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Thermal Plasticity Across Insect Life Stages and Its Consequences for Development, Performance, and Fitness

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ABSTRACT

Thermal plasticity is often evaluated within a single insect life stage and then generalized to whole-organism performance or climatic vulnerability. That approach is problematic because temperature acts on a developmental sequence in which sensitivity, physiological capacity, resource demand, mobility, and reproductive function change over time. This integrative review examines how thermal responses arising during embryonic, larval or nymphal, metamorphic, pupal, and adult stages can persist or change across ontogeny. The evidence indicates that stage-specific thermal responses are frequently endpoint dependent: hardening capacity can differ from basal tolerance, metabolic adjustment need not preserve adult phenotype, and developmental thermal history can affect reproduction even after adult conditions change. Conversely, context-specific thermal matching can improve gametic performance, showing that plasticity is not intrinsically harmful. We propose that cross-stage thermal effects be interpreted through four separable questions: where the thermal exposure occurs, which trait responds at that stage, whether the response persists or is transformed across developmental transitions, and whether the eventual endpoint is performance, reproduction, or a defensible fitness component. This framing prevents physiological response, phenotypic carry-over, and adaptive value from being treated as interchangeable. It also highlights the need for stage-resolved, fluctuating-temperature, resource-aware, and sex-specific experiments that connect laboratory phenotypes to ecologically relevant thermal sequences.

Keywords: Developmental plasticity, Thermal acclimation, Ontogeny, Carry-over effects, Metamorphosis, Reproductive performance

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Introduction

Insects encounter temperature as a sequence of exposures distributed across development, not as a single adult challenge. Yet thermal biology is still frequently summarized by one tolerance limit, one acclimation treatment, or one performance curve. This compression can obscure biologically important ontogenetic variation: thermal sensitivity can differ among life stages, such that vulnerability inferred from one stage need not represent the remainder of the life cycle [1]. The ecological meaning of a developmental response also depends on seasonality, because temperature-driven changes in developmental rate can alter timing and potential generation turnover without guaranteeing improved realized fitness [2]. The inferential problem is therefore not simply whether insects are thermally plastic, but whether the measured plasticity occurs at the stage, trait, and temporal scale that determine later performance.

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A second problem is that plasticity, acclimation, and adaptation are often allowed to blur. Acclimation effects can be sensitive to assay design and require ecological validation before they can be interpreted as meaningful climate adaptation [3]. Incorporating within-species or plastic variation in tolerance can change vulnerability forecasts, but the direction of that change is not uniformly protective [4]. Geographic variation in thermal performance curves likewise changes ecological predictions without implying that populations respond to warming through a common shift in thermal optima [5]. These distinctions matter especially in multistage insects because a phenotype that appears beneficial within one developmental window can be neutral, costly, or overwritten when evaluated at another endpoint.

Thermal history itself is multidimensional. Daytime and nighttime warming can have different consequences because activity, physiology, and species interactions are distributed unevenly across the diel cycle [6]. Daily variability and extreme temperatures can affect performance in ways not recoverable from changes in the mean alone [7]. Even within *Drosophila*, reaction norms for cold tolerance can be more predictable than those for heat tolerance, cautioning against treating "thermal plasticity" as a single scalar trait [8]. Temperature–body size relationships also change with the environmental gradient used for inference; patterns seen across laboratory, seasonal, and latitudinal contrasts were not reproduced consistently across altitude [9]. Consequently, body size, development rate, tolerance, fecundity, fertility, and survival should remain analytically distinct unless evidence establishes how they covary.

This review therefore treats thermal plasticity as a life-course inference problem. We use "stage-local response" for a phenotype measured within the exposed stage, "carry-over" descriptively for an effect detected after a developmental transition, and "adult-context modulation" for cases in which the adult thermal environment changes the expression of an earlier effect. These are proposed organizing terms, not mechanistic categories. Their purpose is to ask whether metamorphosis erases, transforms, or transmits earlier thermal effects and whether the resulting adult phenotype constitutes physiological adjustment, performance change, reproductive consequence, or evidence of adaptive value. This stage-resolved approach is used below to integrate embryonic sensitivity, juvenile plasticity, metamorphic carry-over, and adult reproductive outcomes without converting heterogeneous endpoints into a single index of thermal benefit.

