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Developmental Time Functions as a Dynamic Currency Balancing Growth, Maturation, Resource Use, and Seasonal Risk in Insects

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ABSTRACT

Development time is commonly treated as an outcome of temperature, nutrition, seasonality, or stress, yet elapsed time also changes the biological conditions under which development continues. Additional time before maturation may permit further resource acquisition, tissue growth, physiological preparation, or repair, while simultaneously extending maintenance expenditure, delaying reproduction, increasing exposure to stage-specific mortality, and consuming finite seasonal opportunity. We develop the proposed developmental-time currency concept, in which the biological value of remaining in a developmental state is determined by the changing balance between marginal benefits of continued development and marginal costs of delay. The framework does not assume that faster development is universally advantageous, that longer development necessarily improves adult phenotype, or that observed developmental schedules are evolutionarily optimal. Instead, developmental time is treated as state dependent: its value changes with resource availability, thermal history, developmental stage, diapause state, seasonal information, mortality exposure, and inherited constraints. Evidence from insects supports these component relationships but not their complete integration into a single validated mechanism. The framework therefore generates conditional rather than universal expectations and separates organismal timing responses from fitness, population persistence, and evolutionary adaptation. Its central implication is that developmental duration should be interpreted not simply as a rate outcome but as a dynamic life-history allocation problem.

Keywords: Developmental timing, Life-history trade-offs, Diapause, Seasonal constraint, Resource allocation, Predation risk.

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Introduction

Developmental duration is among the most frequently measured life-history traits in insects, but its biological interpretation is often narrower than its consequences. Climate-driven responses can involve seasonal timing and thermal physiology that evolve along partly independent trajectories, making development time only one component of a larger timing problem [1]. Temperature has strong effects on butterfly development, yet effect magnitudes and associated body-mass responses remain heterogeneous rather than defining a universal insect reaction norm [2]. Thermal sensitivity also changes across ontogeny because developmental stages differ in exposure, mobility, microhabitat, and physiological capacity [3]. A whole-life development time can therefore conceal biologically important stage-specific histories.

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A second limitation is that developmental rate is frequently treated as though it summarizes environmental performance. Integrating development with survival shows why this is unsafe: low-temperature limits may be imposed predominantly by development whereas high-temperature limits can be imposed more strongly by survival [4]. Adult size adds another dimension, because warmer developmental conditions commonly produce smaller mature size through several competing physiological and allocation mechanisms rather than through one simple duration-dependent process [5]. Evolutionary responses are likewise conditional on exposure, environmental variability, plasticity, and historical constraints, so an observed developmental schedule cannot automatically be interpreted as an adaptive optimum [6].

This article develops a proposed theoretical interpretation of developmental time as a dynamic currency. "Currency" is used in an accounting sense, not as a literal metabolite: each additional interval before a developmental transition can create biological returns while simultaneously accumulating costs. The central question is therefore not whether fast or slow development is generally preferable, but when continued development has positive marginal value and when transition, diapause, maturation, or another state change becomes comparatively favorable. The theory retains distinctions among growth, maturation, maintenance, seasonal exposure, predator-mediated mortality, physiological constraint, and evolutionary history rather than collapsing them into one latent pace-of-life variable.

Developmental time as opportunity cost

An additional unit of developmental time has opportunity cost because remaining in one life-history state delays access to alternatives. In a developing insect, this can mean postponing reproduction, dispersal, a less vulnerable stage, overwintering, or exploitation of a temporally restricted resource. Yet remaining immature can also preserve opportunities for further feeding, storage, structural growth, or physiological preparation. Experimental evolution in Callosobruchus maculatus shows that warming can alter resource acquisition, maintenance, reproduction, and other life-history components together rather than changing development in isolation [7]. The inference relevant here is not that warming produces one general allocation rule, but that acquisition and expenditure can shift jointly while developmental schedules change.

Resource opportunity is itself state dependent. In Drosophila melanogaster, nutritional optima for life-history traits differ across temperature and population background, demonstrating that the value of available nutrients cannot be specified independently of thermal context [8]. Thus, the proposed developmental-time currency assigns no fixed benefit to "more feeding time." Continued feeding has positive value only if resources can be acquired and converted into biologically relevant gains at that stage and under those conditions.

