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Developmental Pace Across the Insect Life Cycle Depends on Growth, Maturation, Dormancy, and Adult Performance Rather Than a Single Trait

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ABSTRACT

Developmental rate in insects is commonly represented by the time required to reach a stage or complete pre-adult development. This scalar description is operationally useful but biologically incomplete because similar durations can arise through different combinations of growth, maturation, developmental arrest, and compensatory change among stages. Evidence from nutritional, endocrine, diapause, thermal, and carry-over studies further shows that these components need not vary in parallel and that juvenile timing alone may poorly represent later organismal consequences. This article develops a proposed conceptual architecture in which developmental pace is treated as a multidimensional life-cycle property rather than a synonym for development time. Growth describes biomass and structural acquisition; maturation describes progression in developmental identity and competence for transition; dormancy alters the temporal state itself; and adult performance captures deferred consequences that may remain after apparent juvenile compensation. The framework does not assume that these dimensions are independent, universally measurable in the same way, or governed by a common mechanism. Instead, their coupling is treated as taxon-, stage-, genotype-, and environment-dependent. This separation generates testable predictions about stage compensation, growth–maturation coupling, dormancy-state effects, and transstadial carry-over while preserving explicit laboratory-to-field and mechanism-to-fitness boundaries.

Keywords: Insect development, Developmental timing, Growth regulation, Metamorphosis, Diapause, Transstadial carry-over

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Introduction

Insect development is often summarized by an interval: egg-to-hatch, instar duration, time to pupation, or egg-to-adult development time. Such endpoints are indispensable for comparative physiology and phenology, but elapsed time alone cannot reveal how development was assembled. Nutritional regulation of insect body size, for example, can operate through changes in growth rate, the duration of growth, or both, and those routes need not have identical consequences across organs or species [1]. Development time is therefore a phenotype, but it is not necessarily a sufficient description of developmental pace.

Experimental evolution reinforces this distinction. Bidirectional selection on pre-adult development time in *Drosophila montana* produced an asymmetric response: slower development evolved more readily than faster

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development, while diapause timing changed as a correlated trait [2]. Developmental duration can thus reflect constraints and correlations that remain hidden when the phenotype is interpreted as a single continuously adjustable rate. Stage composition also matters. In *Calliphora vicina*, individuals developing rapidly during the feeding phase subsequently developed more slowly, whereas *Lucilia sericata* showed a different interstage pattern [3]. Equal or similar totals may therefore conceal contrasting temporal trajectories.

The present article proposes that developmental pace be used more narrowly and analytically: not as another term for development time, but as the organization of growth, maturation, dormancy state, and later functional consequences across the life cycle. These dimensions are not assumed to be orthogonal. Their degree of coupling is itself biologically informative. The purpose is consequently not to replace development time, but to define when its interpretation requires decomposition.

Why developmental pace cannot be reduced to development time

A scalar timing phenotype becomes especially problematic when its environmental and genetic determinants change rank across conditions. In *Drosophila melanogaster*, mitochondrial-genotype effects on developmental time depended on diet and temperature, demonstrating that a genotype cannot simply be assigned an environment-independent developmental rate [4]. Developmental pace must therefore preserve the environmental context in which duration was generated.

Body size provides a second example. Across three Australian *D. melanogaster* populations exposed to multiple diets, body-size plasticity differed among populations even though their development-time responses did not show corresponding population differentiation [5]. This does not establish that growth rate and development time are generally independent, but it shows that final size and elapsed duration can contain different biological information. Nutritional-geometry experiments likewise indicate that developmental rate, survival, and secondary sexual morphology need not share the same dietary optimum [6]. A shorter interval cannot consequently be classified as advantageous without specifying which other traits changed with it.

The problem persists within the organism. Relative-growth research emphasizes that body parts need not grow at identical rates and that systemic and local signals coordinate heterogeneous tissue trajectories [7]. Even where total development time is known precisely, it cannot indicate whether altered timing resulted from faster acquisition of mass, altered allocation among structures, shortened growth duration, earlier developmental transition, or compensation in a subsequent stage.