Thermal plasticity during embryonic development

Embryogenesis is sometimes treated as a thermally passive prelude to the more mobile larval or adult stages, but developmental sensitivity can change within the egg itself. In winter moth, temperature sensitivity increased around the fully extended germband stage and coincided with developmental events involving the nervous system and ecdysone-related processes [10]. The temporal coincidence is mechanistically suggestive but not causal evidence that neural or hormonal development produces thermal sensitivity. It instead demonstrates that "embryonic temperature" can conceal a narrower developmental window in which the same thermal change has a different phenological effect.

Embryonic exposure can also remain detectable after the egg stage. In *Drosophila melanogaster*, adult size depended on embryonic temperature and on the subsequent thermal sequence, showing that an early exposure can contribute to an adult phenotype rather than being fully reset during later growth [11]. That adult-size signature should not be translated directly into fitness, because size is a context-dependent trait and the mechanism connecting early temperature to final size was not established. More directly negative carry-over was reported in *Bicyclus anynana*, where egg-stage heat stress reduced performance in later stages [12]. This provides evidence that metamorphosis does not necessarily erase early thermal injury.

The appropriate interpretation is therefore narrower than "thermal programming." Ontogenetic differences make persistence across stages biologically plausible [1], but persistence alone does not distinguish regulated developmental plasticity from damage, energetic depletion, or altered developmental timing. Likewise, an acclimation phenotype should not be treated as adaptive without validation at an ecologically relevant endpoint [3]. We propose an embryonic timing-gate concept only as an analytical device: the consequences of egg temperature should be resolved by exposure window, subsequent thermal sequence, and later endpoint before mechanistic or adaptive significance is assigned.

Larval and nymphal plasticity

Juvenile stages add mobility, feeding, and rapidly changing resource demands, making thermal responses inseparable from developmental state and, often, nutritional environment. In the grain aphid *Sitobion avenae*,

nymphal instars and adults differed in basal thermal performance and hardening response despite experiencing broadly similar thermal conditions; the benefits and reproductive costs of hardening also depended on stage and stress dosage [13]. Similar exposure therefore does not imply similar physiological capacity, and greater inducible tolerance in one juvenile stage cannot be generalized to superior lifetime performance.

Resource state further changes the response surface. In *D. melanogaster* larvae, diet modified the effects of developmental temperature on viability, development, and body size [14]. Nutrition could buffer or magnify thermal effects depending on the outcome measured, making temperature × resource interaction a more defensible unit of interpretation than temperature alone. This does not establish a universal nutritional mechanism for thermal plasticity; it shows that experiments holding diet constant may estimate only one part of the developmental response.

Thermal variability introduces another layer. Across five *Drosophila* species from different thermal niches, developmental fluctuations produced species- and trait-specific life-history responses that were not fully predicted by constant-temperature performance [15]. The result argues against assuming that a fluctuating treatment is either automatically more stressful or automatically more realistic in its biological consequences. In the parasitoid *Aphidius colemani*, developmental temperature altered adult life-history traits and heat tolerance, but the pattern gave only partial support to beneficial acclimation [16]. The important distinction is between a changed tolerance phenotype and an improvement in the adult functions that matter under field conditions. Juvenile plasticity is therefore best represented as a set of trait-specific reaction norms conditional on stage, resources, and thermal regime rather than as one generalized capacity to acclimate.

Metamorphic and pupal carry-over

Metamorphosis creates a strong developmental discontinuity, but it is not a guaranteed physiological reset. In *D. melanogaster*, heat-hardening capacity varied markedly across life stages: adults showed relatively high basal heat resistance, whereas inducible hardening was stronger in some juvenile immobile stages [17]. Basal resistance and plastic capacity are therefore separable properties. The pattern does not establish that immobility evolutionarily caused high juvenile plasticity; it demonstrates that the stage with the greatest inducible response need not be the stage with the greatest untreated tolerance.

Pupae can also adjust physiologically while a later phenotype still changes. In the dung beetle *Onthophagus taurus*, temperature mean and variance altered pupal metabolism, yet warmer and more variable developmental regimes were associated with smaller adult body size [18]. Metabolic plasticity consequently cannot be assumed to preserve the downstream phenotype, and smaller size cannot itself be treated as a measured fitness loss. Short high-temperature exposures in *Bactrocera tau* likewise produced stage- and temperature-dependent effects extending into development and reproduction [19]. Together with the persistent egg-stage effects reported in *B. anynana* [12], these findings show that a thermal episode before adulthood can leave a detectable legacy after major developmental transitions.