This distinction also separates environmental resource abundance from physiological usability. Nitrogen homeostasis in insects depends on coordinated intake, assimilation, storage, conversion, and excretion processes that influence growth and development [9]. At a more specific molecular scale, disruption of the amino-acid transporter BmSLC7A5 in Bombyx mori impairs TORC1-related signalling, silk synthesis, and larval development [10]. Such findings illustrate lower-level constraints on resource conversion, but they do not establish a universal molecular controller of developmental timing. In the proposed theory, resource availability therefore modifies the marginal value of time only through the organism's capacity to use that resource.

Growth benefits of delayed maturation

Delayed maturation is often expected to permit larger size, greater reserves, or more complete development, but the evidence requires separation of time available for growth from growth achieved per unit time. In Trypoxylus dichotomus, higher-latitude populations showed faster larval growth in a common environment, with increased food intake contributing to the cline [11]. Short seasonal opportunity can therefore be met by altered growth rate rather than simply by reducing final size or extending development.

Developmental physiology further complicates any simple time-size exchange. Development under different thermal conditions in D. melanogaster alters body and cell size, while physiological responses to hypoxia also depend on evolutionary thermal history [12]. Adult phenotype is consequently produced by the conditions under which time is spent, not merely by elapsed duration. Stage-specific temperature-shift experiments reinforce this point: larval temperature can dominate total development time and adult body size, whereas earlier-stage exposures generate carry-over effects and sex-dependent responses [13].

The theoretical implication is that the benefit term associated with additional developmental time must be conditional on growth rate, developmental stage, prior environment, sex where relevant, and physiological state.

Longer development may increase size in one context, compensate for low instantaneous growth in another, or merely prolong exposure without a proportionate somatic return. Population differentiation cannot by itself resolve which interpretation applies. In a widespread diving beetle, thermal-tolerance differences among populations were detected, but predicted climatic and elevational patterns of local thermal adaptation were weak [14]. Realized developmental schedules must therefore remain conceptually distinct from an assumed evolved optimum.

Resource and maintenance costs

Time spent developing is also time spent maintaining a living organism. Maintenance costs include turnover, ion regulation, cellular repair, immune activity, locomotion, osmoregulation, and protection against environmental injury, but their magnitude cannot be inferred simply from duration. Cold-storage research illustrates the distinction: fluctuating thermal regimes can permit repair of chill injury, yet the energetic and reproductive costs of those repair processes remain incompletely quantified [15]. Additional time can therefore preserve future function while simultaneously consuming resources.

Dormancy further demonstrates that slow or arrested visible development is not physiologically equivalent to cost-free waiting. In Helicoverpa armigera, AMPK-associated regulation contributes to pupal diapause through interactions involving HIF-1α-related signalling and metabolic suppression [16]. This is a species- and stage-specific mechanism, but it illustrates why the proposed framework separates active growth time, maintenance-dominated time, and dormant developmental time rather than assigning each the same energetic meaning.

Costs may also precede the dormant stage. In two mirid species, production of diapause-oriented eggs was associated with longer pre-oviposition periods and reduced egg production relative to nondiapause-oriented reproduction [17]. Diapause can therefore redistribute costs across generations and stages rather than simply preserving individuals through adverse conditions. The proposed developmental-time currency consequently treats maintenance and dormancy costs as conditional debits whose magnitude must be measured rather than presumed.

Seasonal time constraint

Seasonality changes the value of developmental time because the remaining interval before winter, drought, host disappearance, migration, diapause entry, or another environmental transition progressively alters the consequences of delay. A fixed calendar threshold is often too coarse for this problem. Population-level diapause induction and termination can be represented more realistically as continuous responses to environmental information even when individual developmental decisions remain discrete [18]. The proposed theory therefore treats remaining seasonal opportunity as a state variable whose value can change continuously as development proceeds.

Seasonal timing must also be distinguished from seasonal success. In the butterfly Lasiommata megera, seasonal timing traits evolved rapidly during climate-associated range expansion, yet winter survival still restricted establishment beyond the range margin, and prewinter mass did not explain that limitation [19]. Adjusting when development occurs is therefore not equivalent to removing the mortality costs encountered after that adjustment.