Taken together, nutrition, genotype and environment can alter size-related and temporal components non-equivalently [1, 4, 5]. The appropriate inference is not that development time is uninformative; rather, it is that its biological meaning is conditional. The proposed framework therefore treats chronological duration as an observation that must be interpreted alongside the developmental processes occupying that interval.

Conceptual basis and trait selection

A multidimensional description requires biologically defensible dimensions rather than an arbitrary list of life-history traits. The first criterion is that a candidate dimension should capture a process that can vary without being reducible to elapsed time. Metamorphosis satisfies this requirement. Insect metamorphic transitions involve stage- and tissue-specific regulatory processes, including microRNA-mediated control whose roles differ among developmental modes and taxa [8]. Maturation therefore concerns a change in developmental state, not simply the accumulation of time.

Temporal stage identity provides a stronger mechanistic basis for this distinction. The metamorphic gene network, including Kr-h1, E93 and Broad-Complex under juvenile-hormone and ecdysteroid regulation, helps specify successive developmental identities [9]. These findings do not imply that one molecular architecture fully determines developmental pace in all insects, but they show why chronological age and biological developmental state cannot be assumed to be interchangeable.

A second criterion is sensitivity to physiological constraint. Functional hypoxia can depend on tissue, age, instar, temperature and oxygen demand, with consequences for growth and activity that differ across developmental contexts [10]. Environmental effects on developmental duration can therefore originate from constraints that are stage-specific rather than from a uniform slowing of all developmental processes.

A third criterion is inferential separability. Environmentally induced developmental plasticity in orthopteroid insects can involve epigenetic regulation, but the observation of plasticity does not itself establish adaptive evolution [11]. Similarly, insect polyphenisms show how nutrition, temperature, photoperiod or crowding may be

integrated through insulin, juvenile-hormone and ecdysteroid systems to generate alternative trajectories [12]. These cases justify retaining environmental routing and developmental state in the framework while prohibiting an automatic transition from plastic response to adaptive interpretation.

Accordingly, the proposed architecture selects dimensions because they represent distinguishable biological operations or consequences: active growth, maturation/state transition, dormancy, and later performance. Their separation is analytical, not an assertion that they operate independently.

Growth and maturation as partially independent axes

Growth and maturation are often correlated because insects must acquire resources and construct tissues before completing stage transitions. Correlation, however, does not establish identity. Growth has experimentally tractable regulatory control. In *Tribolium castaneum*, depletion of target of rapamycin reduced body and appendage growth, including effects on cellular growth, without evidence that reduced food consumption alone explained the phenotype [13]. This establishes TOR as a growth regulator in that system, not as a universal controller of whole-life developmental pace.

Conversely, maturation can be experimentally shifted without preserving the normal relation to size. In *T. castaneum*, increased E93 expression triggered premature metamorphosis independently of the usual threshold-size relationship [14]. The result provides unusually direct evidence that attainment of size and initiation of metamorphic identity can be uncoupled under experimental manipulation. It does not demonstrate that size is irrelevant to maturation under normal conditions, or that all insects show the same degree of independence.

Comparative physiology further argues against treating the coupling as fixed. In *D. melanogaster* and *Manduca sexta*, nutritional and endocrine regulation of prothoracic-gland activity differs around developmental checkpoints, indicating distinct relationships among nutritional state, body-size thresholds and endocrine progression [15]. At the transition itself, ecdysteroid production and secretion are regulated by interacting intrinsic and extrinsic signals that control metamorphic timing [16]. Thus, maturation has its own temporal regulatory architecture even when it remains tightly integrated with growth.

Integration is equally important. The insect fat body participates in nutrient sensing, endocrine communication, growth, diapause, reproduction and longevity, providing routes through which growth and later developmental states can remain physiologically linked [17]. Size regulation, nutritional checkpoints and endocrine transition can therefore be differently coupled across systems [14-16]. The framework consequently defines growth and maturation as partially independent axes: separable enough to require distinct measurement, but sufficiently connected that the strength and direction of their coupling should itself be treated as a biological variable.

For empirical use, growth should be represented by directly measured acquisition or structural change where feasible, whereas maturation should be represented by stage identity, developmental competence, endocrine state, or transition timing appropriate to the taxon. Development time alone cannot substitute for either measurement unless their relation has been independently established.