The central analytical problem is to distinguish stage-local compensation from downstream preservation. A physiological change during pupation may reduce immediate stress while leaving adult size, timing, or reproduction altered; alternatively, a later phenotype may remain stable despite large within-stage physiological adjustments. Because the current evidence does not provide a common metric for such outcomes, "thermal legacy" is used here descriptively rather than as a mechanistic or quantitative construct.

A comparative adjudication matrix is useful here because the same observation—plasticity during a metamorphic stage—has different implications depending on whether basal tolerance, inducible hardening, metabolic adjustment, or a later adult phenotype is being evaluated.

Table 1. Metamorphic persistence is not equivalent to phenotypic preservation: adjudicating thermal carry-over across pupal and developmental transitions

Across metamorphosis		Inference after transition
Metamorphic carry-over class	**Persistence pattern**	**Longitudinal adjudication**
Stage-local hardening dominance. Drosophila across juvenile, puparial/pupal, and adult stages	Inducible heat-hardening capacity differs from untreated basal heat resistance across ontogeny. Strong within-stage plasticity does not demonstrate protection of later-stage phenotype	Acute laboratory hardening protocol; evolutionary cause unresolved. Pair stage-specific hardening assays with post-transition performance and reproduction. Proposed synthesis from stage-resolved evidence.

Metabolic adjustment with incomplete phenotype preservation. Onthophagus pupae exposed to different temperature means and variances	Pupal metabolism changes while adult body size also shifts. Physiological adjustment during metamorphosis can coexist with altered adult phenotype	Adult size is a proxy, not a direct measure of fitness; proximate pathway incomplete. Measure metabolic response together with adult function rather than treating metabolism as sufficient evidence of resilience. Proposed synthesis from physiological and adult-trait evidence.
Persistent thermal legacy. Immature Bactrocera and egg-stage Bicyclus exposed to high temperature	Later development, performance, or reproduction remains altered after the original exposure. Metamorphosis does not necessarily erase an earlier thermal effect	Damage, developmental reorganization, and resource depletion are not distinguished by persistence alone. Use stage-specific exposure, recovery intervals, and multiple post-metamorphic endpoints to identify persistence versus recovery. Proposed synthesis from cross-stage carry-over evidence.

Adult performance and reproduction

Adult thermal phenotype cannot be interpreted independently of developmental history. In *D. melanogaster*, reproductive performance was maximized by an intermediate developmental temperature across the tested adult thermal environments rather than by a simple rule in which developmental and adult temperatures should match [20]. In *Drosophila subobscura*, high developmental temperature depressed later reproduction even when the adult thermal environment changed [21]. These experiments make adult temperature an incomplete predictor of reproductive outcome: developmental conditions can persist as a constraint, although the magnitude and expression of that constraint remain population- and design-specific.

Reproductive tissues also reveal why "plasticity" cannot be assigned a single sign. In *Tribolium castaneum*, thermal plasticity of sperm and eggs improved reproductive performance when the environment of gamete production matched the reproductive environment [22]. In the same model insect, experimental heatwaves substantially impaired male sperm function, repeated exposure intensified reproductive damage, and downstream offspring effects were detected [23]. These findings are not contradictory once exposure regime and endpoint are retained: modest or matched thermal conditions can generate conditionally beneficial gametic plasticity, whereas extreme heat can produce direct reproductive injury. *Drosophila suzukii* provides a further cross-generational complication: juvenile heat stress impaired viability, lifespan, and fertility, particularly male reproductive performance, while maternal thermal history modified offspring egg-to-adult viability under heat in the tested setting [24]. A maternal effect therefore can coexist with broad direct costs rather than cancelling them.

We propose that adult reproductive consequences be interpreted as a reconciliation problem involving at least four separable inputs: developmental thermal history, the current adult thermal environment, acute thermal extremes, and sex- or gamete-specific state. Parental thermal history becomes a fifth input when offspring responses are measured. The output should then be named by the endpoint actually demonstrated—gamete function, fecundity, fertility, viability, or another reproductive component—rather than elevated automatically to lifetime fitness. This formulation also accommodates apparently divergent evidence: developmental history may impose persistent costs, thermal matching may improve gametic performance, extreme events may cause injury, and cross-generational effects may modify offspring phenotype. **Figure 1** compresses these relationships while retaining the boundaries between evidence-supported responses and the proposed integrative classification.