Inherited architecture can influence seasonal response without defining one universal timing mechanism. Repeated evolution of photoperiodic plasticity in a butterfly involved different genetic architectures across colonization histories [20]. Conversely, in H. armigera, a large inversion containing functionally implicated circadian genes contributes strongly to facultative diapause variation [21]. These cases together support genetic contingency rather than a single conserved developmental clock. Timing of diapause termination is similarly complex: selection and crossing in Cydia pomonella indicate contributions from Z-linked, autosomal, and additional nonchromosomal components [22].

Environmental history remains equally important. Multi-year field experiments with Anabrus simplex eggs show that elevation and associated microenvironment strongly alter diapause duration, hatching, and mortality, while parental photoperiod alone does not determine the outcome [23]. Seasonal information can also be degraded anthropogenically; artificial light at night can disrupt photoperiodic control of diapause, although species differ in sensitivity and field transfer remains incompletely resolved [24].

These observations motivate a specific distinction in the proposed theory. Seasonal time is not simply “days remaining.” It combines at least four biologically separable properties: cue reliability, developmental state at cue perception, expected conditions after transition, and mortality associated with failing to reach the appropriate state

in time. **Table 1** separates these seasonal-time states because prose alone can obscure how similar changes in calendar time lead to different biological interpretations.

Table 1. Seasonal-time states that change the biological value of remaining in development

Biological setting	Observable basis	Consequence for interpreting developme, boundary or uncertainty, and discriminating check
Continuous cue-responsive timing		
Evidence-supported premise		
Diapause induction or termination across insect populations	Reaction norms relating seasonal cues to state transition	Remaining time changes gradually in value as cue conditions shift Individual decisions may still be discrete; reaction norms are population- and species-specific Measure full cue–response functions rather than a single nominal threshold
Timing–survival decoupling		
Evidence-supported premise		
Range-edge or overwintering populations	Seasonal timing changes accompanied by independent winter-survival measurements	Earlier or better-aligned transition does not guarantee successful overwintering Post-transition mortality may dominate developmental benefits Couple phenology with stage-specific survival in field settings
Genetically contingent seasonal response		
Evidence-supported premise		
Photoperiodic plasticity and diapause systems	Crosses, genomic variation, selection responses	Similar developmental schedules can arise through different inherited architectures No single genetic implementation can be assumed across taxa Test phenotype-level predictions independently of molecular architecture
Environmentally prolonged developmental arrest		
Evidence-supported premise		
Eggs or other dormant stages exposed to contrasting microclimates	Hatching timing, diapause duration, mortality across environments	Calendar delay can reflect environmental constraint rather than maladaptive developmental inertia Multi-year dormancy cannot be equated with actively growing development Separate active, maintenance-dominated, and dormant intervals
Seasonal-information degradation		
Evidence-supported premise		
Species using photoperiodic cues in artificially illuminated environments	Altered diapause induction or termination under night lighting	Time may be valued using unreliable environmental information Sensitivity depends on taxon, spectrum, intensity, and ecological context Compare cue perception with subsequent environmental conditions and survival
Remaining seasonal opportunity		
Proposed synthesis		
Any developing stage approaching an adverse seasonal transition	Time to transition integrated with stage, resource state, and post-transition survival	The marginal cost of another developmental interval is predicted to rise when missed transition becomes more consequential Functional form and magnitude are not established Manipulate developmental delay while independently varying seasonal proximity

Seasonality also requires a visual representation because developmental trajectories can enter different states from the same calendar position depending on cue information, energetic state, inherited responsiveness, and the conditions expected after transition. **Figure 1** therefore separates evidence-supported seasonal pathways from the proposed valuation step that converts those pathways into a changing marginal cost of developmental delay.