Dormancy as a temporal state modifier

Dormancy presents the clearest case in which elapsed time and developmental pace can diverge conceptually. Diapause is not merely an interval added to otherwise continuous development. Photoperiodic timing systems can use different forms of time measurement, including oscillator-like and hourglass-like organization, and their expression varies among insect taxa [18]. During a diapause interval, chronological time therefore continues while the biological meaning of developmental progression changes.

This distinction requires two analytical boundaries. First, cue detection, diapause entry, diapause maintenance and subsequent developmental resumption should not be compressed into a single “slow development” state. They represent different temporal functions. Second, evidence for a gene or transcript associated with diapause should not automatically be interpreted as evidence that the factor mechanistically controls dormancy.

Diapause genetics contains a recognized gap between genomic association and functional validation [19]. Developmental-pace models must preserve that evidence boundary.

Population context provides another constraint. In *Aphidius ervi*, diapause and associated life-history responses differed between a commercial strain and a Canadian field-derived strain across generations. Exposure to diapause-inducing conditions increased diapause in the Canadian strain, whereas responses in the commercial strain differed, and a crossed-generation test did not support a uniform maternal-temperature effect on diapause [20]. Dormancy response is therefore not adequately represented by a universal environmental coefficient.

Within the proposed framework, dormancy functions as a temporal state modifier. It changes how elapsed time should be interpreted rather than simply extending a common developmental clock. A long developmental interval can therefore represent slow active growth, delayed maturation, residence in dormancy, or a combination of these states. Distinguishing these possibilities is essential before comparing "developmental speed" across populations or species.

A compact adjudication matrix is useful here because the same chronological delay can correspond to mechanistically and inferentially different dormancy states, while prose alone makes those distinctions difficult to compare simultaneously.

Table 1. When a longer developmental interval does—and does not—represent slower development: adjudicating dormancy as a temporal state modifier

Dormancy-related state or inference scenario	Evidence · Consequence for developmental-pace interpretation	Limits and uncertainty · Biological setting	Research or test · Evidential standing
Photoperiodically induced diapause	Developmental arrest or altered progression associated with photoperiodic induction Added chronological time should not automatically be classified as reduced active developmental rate	Timing mechanisms differ among taxa and stages Diapause-capable insects responding to seasonal cues	Measure diapause state separately from total duration Evidence-supported distinction
Oscillator-like versus hourglass-like timing	Repeated-cycle versus interval-like temporal organization Similar diapause phenotypes may arise through different temporal mechanisms	Mechanistic architecture is species dependent Species with different photoperiodic time-measurement systems	Test time-measurement mechanism before transferring timing rules among taxa Evidence-supported comparison
Diapause-associated molecular signal	Statistical or expression association with diapause phenotype Association can locate a candidate component but cannot by itself define a causal pace mechanism	Functional causation may remain unresolved Genomic, transcriptomic or candidate-gene studies	Pair association studies with perturbation or functional validation Evidence-supported inference boundary
Strain-specific diapause responsiveness	Divergent diapause incidence or associated life-history responses under common induction conditions The same environmental cue need not produce the same temporal state	Population history and laboratory maintenance may alter responsiveness Populations or laboratory/commercial strains with different histories	Replicate across independently derived populations Evidence-supported boundary
Cross-generational dormancy effect	Offspring diapause or development evaluated after different parental environments Parental environment should be treated as a possible modifier rather than assumed control of offspring pace	Null or trait-specific transgenerational responses are possible Maternal and offspring environments considered jointly	Use crossed-generation designs that separate parental and offspring environments Evidence-supported boundary
Chronologically long but biologically heterogeneous development	Equal or similar total durations composed of different amounts of active development and dormancy Total time alone cannot resolve developmental pace	Requires explicit state-resolved measurements Comparative use of total development time	Partition active growth, maturation and dormancy intervals before cross-taxon comparison Proposed synthesis

The central visual problem is therefore not how to add diapause onto a developmental timeline, but how to distinguish elapsed chronology from the biological states occupying that chronology while retaining boundaries between evidence, mechanism and cross-population generalization.

