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Insect Body Size Emerges from Competing Resource Demands for Reproduction, Flight, Stress Resistance, and Maintenance in Insects

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ABSTRACT

Adult insect body size is commonly treated as an integrated indicator of developmental conditions, resource availability, or organismal quality. Such interpretations become problematic when acquired resources can be diverted among structural growth, stored reserves, locomotor machinery, reproduction, stress resistance, and somatic maintenance. Here, we develop a mechanistic model in which insect body size emerges from conditional allocation rather than from resource acquisition alone. The model distinguishes resource quantity from nutrient composition, structural tissue from reserve storage, developmental growth from metamorphic timing, locomotor capacity from realized movement strategy, reproductive output from per-offspring investment, and stress resistance from maintenance. Evidence across insects indicates that these components need not change in parallel: smaller adults can retain more energetic reserves, movement syndromes differ in their reproductive associations, nutrient identity can constrain reproduction and longevity independently of bulk macronutrient supply, and thermal or hypoxic responses are strongly context dependent. We therefore propose that body size should be interpreted as one outcome of a multicomponent developmental resource budget whose allocation rules vary with sex, life stage, physiology, movement ecology, reproductive strategy, and environment. The framework predicts that no single size optimum should apply across ecological contexts and that mechanistic validation requires simultaneous measurement of structural growth and competing allocation sinks rather than body size alone.

Keywords: Insect body size, Resource allocation, Developmental plasticity, Flight–reproduction trade-offs, Stress resistance, Life-history energetics

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Introduction

Body size is among the most frequently measured insect traits because it covaries with development, resource use, locomotion, reproduction, thermal exchange, and survival. Yet a final linear dimension or adult mass compresses several developmental processes into one endpoint. Nutritional physiology already demonstrates that adult size can change through altered growth rate, growth duration, developmental thresholds, and endocrine regulation rather than through a single resource-to-size pathway [1]. Bees provide a complementary example: developmental provisioning, temperature, social organization, and caste-related biology can all influence body-size variation, while the consequences of being larger depend on ecological and social context rather than conforming to an invariant advantage [2].

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Environmental patterns further caution against treating size as a simple physiological readout. Temperature–body size relationships observed across laboratory, seasonal, or latitudinal contrasts do not reproduce consistently across elevational gradients [3]. In tropical *Cephaloleia* beetles, evolutionary history explained substantial size variation, and simple ecogeographic expectations did not adequately describe most within-species elevational patterns [4]. Thus, an observed size difference can reflect developmental plasticity, historical differentiation, resource composition, environmental constraints, or combinations of these processes. Even the widely discussed relationship between warming and shrinking body size admits several nonexclusive mechanistic explanations, with oxygen limitation acting as a conditional rather than universally sufficient explanation [5].

The central problem is therefore not merely why insects become large or small. It is how limited and compositionally heterogeneous resources are partitioned among biological demands while development is occurring. Structural tissue is only one potential destination. Resources may instead remain in lipid or carbohydrate stores, support flight morphology and locomotor performance, enter egg production, sustain immune or thermal resistance, or maintain adult function. These destinations need not be energetically interchangeable, temporally simultaneous, or regulated by the same signaling pathways.

We consequently propose a resource-budget interpretation in which final body size is an emergent developmental outcome of competing and interacting demands. The model does not assume a fixed energetic currency, a universal trade-off coefficient, or a single optimal size. It instead distinguishes direct allocation competition from endocrine regulation, developmental timing, environmental constraint, and later ecological consequences of attained size. The sections below develop the evidential premises required for that synthesis while retaining taxonomic, sex-specific, life-stage, and laboratory-to-field boundaries.

Resource acquisition and allocation

Resource acquisition cannot be represented adequately by food amount alone. In *Drosophila melanogaster*, manipulating diet quality and quantity produces different morphological responses, and those responses differ between females and males [6]. This distinction matters mechanistically because the same nominal reduction in intake can alter protein, carbohydrate, sterol, micronutrient, or other substrate availability differently. A developmental resource budget should therefore begin with physiologically usable resources rather than bulk calories.

The conversion from diet to structure is also sex dependent. Female-biased activity of insulin signaling contributes to stronger nutritional plasticity of body size in *D. melanogaster*, showing that identical dietary environments need not be translated into equivalent growth responses in the two sexes [7]. This does not establish an insect-wide rule for insulin signaling, but it demonstrates that resource allocation can be modified by sex-specific regulatory architecture before adult size is expressed.

Acquisition is further transformed by host–microbial interactions. Work in *Drosophila* emphasizes that microbial contributions to nutrient use and host physiology vary with diet, host genotype, microbial identity, and physiological state [8, 9]. Consequently, consumed food and developmentally available substrate should not be treated as synonymous quantities. The proposed budget begins after this physiological filtering, while recognizing that the filtering process itself can change across environments and genotypes.