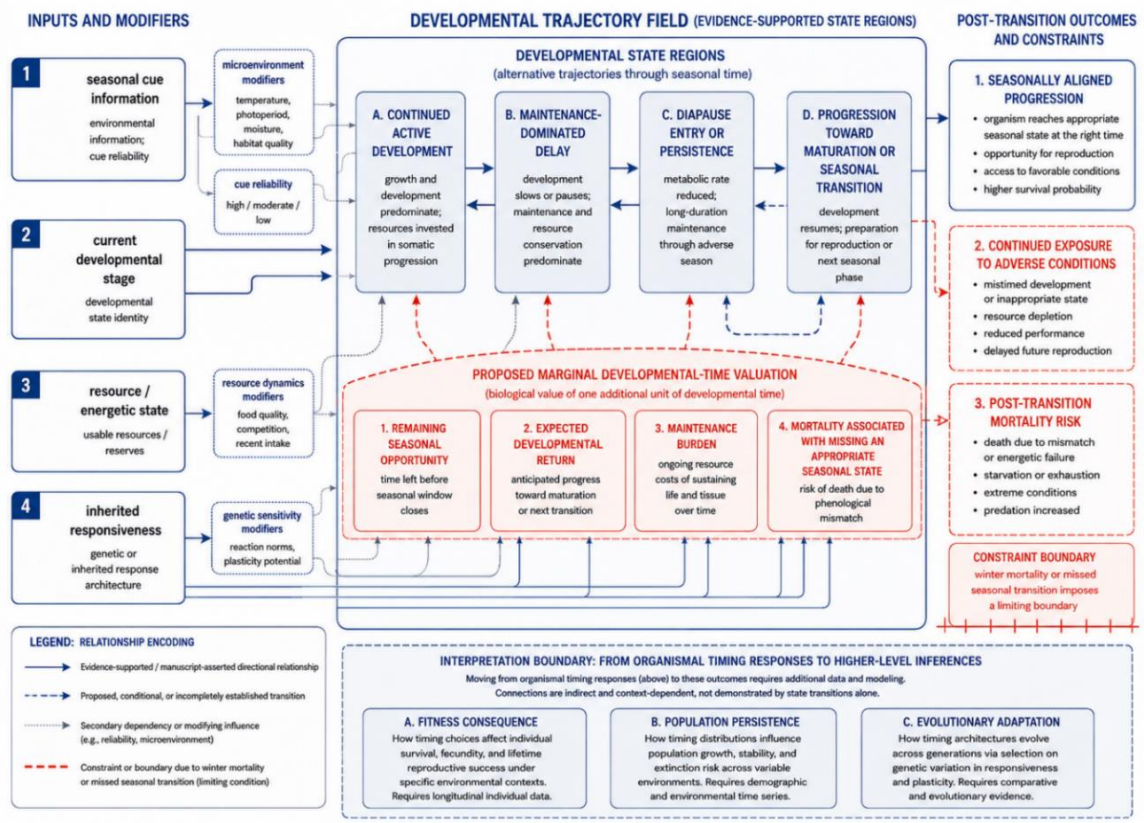


Figure 1. Seasonal trajectories diverge when the same elapsed time carries different developmental consequences

Predation and mortality risk

Mortality changes the developmental-time calculation because remaining in a vulnerable stage can extend exposure even when additional time provides nutritional or growth benefits. In Ischnura elegans, seasonal time constraint, warming, and predator cues interact: late-season larvae can accelerate development under warming, while predator cues can counteract aspects of that acceleration [25]. The direction of timing change is therefore not predictable from seasonal urgency alone.

Risk also has non-consumptive physiological consequences. Chronic larval exposure to predators in two Anopheles species produced different carry-over effects on adult life-history and physiological traits, with responses varying between species and sexes [26]. This heterogeneity argues against representing predator risk as a single fixed mortality coefficient. Risk can change resource allocation before any predation event occurs, thereby altering the marginal benefit of additional developmental time.

The duration of the vulnerable stage provides a second route by which developmental timing affects risk. Experiments on stage-structured dragonfly–mosquito interactions show that temperature can alter predator feeding and prey developmental progression asymmetrically [27]. Faster development may reduce the period during which prey are exposed to a predator, yet a thermal environment that speeds prey development can also increase predator consumption. Consequently, “developmental escape” is conditional on the relative temperature sensitivities of predator attack and prey maturation rather than on development rate alone.