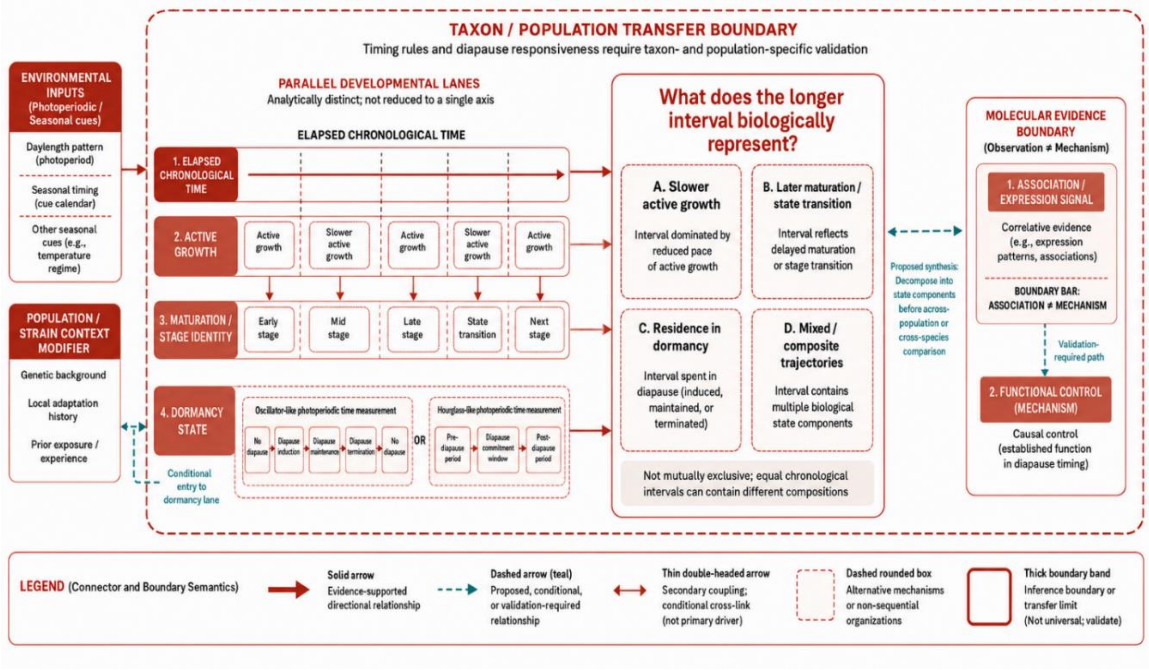


Figure 1. Dormancy rewrites the meaning of elapsed time by separating chronology, developmental state, and inferenc

Adult performance and deferred developmental costs

Developmental interpretation remains incomplete at emergence if juvenile conditions leave persistent effects on adult function. Such carry-over need not follow simple expectations based on body size. In the mango stem borer *Batocera rufomaculata*, poorer larval growth conditions produced smaller adults, yet those adults showed greater long-distance flight endurance in flight-mill tests [21]. A related biomechanical study found that smaller and larger adults did not differ in the expected simple direction for mass-specific flight power or cost of transport [22]. These findings are confined to particular flight measures in one beetle species; they do not establish that small adults generally outperform large ones.

The broader point is that body size is an imperfect universal proxy for adult function. In bees, the developmental regulation and consequences of body-size variation depend on species, caste or social organization and ecological role [23]. Adult performance must therefore remain a distinct outcome domain rather than being inferred automatically from juvenile development duration or final size.

Transstadial physiology provides an even clearer example of deferred effects. Nutrient-limited *Aedes albopictus* larvae prolonged their developmental period, partially compensating for restricted resource acquisition, but adult females retained altered metabolic characteristics [24]. Longer juvenile development therefore reduced one immediate constraint without erasing the developmental history carried into adulthood. This result supports a distinction between temporal compensation and biological compensation: the former occurs when additional time permits developmental completion, whereas the latter would require the relevant later-life consequences also to converge.