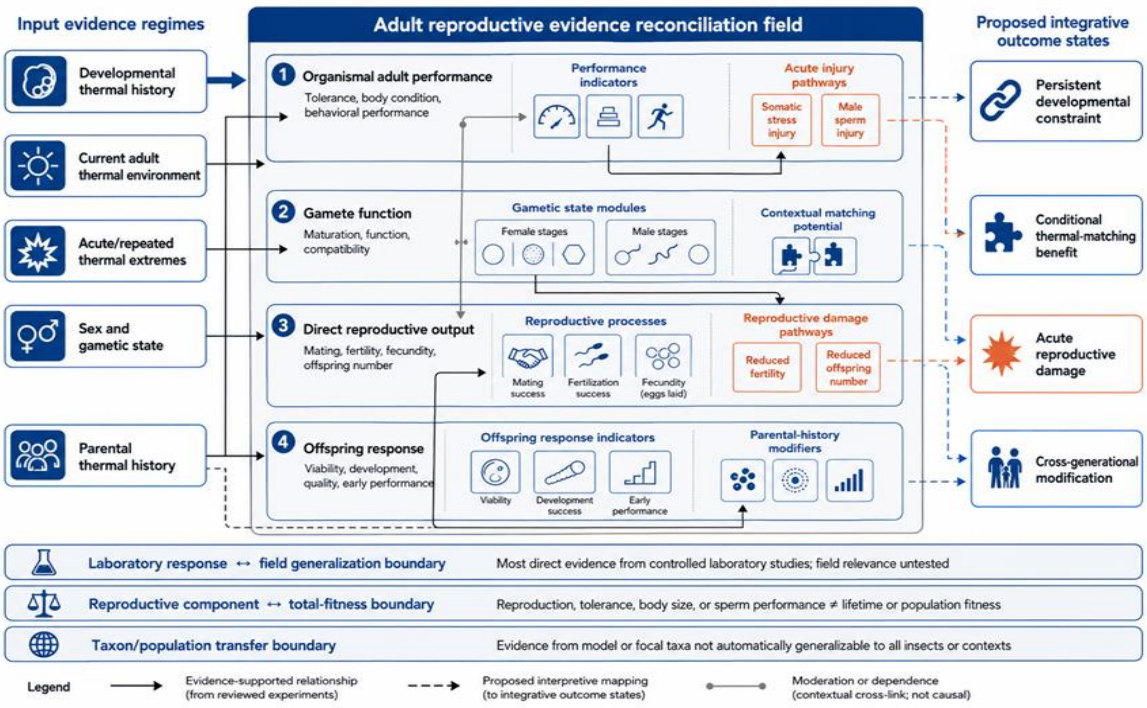


Figure 1. Divergent reproductive outcomes under similar adult temperatures: reconciling developmental history, acute heat, and gametic state

Cross-stage integration

Cross-stage integration requires more than connecting successive developmental boxes. Behavioral exposure and physiological tolerance are distinct processes: thermal preference differs among *Drosophila* life stages and species and does not map uniformly onto climatic origin or a demonstrated performance optimum [25]. Physiological plasticity is similarly multidimensional. In *Tuta absoluta*, hardening and acclimation affected larval and adult tolerance traits differently, with some responses beneficial for one endpoint but absent or unfavorable for another [26]. Thus, neither preferred temperature nor one improved tolerance metric provides a sufficient estimate of whole-life thermal performance.

Trait discordance persists even within a single stage. In the water beetle *Enochrus jesusarribasi*, warm acclimation modified locomotor and metabolic thermal-performance components unevenly rather than shifting the entire performance curve beneficially [27]. Such findings reinforce the broader ontogenetic conclusion that stage identity can substantially alter thermal sensitivity [1]. Short-term heat effects extending across development and reproduction in *Bactrocera tau* further show that later outcomes may preserve information about earlier exposure without identifying the process responsible for that persistence [19].

We therefore propose a three-part cross-stage distinction: response, the phenotype altered during or immediately after exposure; persistence, whether that alteration remains detectable after a developmental transition; and consequence, the later endpoint on which biological interpretation rests. The three can be concordant, compensatory, or discordant. **Table 2** makes these states explicit because a single descriptor such as "thermal resilience" would erase whether exposure behavior, tolerance, developmental carry-over, and reproduction actually move together.