Resource state can further modify this relationship. In larval Colorado potato beetles, nutritional condition changes behavioural and physiological responses to predator risk [28]. Field-mesocosm experiments with aquatic insects likewise show that colonization decisions can integrate nutrient rewards and predator-associated costs in species-specific ways [29]. These studies do not demonstrate a developmental-time optimum directly, but they establish that insects can integrate resource and risk information rather than responding to each dimension independently.

The broader enemy-risk literature reinforces the need for scale discipline. Non-consumptive predator effects can alter insect behaviour, physiology, and life history, but their ecological consequences remain strongly context dependent [30]. More importantly, a critical evidence review found very few studies that directly linked predator-induced prey traits to population size, with positive, negative, and null outcomes represented [31]. The proposed

developmental-time currency should therefore remain an organismal life-history theory unless higher-level consequences are measured directly.

Within that boundary, mortality risk modifies developmental time in two separable ways. First, it changes the expected cost of remaining in a vulnerable state. Second, through behavioural or physiological responses, it can alter the resource gains available during that state. The resulting prediction is not that predators universally accelerate or delay maturation. Rather, the sign of the timing response should depend on whether an additional developmental interval provides enough growth, maturation, or resource benefit to compensate for its maintenance cost and its added exposure to mortality. This conditional interaction provides the immediate foundation for the Dynamic Resource–Risk Model developed in the next section.

Dynamic resource–risk model

Life-history responses to environmental change do not support a universal expectation that selection should move insects toward faster or slower development. A meta-analysis of warming, predation, and competition found weak overall directional evolutionary responses across major life-history traits, despite significant responses within some individual studies [32]. The proposed model therefore does not equate its theoretical optimum with an evolved adaptation.

Trait-specificity provides a second constraint. During poleward expansion of Ischnura elegans, cold tolerance and thermal plasticity changed differently among life-history, behavioural, and physiological traits, without a generalized acceleration of life history at the expanding edge [33]. Developmental "pace" should consequently not be treated as a single latent phenotype.

The proposed Dynamic Resource–Risk Model instead evaluates the marginal value of remaining in the present developmental state. Let another developmental interval be favored when expected gains from growth, maturation, resource acquisition, physiological preparation, or repair exceed the combined costs of maintenance, delayed access to the next life-history state, seasonal opportunity loss, and added mortality exposure. These components are conceptual terms rather than fitted quantities. Their magnitudes, functional forms, and interactions are not assumed to be identical across taxa or stages.

The model is explicitly state dependent. Resource abundance matters only when resources remain usable; growth benefits depend on developmental and thermal history; seasonal costs depend on cue reliability and post-transition conditions; and mortality costs depend on vulnerability duration and predator context. Feedback is also possible: predator avoidance may reduce feeding, thereby lowering the return from prolonging development, whereas improved resource acquisition may increase the benefit of remaining immature. Such interactions make the theoretical transition point conditional rather than fixed.

Optimal developmental timing across environments

Environmental heterogeneity does not guarantee that populations can evolve corresponding physiological optima. Across ten Aedes sierrensis populations spanning a broad climatic range, upper thermal limits for several life-history traits varied relatively little, although pupal development showed evidence of differentiation [34]. Physiological constraint can therefore coexist with substantial environmental variation.

Within the proposed theory, optimal developmental timing is the state at which the expected marginal value of continued development no longer exceeds the expected marginal value of transition. This optimum may occur earlier under strong seasonal or mortality costs, but later where growth returns remain high and exposure costs are low. Importantly, this is a theoretical comparison, not evidence that insects perform such calculations or that realized schedules maximize fitness.

Realized development can depart from the theoretical optimum because cue information is imperfect, thermal limits are constrained, genetic architectures differ, developmental histories generate carry-over, and environments change after a developmental decision. **Table 2** reconciles apparently conflicting empirical patterns by separating the theoretical direction expected from the model from constraints that can prevent the corresponding phenotype from appearing.