Resource-responsive changes may also occur at levels below whole-body growth. In the adult *Drosophila* midgut, diet-dependent organ plasticity can arise through changes in both cellular number and enterocyte size [10]. Such multilevel responses illustrate why changes in organ or body dimensions should not automatically be interpreted as proportional changes in all structural components. Nutrient identity can additionally enter endocrine control directly. Dietary cholesterol influences insulin-associated growth and maturation in *Drosophila*, demonstrating that a specific nutrient can alter developmental progression rather than simply contribute generic energetic substrate [11].

These findings motivate a first distinction in the proposed model: resource acquisition, physiological availability, and allocation are separate stages. Acquisition describes what enters the organism; availability describes what can be metabolically or developmentally deployed; allocation describes where those resources are used. Final size integrates all three, but cannot uniquely identify any one of them.

Structural growth versus reserve storage

Even after resources become physiologically available, structural growth is not a homogeneous sink. Insect organs and dimensions exhibit differential relative growth, so changes in one morphological component need not predict proportional change in another [12]. Wing area, thoracic investment, abdominal volume, reproductive structures,

and overall linear dimensions may therefore respond differently to the same developmental environment. Treating "body size" as a single structural compartment risks concealing the architecture through which resources become adult phenotype.

A more consequential distinction separates structural growth from stored reserves. Under larval food restriction, male *D. melanogaster* can emerge smaller while retaining greater lipid stores and showing greater starvation resistance as adults [13]. This result directly rejects the assumption that a smaller adult must necessarily contain fewer usable reserves or represent uniformly poorer physiological condition. The direction of the association is context specific and should not be generalized into a claim that developmental restriction is beneficial. Its mechanistic importance is narrower: structural size and reserve storage can move in opposite directions.

Starvation resistance itself is also more complex than accumulation of one metabolite. Selection for starvation resistance in *Drosophila* is associated with coordinated developmental, behavioral, feeding, sleep, and metabolic changes [14]. Hence a resource budget cannot assign stress resistance to a single static reservoir. Stored fuels interact with expenditure rates, behavior, and developmental programming.

Developmental timing creates an additional constraint. Interorgan communication links nutritional and growth state with endocrine control of metamorphosis, thereby influencing when structural growth terminates [15]. Two larvae with similar accumulated resources may therefore achieve different adult structures if they differ in the timing of growth cessation or in the signaling thresholds governing maturation. In the proposed framework, final structural size is consequently determined not only by the amount allocated to tissue production but also by when allocation to structural growth is permitted to stop.

This separation has an important interpretive consequence. Adult mass or linear size cannot simultaneously stand as an unqualified proxy for resource acquisition, storage, and developmental condition. These dimensions should be measured independently whenever the objective is to infer allocation.

Flight machinery and mobility costs

Flight introduces a particularly important competing demand because locomotor capacity depends on morphology established during development but may affect energetic expenditure throughout adult life. Wing-polymorphic insects show that investment in dispersal morphology and reproduction can be coordinated through endocrine systems, with environmental cues contributing to alternative developmental trajectories [16]. Such systems provide direct precedent for developmentally organized allocation between mobility-related and reproductive phenotypes, although the specific hormonal mechanisms cannot be assumed to apply across all winged insects.

Movement strategy must also be distinguished from the mere presence of wings. Comparative work on butterflies indicates that dispersal and migration are associated with contrasting combinations of flight morphology and reproduction [17]. A short-distance disperser, a long-distance migrant, and a largely sedentary but fully winged insect therefore should not be assigned a common "flight cost." Realized movement regime determines which structural and energetic components of locomotion are likely to matter.

Nor does body size generate a universal monotonic locomotor penalty. Measurements of the mango stem borer *Batocera rufomaculata* do not support a simple expectation that increasing size necessarily produces progressively poorer mass-specific flight performance or a straightforward size-dependent cost [18]. This taxon-specific result does not show that flight costs are independent of size generally. Instead, it prevents the proposed model from encoding body size and flight expenditure with a universal positive or negative slope.

A complementary mechanistic hypothesis proposes that resources acquired during larval development may pass through sequential adult pools, potentially connecting flight expenditure and fecundity in herbivore–pollinator systems [19]. That proposal is useful because it makes temporal ordering explicit, but it remains hypothesis-level rather than an insect-wide demonstrated pathway. Accordingly, the present model distinguishes three quantities: developmental investment in flight machinery, resources consumed by realized adult movement, and the opportunity costs imposed on later reproduction or maintenance. They may interact, but they are not interchangeable.