The two beetle flight studies likewise show that adult performance cannot be inferred monotonically from body size [21, 22]. The proposed developmental-pace architecture therefore treats adult performance as a downstream validation domain. Juvenile trajectories may be described adequately only when the question concerns stage completion; they are insufficient when the biological question concerns dispersal, reproduction, longevity, metabolic condition, or other adult functions. These domains must be measured directly and interpreted within their taxonomic and environmental setting.

Deferred costs should also not be presumed. A juvenile delay may sometimes be compensatory without detectable later impairment, and an adult difference may arise through pathways not captured by the developmental variables selected here. The framework consequently uses adult outcomes to test whether apparent juvenile convergence represents genuine life-cycle convergence rather than assuming that every altered developmental trajectory carries a later cost.

Integrated developmental-pace architecture

The evidence considered above does not support replacing development time with another single index. It instead supports a proposed architecture in which developmental pace is reconstructed from the biological composition of time. Thermal history illustrates why such reconstruction is necessary. In *Onthophagus taurus*, both temperature mean and thermal variability affected pupal metabolic responses and adult body size, so a single environmental average would have omitted relevant developmental information [25]. Likewise, in *Lobesia botrana*, heat-wave effects depended on developmental stage and post-stress food quality, and the stage appearing most vulnerable differed among measured traits [26].

The proposed architecture therefore contains four analytically separable components: growth trajectory, maturation trajectory, dormancy-state occupancy, and adult-performance consequence. Chronological development time remains an observable overlay rather than becoming a fifth equivalent mechanism. Component coupling is expected to vary. Stage compensation in blowflies demonstrates that temporal effects can redistribute within development [3]; experimental E93 manipulation demonstrates that size attainment and metamorphic initiation can be uncoupled in a specific beetle system [14]; diapause changes the biological interpretation of elapsed time [18]; and nutritional compensation in mosquitoes can coexist with persistent adult metabolic differences [24].

Accordingly, two insects completing development in the same number of days need not occupy the same developmental-pace state. Conversely, unequal total durations need not imply proportionally unequal growth or maturation. The architecture is therefore a proposed descriptive and hypothesis-generating system, not a validated metric, fitness function, or universal mechanistic model.

Testable predictions across insect life histories

The principal value of the architecture is that it makes disagreements among developmental components testable. Field relevance is especially important because altered temperature regimes can influence insects directly through physiology and indirectly through phenological mismatch, host quality, enemies, and other ecological interactions [27]. Laboratory differences in developmental timing should therefore not be assumed to predict population consequences without external ecological validation.

A first prediction is equal-duration divergence: individuals or taxa with similar total development time may differ in growth allocation, maturation timing, dormancy occupancy, or adult performance. A second is stage compensation, in which acceleration in one interval is partly offset later rather than propagated uniformly through the life cycle. A third is variable growth–maturation coupling; comparative endocrine evidence already indicates that nutritional control of developmental checkpoints differs between *Drosophila* and *Manduca* [15]. A fourth is context-dependent dormancy routing, for which strain-dependent diapause responses provide an empirical precedent [20]. A fifth is incomplete life-cycle compensation, where additional juvenile time restores developmental completion without eliminating adult carry-over, as observed under larval nutritional limitation in *Aedes albopictus* [24].

These predictions require different observations and different failure criteria. They are summarized below as a validation ledger rather than as expected outcomes, because none has yet been demonstrated as a universal rule.

Table 2. Tests that distinguish identical development times from genuinely similar developmental trajectories

Proposed test state	Equal-duration divergence	Stage compensation	Variable growth–maturation coupling	Dormancy-state divergence	Incomplete life-cycle compensation	Laboratory-to-field transfer
Interpretation if supported · Principal alternative or boundary	Chronological equivalence conceals biological divergence Measurement error or unmeasured environmental history	Early acceleration is offset by later slowing Independent stage responses without compensation	Coupling strength changes among biological contexts Apparent differences caused by incompatible measurements	Equal cue exposure produces different temporal-state trajectories Laboratory history or population-	Added developmental time restores completion but not later phenotype Adult difference generated after emergence	Laboratory pattern persists under realistic ecological context Phenology, trophic interactions or spatial