Table 2. Reconciling environmental timing expectations with realized developmental schedules

Timing scenario — evidential organization		Interpretive reach, restraint, and verification	
Timing scenario with evidential standing	**Biological context with observed basis**	**Interpretation for devel within its limit**	**Discriminating test**

High resource return with low immediate risk **Proposed synthesis**	Actively feeding immature stages Resource availability can improve performance, but responses depend on temperature and population background	Additional developmental time may retain positive marginal value Resource conversion, stage history, and future conditions may limit returns	Manipulate resource level and developmental opportunity independently
Approaching seasonal transition **Proposed synthesis**	Diapause-prone or seasonally limited stages Timing responses vary continuously and can evolve rapidly	Delay is expected to become increasingly costly as viable seasonal opportunity contracts Cue reliability and post-transition survival can decouple timing from success	Pair phenology manipulations with overwinter or post-transition survival
High vulnerability during prolonged immature development **Proposed synthesis**	Predator-exposed larvae or nymphs Predator effects depend on temperature, resource state, and predator identity	Earlier transition may reduce exposure when developmental escape exceeds lost growth benefit Faster development may coincide with increased predator attack or reduced adult condition	Measure attack, development, resource gain, and carry-over jointly
Strong physiological or evolutionary constraint **Evidence-supported boundary**	Populations across climatic gradients Thermal limits and life-history responses can remain weakly differentiated	Realized timing may remain distant from the theoretical environmental optimum Limited plasticity, genetic constraint, or historical contingency	Compare field timing with common-garden reaction norms and survival
Rapidly changing or misleading seasonal cues **Proposed synthesis**	Artificially altered or climatically novel environments Cue–environment relationships can become unreliable	A historically useful developmental rule may produce mistimed transition Future environmental state cannot be inferred from cue response alone	Measure cue response and subsequent realized environmental match

The relationship among theoretical optima, realized schedules, and biological constraints is easier to recover visually when evidence levels remain separated. **Figure 2** therefore reconciles environmental drivers with organismal timing responses while retaining an explicit boundary between a theoretically favored transition and an empirically observed phenotype.

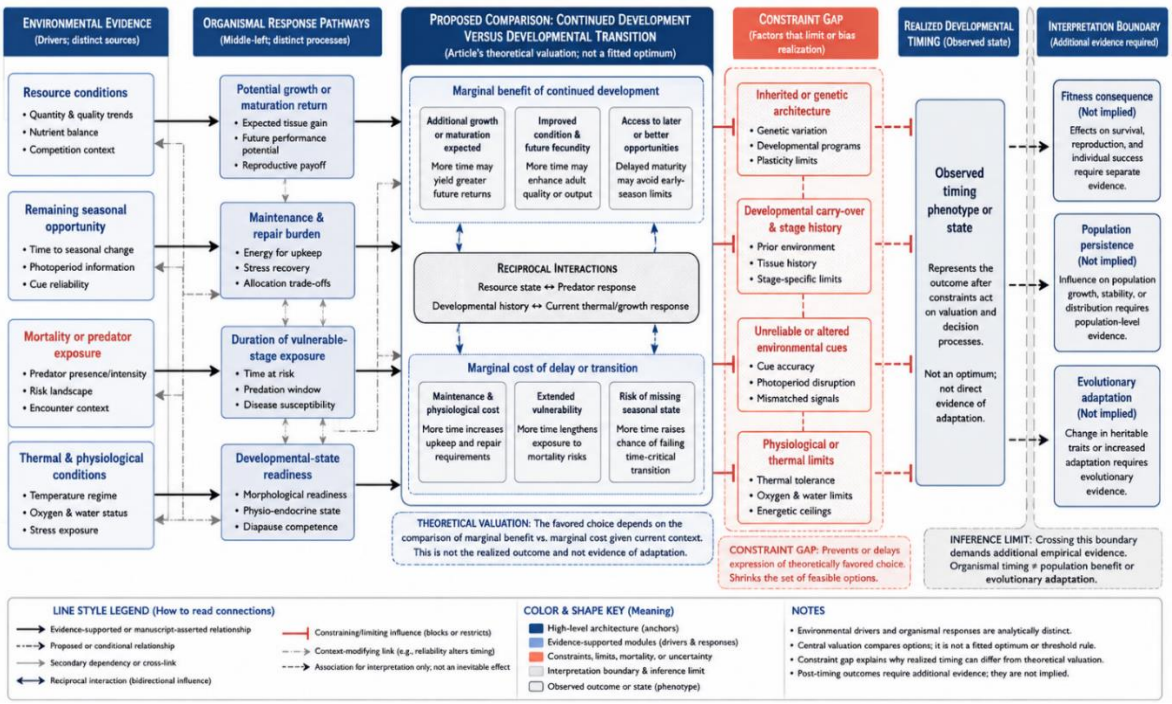


Figure 2. Constraint gaps separate environmentally favored transition timing from realized insect development