Table 2. Cross-stage response states linking thermal exposure, persistence, and downstream consequence

Cross-stage state	Exposure and organism context	Signature → later consequence	Persistence test and scope
Exposure-choice shift	Mobile larval or adult stage	Preferred temperature changes. Experienced temperature may change without altered physiological limits	Preference–performance relationship unresolved. Pair choice with performance assays. Proposed.

Trait-selective plasticity	Larvae or adults after hardening/acclimation	One tolerance component changes more than another. No unitary improvement in thermal phenotype	Trait and pretreatment dependent. Measure multiple tolerance endpoints. Proposed.
Persistent carry-over	Exposure precedes a developmental transition	Later phenotype retains exposure effect. Earlier temperature remains biologically relevant	Persistence does not identify mechanism. Track the same cohort across stages. Proposed.
Cross-endpoint discordance	Performance components respond differently	Locomotion, metabolism, tolerance, or reproduction diverge. Composite "resilience" can mislead	Endpoints are not interchangeable. Link stage traits to later reproduction or survival. Proposed.

When plasticity becomes maladaptive

A plastic response is not maladaptive merely because it is small, variable, or costly under an artificial assay. In *Drosophila mojavensis*, within- and transgenerational heat-tolerance plasticity differed across stages and climatic regions, while interpretations of adaptive value depended partly on environmental predictability [28]. Environmental matching therefore matters, but predictability cannot be converted into a universal rule that transgenerational plasticity is beneficial.

Measurement can also create apparent biological trade-offs. Across *Drosophila* species, static and dynamic heat-tolerance assays could be reconciled through time–temperature injury accumulation, undermining an assumed intrinsic trade-off between acute and chronic heat tolerance [29]. Cold injury in *D. suzukii* likewise depended jointly on exposure intensity, duration, and acclimation rather than on one critical temperature [30]. These results make thermal dose and assay architecture part of biological interpretation.

Costs nevertheless can be real. Aphid hardening benefits can coexist with reproductive costs [13], and high developmental temperature can depress later reproduction despite changed adult conditions [21]. We therefore reserve "maladaptive" for cases in which plastic expression produces or contributes to a demonstrable mismatch, downstream cost, or unfavorable trade-off in a relevant environment. **Table 3** separates those cases from weak plasticity, assay-dependent patterns, and direct thermal damage.

Table 3. Distinguishing maladaptive thermal plasticity from mismatch, measurement artefact, and direct injury

Candidate explanation			**Claim control**	
Interpretation problem	**Observed thermal pattern**	**Mechanistic reading**	**Exclusion boundary**	**Evidence needed for stronger inference**
Environmental mismatch	Plastic phenotype poorly aligned with realized conditions	Plasticity may impose a context-dependent cost	Environmental predictability must be established	Performance or reproduction measured under the realized environment. Proposed criterion.
Endpoint trade-off	One trait improves while another worsens	Benefit is trait-specific, not organism-wide	Tolerance and reproduction remain separate	Joint measurement of competing endpoints. Proposed criterion.
Assay-dependent discordance	Static and dynamic tests imply different rankings	Time–temperature integration may explain discrepancy	Laboratory protocol can generate apparent trade-offs	Cross-assay validation. Evidence-based boundary.
Dose-dependent injury	Outcome worsens with exposure intensity or duration	Direct damage may dominate plastic adjustment	Injury is not synonymous with maladaptive plasticity	Recovery and acclimation treatments separating damage from response. Proposed criterion.

These distinctions are synthesized visually in **Figure 2** to show where claims about beneficial or maladaptive plasticity cross from observed phenotype into conditional interpretation.