				specific cue thresholds		heterogeneity alter response
Evidential standing · Biological comparison	Proposed prediction Individuals, populations or taxa with similar total duration	Proposed prediction Sequential juvenile stages	Proposed prediction Taxa or environments differing in nutritional/endocrine regulation	Proposed prediction Populations or strains exposed to common seasonal cues	Proposed prediction Juveniles experiencing resource or environmental limitation	Proposed validation boundary Laboratory developmental responses compared with natural populations
Required observation · Empirical test requirement	Stage-resolved growth, maturation, dormancy and adult outcomes Compare matched total-duration groups using component-specific measures	Duration or rate measured separately for successive stages Longitudinal stage-specific tracking	Growth state and transition competence measured independently Comparative experiments using homologous developmental landmarks	Diapause state, entry/resumption timing and total duration Replicated population and reciprocal-environment tests	Juvenile completion plus adult physiological or functional outcomes Follow individuals across metamorphosis into adult performance assays	Component trajectories plus ecological exposure and population outcome Independent field or semi-field validation

The figure below separates the proposed trajectories from the empirical tests required to decide whether they meaningfully improve interpretation beyond total development time.

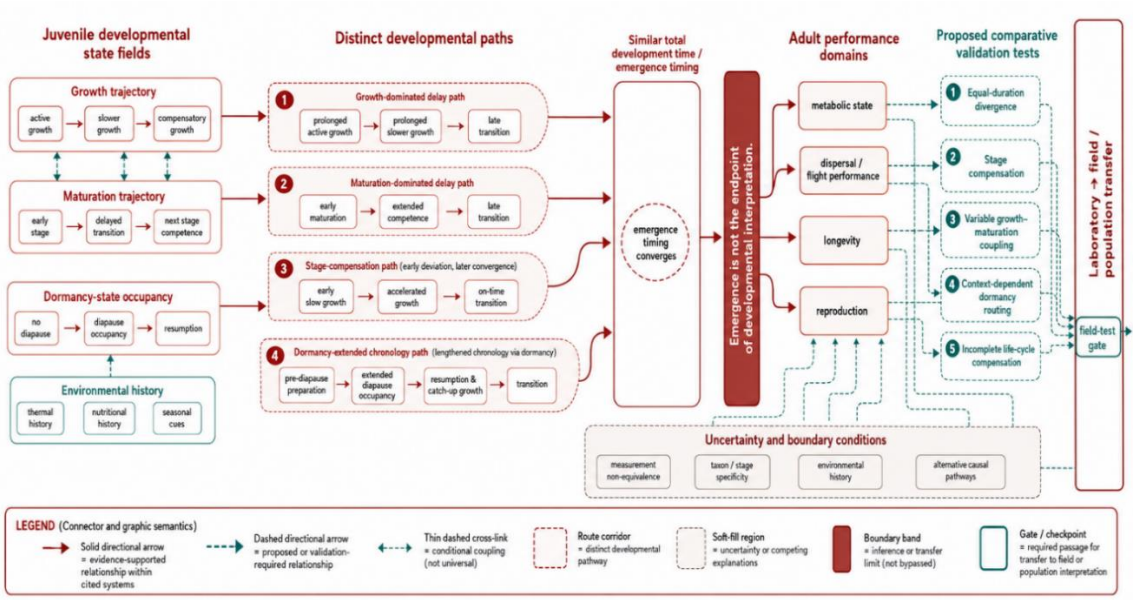


Figure 2. Convergent development times can conceal divergent life-cycle trajectories and validation outcomes

Results and Discussion

The proposed architecture changes the question asked of developmental-time data. Instead of asking only whether one insect develops faster than another, it asks which biological processes account for the temporal difference and whether those processes converge later in the life cycle. This distinction retains information otherwise lost when stage durations, growth, maturation and dormancy are collapsed into one total.

The evidence also argues against treating the proposed dimensions as fully independent. Nutritional plasticity can affect body size without a corresponding population difference in development-time plasticity [5], while fat-body physiology provides routes through which nutritional and endocrine signals remain integrated across stages [17]. Dormancy and transstadial effects add further coupling. The more defensible interpretation is therefore conditional

independence: dimensions should be measured separately when biologically distinguishable, while their coupling becomes an empirical property rather than an assumption.