Predictions

The theory generates conditional predictions rather than a universal direction of developmental change. First, additional developmental time should be favored under resource-rich conditions only while growth, maturation, storage, or physiological returns remain greater than the accumulated costs of delay. Increasing resources should therefore not necessarily lengthen development if conversion is constrained or if mortality risk rises simultaneously.

Second, the marginal cost of delay should increase as a consequential seasonal transition approaches, but only when environmental cues reliably indicate future conditions. Manipulations that alter apparent season without altering subsequent survival conditions should therefore separate cue response from actual seasonal benefit.

Third, predator effects should depend on the interaction between vulnerable-stage duration and resource state. Where faster development markedly shortens exposure, risk may favor earlier transition; where predator avoidance suppresses feeding or where attack rates rise with temperature, the same environmental change may yield a different response.

Fourth, stage-resolved environmental histories should explain developmental outcomes better than whole-life mean exposure when carry-over is substantial. Finally, realized schedules should depart most strongly from the theoretical optimum in populations or stages constrained by thermal physiology, inherited architecture, or unreliable seasonal information. These predictions require direct experimental and field validation; none constitutes a demonstrated performance advantage.

Results and Discussion

Treating developmental time as a dynamic currency changes the question asked of insect life histories. The relevant contrast is not simply fast versus slow development, but whether remaining in the current state still generates sufficient return relative to the accumulating costs of delay. This interpretation preserves distinctions that conventional duration measures can obscure: growth differs from survival [4], thermal responses differ among developmental stages [3], and physiological or population variation need not demonstrate local adaptation [14].

The framework is deliberately pluralistic about mechanism. Molecular nutrient sensing, diapause regulation, predator-induced physiology, seasonal cues, and thermal constraints can all influence developmental timing without forming one conserved pathway. The proposed currency is therefore an analytical common denominator rather than a molecular substance or hidden physiological variable. Likewise, the model parameters cannot be assumed to transfer among holometabolous and hemimetabolous insects, aquatic and terrestrial stages, sexes, geographic populations, or laboratory and field environments.

A second boundary concerns evolutionary interpretation. Rapid change in seasonal timing can coexist with severe winter-survival limitation [19]. Across broader experimental literature, warming and predation do not produce one consistently directional evolutionary response [32]. Even during range expansion, component traits can evolve differently [33], while substantial climatic gradients may coexist with relatively constrained thermal limits [34]. The theoretical optimum defined here must therefore remain distinct from the realized phenotype and from claims of adaptation.

A third boundary concerns biological scale. Predator-induced changes in development, behaviour, or physiology cannot be assumed to alter population size without direct demographic evidence [31]. Similarly, adult size, development rate, or successful diapause cannot individually substitute for lifetime fitness. Strong tests of the model should consequently combine stage-resolved manipulations of resources and risk with field-relevant seasonal conditions, common-garden comparisons among populations, and independent measures of survival and reproduction.

The framework is most useful as a generator of discriminating experiments. Its value will depend on whether measuring marginal benefits and costs of continued development explains timing better than simpler alternatives such as temperature-dependent rate models, fixed seasonal thresholds, or single-trait optimality assumptions. Failure under those comparisons would narrow its domain rather than invalidate the well-established component relationships from which it was constructed.

Conclusion

Developmental time is proposed here as a dynamic life-history currency whose value changes as growth opportunities, resource processing, maintenance demands, seasonal opportunity, and mortality exposure change. The framework does not prescribe universally faster or slower development and does not equate realized timing with adaptation. Its principal contribution is to recast developmental duration as a state-dependent allocation problem in which the biological value of another interval before transition depends on what can still be gained, what must be paid, and which future opportunities may be lost. Testing that proposition requires stage-resolved, taxon-aware, and field-linked evidence that separates developmental response from survival, reproduction, population consequence, and evolutionary interpretation.

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