reproductive and survival responses provide a basis for this prediction [13], whereas damage–repair modeling shows why a memoryless performance curve could miss such temporal dependence [15]. Direct sequence-swapping experiments would be needed to determine how broadly this principle applies.

Third, equal developmental means should generate different adult outcomes when stage-specific retention differs. Developmental and adult acclimation can leave different thermal-tolerance signatures [24], and developmental carry-over may even oppose earlier survival effects in later life-history components [29]. The proposed model therefore predicts greater divergence between constant and fluctuating regimes when the fluctuating sequence overlaps a sensitive developmental transition than when the same temperatures occur after that transition.

Finally, predictive performance should depend on whether the experimental history spans the range, sequencing, and population backgrounds relevant to application. Laboratory estimates should transfer most reliably within environmental domains resembling those used to construct them, whereas unrepresented field histories and colony backgrounds should increase uncertainty [31]. These predictions are falsifiable conceptual outputs: they require experiments that manipulate mean, amplitude, sequence, duration, stage, and recovery independently rather than assuming that one thermal summary represents them all.

Results and Discussion

The reviewed evidence resolves an apparent contradiction in thermal-variability studies by replacing a directional question—whether fluctuation is “good” or “bad”—with a conditional one: under what thermal histories do

particular traits diverge from constant-mean expectations? Two noctuid experiments demonstrate that effects of fluctuation depend strongly on the underlying mean and on the response being measured [5, 6]. This framework therefore interprets conflicting outcomes as potentially informative about thermal position, stage, duration, or trait sensitivity rather than as noise around a universal effect.

Heterogeneity remains a major limitation. Congeneric *Drosophila* species differ in developmental responses to thermal fluctuation [21], water-beetle populations and species differ in thermal-tolerance plasticity [25], and thermal stress can interact with species and sex [28]. These contrasts argue against transferring response functions among taxa without validation. They also constrain evolutionary interpretation: plasticity, population differences, and persistence of thermal effects should not automatically be called adaptation, because the necessary genetic and fitness evidence is not supplied by many of these studies.

A second limitation concerns trait integration. Development, energetic reserves, morphology, thermal tolerance, and reproduction may respond in different directions or at different times. The framework therefore rejects the use of one measured endpoint as a universal proxy for organismal thermal performance. Similarly, laboratory-to-field transfer remains conditional: reaction norms can lose accuracy under environmental trajectories outside their calibration range, and population or rearing background can alter observed performance [11, 31]. Controlled experiments remain indispensable, but their thermal histories should be reported and interpreted as part of the biological treatment rather than as neutral laboratory context.

The framework also defines a testable research agenda. Experiments should independently manipulate fluctuation amplitude, exposure duration, ordering, developmental stage, and recovery intervals while following multiple traits across stage transitions. Designs that exchange the order of otherwise similar exposures would be especially informative because they distinguish history dependence from effects attributable only to the temperature distribution. Repeated measurements after transfer could identify whether apparent thermal memory persists, decays, or is overwritten. Field validation should then test whether relationships inferred under controlled histories survive realistic microclimatic variation and population backgrounds.

The central theoretical claim is consequently modest but consequential: mean temperature is not necessarily a sufficient state variable for insect development and performance. A thermal history can matter through nonlinear instantaneous responses, cumulative exposure, recovery, state retention, and cross-stage transfer. Which of these processes dominates is an empirical question for each trait, species, and environment, not a property that the framework prespecifies

Conclusion

Fluctuating temperatures can produce biological outcomes that cannot be inferred reliably from mean temperature alone. Their consequences depend on where exposures occur on nonlinear response curves, how long they persist, when they occur during development, whether recovery is possible, and whether physiological or energetic states persist into later stages. Developmental rate, growth, energetic condition, acclimation, and adult performance must therefore remain analytically distinct.

The proposed thermal-history framework organizes these dimensions without assuming that variability is inherently harmful, beneficial, adaptive, or universally persistent. Its principal value is to identify when equal-mean regimes should not be treated as biologically interchangeable and to specify the experiments needed to distinguish curvature effects, accumulated exposure, recovery, and cross-stage carry-over. Validation across taxa, stages, traits, field environments, and population backgrounds remains essential before the framework can support general predictive claims.

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