Adult consequences sharpen this argument. Juvenile conditions can alter later flight performance [21], and body-size effects in bees depend on social and ecological organization [23]. Developmental pace is therefore most informative when the downstream phenotype relevant to the biological question is specified rather than inferred from juvenile timing alone.

Limitations and boundary conditions

The framework is intentionally broader than any single model insect, but the supporting evidence is taxonomically uneven. Mechanistic understanding of stage identity is strongest in tractable hemimetabolous and holometabolous systems [9], comparative growth–maturation evidence remains concentrated in a few model taxa [15], and adult size–function relationships can differ substantially among social and solitary insects [23]. The framework should therefore be tested rather than presumed transferable across orders.

External validity is another major boundary. Strain-specific diapause responses [20], laboratory thermal histories [25], stage-specific heat responses [26], and ecological phenological interactions [27] all indicate that laboratory developmental trajectories cannot automatically be translated into field fitness or population dynamics.

Finally, inference levels must remain separated. Genomic association is not functional proof [19], experimental manipulation in one species does not establish universality [14], and endocrine reviews identify plausible mechanisms without yielding a common quantitative threshold for all insects [16]. The architecture is consequently a proposed organizational framework whose predictive usefulness requires direct comparative and field validation.

Conclusion

Developmental time remains a valuable measurement, but it is not a complete description of developmental pace. Insects can arrive at similar or different chronological endpoints through distinct combinations of growth, maturation, dormancy and carry-over into adult performance. Treating those components separately, while measuring their context-dependent coupling, provides a more discriminating conceptual basis for comparing insect life histories. The proposed architecture is intended to generate testable distinctions, not to replace empirical measurement with a universal developmental score.

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References

1. Koyama T, Mirth CK. Unravelling the diversity of mechanisms through which nutrition regulates body size in insects. Curr Opin Insect Sci. 2018;25:1-8. doi:10.1016/j.cois.2017.11.002
2. Kauranen H, Kinnunen J, Hopkins D, Hoikkala A. Direct and correlated responses to bi-directional selection on pre-adult development time in Drosophila montana. J Insect Physiol. 2019;116:77-89. doi:10.1016/j.jinsphys.2019.04.004
3. Komo L, Charabidze D. Balance between larval and pupal development time in carrion blowflies. J Insect Physiol. 2021;133:104292. doi:10.1016/j.jinsphys.2021.104292
4. Towarnicki SG, Ballard JWO. Drosophila mitotypes determine developmental time in a diet and temperature dependent manner. J Insect Physiol. 2017;100:133-9. doi:10.1016/j.jinsphys.2017.06.002
5. Chakraborty A, Sgrò CM, Mirth CK. The proximate sources of genetic variation in body size plasticity: The relative contributions of feeding behaviour and development in Drosophila melanogaster. J Insect Physiol. 2021;135:104321. doi:10.1016/j.jinsphys.2021.104321