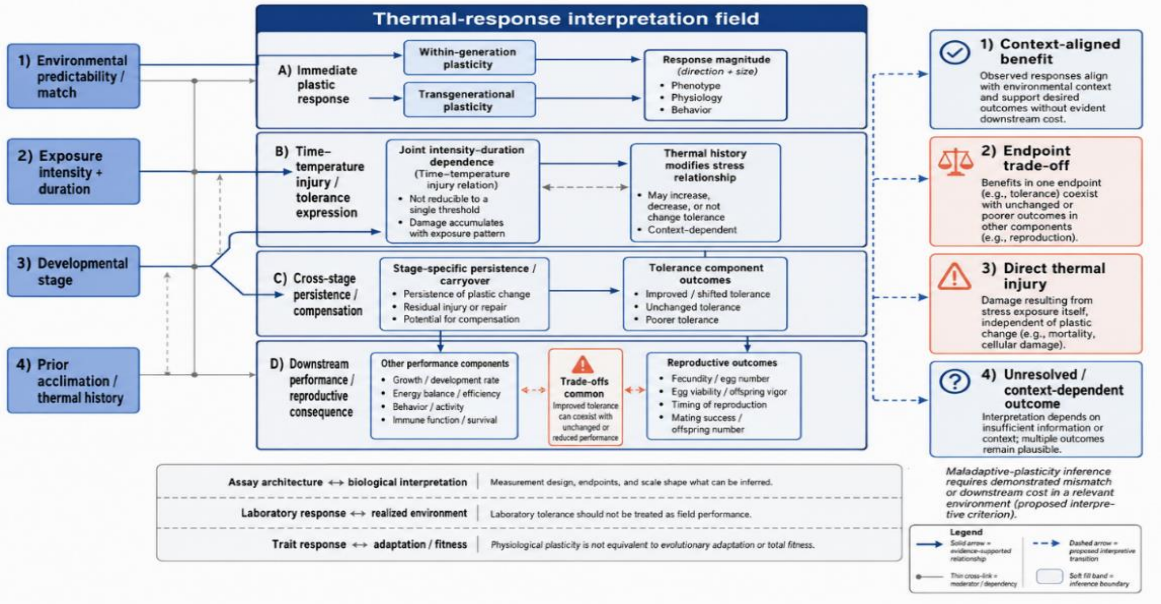


Figure 2. Where thermal plasticity changes biological meaning: mismatch, trade-offs, thermal dose, and inference boundaries

Emerging mechanistic questions

The principal mechanistic gap is not a shortage of candidate processes but the absence of complete causal chains across biological levels. Nutrient-sensitive insulin/IGF and TOR signaling regulate insect growth and offer plausible interfaces through which resource state could alter developmental responses [31], but they cannot be designated universal thermal-plasticity pathways. Embryonic timing effects [10] and pupal metabolic adjustment [18] likewise identify mechanistic touchpoints without demonstrating how those responses propagate to adult fitness.

Reproduction provides stronger proximal endpoints: gamete performance can respond plastically to thermal matching [22], whereas heatwaves can damage sperm function [23]. Yet evolutionary interpretation requires another evidential boundary. Evidence for contemporary thermal evolution differs substantially among traits, and phenotypic responses alone do not demonstrate genetic adaptation [32]. A useful proposed evidence ladder is therefore: candidate molecular or physiological process → stage-specific phenotype → demonstrated persistence or compensation → reproductive consequence → demographic or evolutionary validation. Missing links should remain explicit rather than filled by mechanistic inference.

Future directions

Experiments should now follow individuals and lineages through thermally heterogeneous developmental sequences rather than treating each stage as an independent assay. The evolutionary consequences of plasticity may slow, facilitate, or redirect adaptation depending on how plastic responses alter selection and available variation [33]; these alternatives require multigenerational experiments rather than inference from plasticity magnitude.

Field translation is equally important. Altered temperatures can affect insect populations directly and indirectly through phenological mismatches and changing biotic interactions [34]. Laboratory acclimation measures therefore require ecological validation [3], and geographic variation in thermal-performance relationships should be retained rather than averaged away [5]. Behavioral temperature choice provides an additional exposure filter [25]. Stronger studies should combine microclimate-resolved thermal histories, multiple stage-specific traits, reproduction, and field demographic outcomes while explicitly testing whether laboratory carry-over persists under fluctuating resources, enemies, competitors, and seasonal timing.

Conclusion

Thermal plasticity across insect ontogeny is neither a single capacity nor an inherently beneficial response. Embryonic exposure can persist beyond the egg, juvenile acclimation can differ among traits, metamorphosis can

transform rather than erase thermal legacies, and adult reproduction can reflect both developmental history and current conditions. The central interpretive task is therefore to separate the stage at which exposure occurs, the phenotype that responds, the persistence of that response, and the endpoint used to infer biological consequence. This stage-resolved framework accommodates beneficial matching, compensation, discordance, direct injury, and downstream cost without treating any of them automatically as adaptation or maladaptation. Progress now depends on connecting mechanistic measurements to cross-stage persistence, reproduction, realistic thermal sequences, and ultimately field population consequences.

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