6. Gray LJ, Simpson SJ, Polak M. Fruit flies may face a nutrient-dependent life-history trade-off between secondary sexual trait quality, survival and developmental rate. J Insect Physiol. 2018;104:60-70. doi:10.1016/j.jinsphys.2017.11.010
7. Shingleton AW, Frankino WA. The (ongoing) problem of relative growth. Curr Opin Insect Sci. 2018;25:9-19. doi:10.1016/j.cois.2017.10.001
8. Belles X. MicroRNAs and the evolution of insect metamorphosis. Annu Rev Entomol. 2017;62:111-25. doi:10.1146/annurev-ento-031616-034925
9. Martín D, Chafino S, Franch-Marro X. How stage identity is established in insects: The role of the Metamorphic Gene Network. Curr Opin Insect Sci. 2021;43:29-38. doi:10.1016/j.cois.2020.10.002
10. Harrison JF, Greenlee KJ, Verberk WCEP. Functional hypoxia in insects: Definition, assessment, and consequences for physiology, ecology, and evolution. Annu Rev Entomol. 2018;63:303-25. doi:10.1146/annurev-ento-020117-043145
11. Lo N, Simpson SJ, Sword GA. Epigenetics and developmental plasticity in orthopteroid insects. Curr Opin Insect Sci. 2018;25:25-34. doi:10.1016/j.cois.2017.11.003
12. Nijhout HF, McKenna KZ. The distinct roles of insulin signaling in polyphenic development. Curr Opin Insect Sci. 2018;25:58-64. doi:10.1016/j.cois.2017.11.011
13. Lin X, De Schutter K, Chafino S, Franch-Marro X, Martín D, Smagghe G. Target of rapamycin (TOR) determines appendage size during pupa formation of the red flour beetle Tribolium castaneum. J Insect Physiol. 2019;117:103902. doi:10.1016/j.jinsphys.2019.103902
14. Chafino S, Ureña E, Casanova J, Casacuberta E, Franch-Marro X, Martín D. Upregulation of E93 gene expression acts as the trigger for metamorphosis independently of the threshold size in the beetle Tribolium castaneum. Cell Rep. 2019;27(4):1039-49.e2. doi:10.1016/j.celrep.2019.03.094
15. Xu LC, Nunes C, Wang VR, Saito A, Chen T, Basak P, et al. Distinct nutritional and endocrine regulation of prothoracic gland activities underlies divergent life history strategies in Manduca sexta and Drosophila melanogaster. Insect Biochem Mol Biol. 2020;119:103335. doi:10.1016/j.ibmb.2020.103335
16. Pan X, Connacher RP, O'Connor MB. Control of the insect metamorphic transition by ecdysteroid production and secretion. Curr Opin Insect Sci. 2021;43:11-20. doi:10.1016/j.cois.2020.09.004
17. Li S, Yu X, Feng Q. Fat body biology in the last decade. Annu Rev Entomol. 2019;64:315-33. doi:10.1146/annurev-ento-011118-112007
18. Saunders DS. Dormancy, diapause, and the role of the circadian system in insect photoperiodism. Annu Rev Entomol. 2020;65:373-89. doi:10.1146/annurev-ento-011019-025116
19. Ragland GJ, Armbruster PA, Meuti ME. Evolutionary and functional genetics of insect diapause: A call for greater integration. Curr Opin Insect Sci. 2019;36:74-81. doi:10.1016/j.cois.2019.08.003
20. Tougeron K, Devogel M, van Baaren J, Le Lann C, Hance T. Trans-generational effects on diapause and life-history-traits of an aphid parasitoid. J Insect Physiol. 2020;121:104001. doi:10.1016/j.jinsphys.2019.104001
21. Brown S, Soroker V, Ribak G. Effect of larval growth conditions on adult body mass and long-distance flight endurance in a wood-boring beetle: Do smaller beetles fly better? J Insect Physiol. 2017;98:327-35. doi:10.1016/j.jinsphys.2017.02.008
22. Urca T, Ribak G. The relationship between body size and flight power output in the mango stem borer (Batocera rufomaculata). J Insect Physiol. 2021;133:104290. doi:10.1016/j.jinsphys.2021.104290
23. Chole H, Woodard SH, Bloch G. Body size variation in bees: Regulation, mechanisms, and relationship to social organization. Curr Opin Insect Sci. 2019;35:77-87. doi:10.1016/j.cois.2019.07.006
24. Dittmer J, Gabrieli P. Transstadial metabolic priming mediated by larval nutrition in female Aedes albopictus mosquitoes. J Insect Physiol. 2020;123:104053. doi:10.1016/j.jinsphys.2020.104053
25. Fleming JM, Carter AW, Sheldon KS. Dung beetles show metabolic plasticity as pupae and smaller adult body size in response to increased temperature mean and variance. J Insect Physiol. 2021;131:104215. doi:10.1016/j.jinsphys.2021.104215
26. Iltis C, Louâpre P, Vogelweith F, Thiéry D, Moreau J. How to stand the heat? Post-stress nutrition and developmental stage determine insect response to a heat wave. J Insect Physiol. 2021;131:104214. doi:10.1016/j.jinsphys.2021.104214
27. Abarca M, Spahn R. Direct and indirect effects of altered temperature regimes and phenological mismatches on insect populations. Curr Opin Insect Sci. 2021;47:67-74. doi:10.1016/j.cois.2021.04.008