Flight therefore contributes to body-size evolution and plasticity through more than a simple "large versus small" trade-off. A larger thorax may support locomotor machinery, larger wings may alter aerodynamic performance, and greater mass may simultaneously change power requirements. Which combination is favored depends on taxon, morphology, movement distance, reproductive schedule, and environment.

Reproductive investment

Reproduction imposes another major resource demand, but "reproductive investment" itself contains several separable processes. In *Drosophila*, nutritional regulation of egg production involves both the provision of substrates and nutrient-sensitive developmental signaling [20]. Reproductive output therefore cannot be represented adequately as a direct conversion of surplus calories into eggs. Protein, sterols, and other nutrients can differ in their physiological roles, while regulatory pathways determine whether available substrates are committed to ovarian activity.

Nutrient-responsive signaling also acts at the germline level. Insulin/IGF-related, TOR, GCN2, and associated pathways participate in the regulation of female germline stem-cell activity and oogenesis under changing nutritional conditions [21]. These mechanisms are best supported in *Drosophila* and should not be transferred uncritically across insect orders, but they establish a general analytical point: allocation to reproduction includes regulated commitment, not merely substrate availability.

Reproductive investment must additionally distinguish total output from investment per offspring. In the haplodiploid thrips *Pezothrips kellyanus*, mating status changes reproductive allocation, and egg size participates in sex-allocation patterns while reproductive output varies across the reproductive period [22]. These findings are species- and mating-system specific, yet they demonstrate why egg number alone cannot capture all reproductive expenditure. Larger per-offspring allocation, offspring sex, and lifetime fecundity may respond differently to the same maternal condition.

For the present model, reproduction is therefore separated into reproductive activation, per-offspring provisioning, and cumulative reproductive output. The first concerns whether resources and signaling permit reproductive activity; the second concerns the amount committed to individual offspring; the third integrates reproductive rate and duration. These distinctions matter because each may compete with structural development or adult maintenance at different times.

The resulting stage-specific interpretive problem is condensed in **Table 1**. The table is needed because the same phrase—"greater reproductive investment"—can describe biologically different states that imply different resource-budget consequences and different empirical tests.

Table 1. Reproductive investment cannot be represented by a single fecundity axis in an insect resource budget

Reproductive allocation			Whole-body budget	
Investment destination	**Biological context**	**Tracer or phenotype**	**Resource-allocation meaning**	**Carry-over boundary and test**
Nutrient-enabled reproductive activation	Adult female reproductive physiology	Nutrient-sensitive ovarian or germline activity	Resources may alter whether reproductive allocation is initiated, not only how much material reaches offspring. Evidence-supported distinction.	Mechanistic evidence is strongest in Drosophila; nutrient identity matters. Manipulate specific nutrients while separately measuring ovarian activation and somatic allocation
Substrate commitment to egg production	Egg-producing females	Conversion of dietary substrates into reproductive tissue and eggs	Reproduction competes for compositionally specific resources rather than a generic energy pool. Evidence-supported distinction.	Different nutrients may be substitutable only within limited physiological ranges. Quantify nutrient-specific depletion alongside egg production and adult condition
Per-offspring provisioning	Species in which egg size or composition varies	Egg size, egg composition, or other offspring-provisioning traits	Greater allocation to each offspring need not imply greater lifetime reproductive output. Evidence-supported distinction.	Egg size can also reflect offspring sex, mating system, maternal state, or developmental constraints. Measure offspring provisioning together with offspring number and maternal resource state
Cumulative reproductive output	Reproductively active adults across time	Fecundity rate, reproductive duration, lifetime egg production	Total reproductive expenditure integrates both allocation rate and duration. Proposed resource-budget decomposition.	Egg number alone does not reveal per-offspring cost or nutrient composition. Resolve reproductive rate, duration, and provisioning as separate variables
Development-to-reproduction carry-over	Holometabolous insects with distinct larval	Adult reproduction associated with	Juvenile acquisition can alter the resources available for later reproduction without	Degree of capital versus income breeding differs among taxa and environments. Track resource acquisition and labeled

	and adult resource environments	resources acquired or stored before eclosion	changing adult intake. Proposed cross-stage synthesis.	reserves across metamorphosis into reproductive output

stress-resistance investment

Stress resistance represents a further allocation demand, but it cannot be collapsed into one generic "stress-tolerance" compartment. Oxygen availability illustrates the problem. Functional hypoxia occurs when oxygen supply becomes insufficient relative to tissue demand, and its effects can include reduced activity, altered feeding, constrained growth, or developmental responses [23]. The relevant threshold depends on temperature, developmental stage, tissue demand, activity, and respiratory architecture. Oxygen therefore enters the proposed model primarily as a conditional physiological constraint on resource use rather than as a fixed energetic sink.

Direct tests also caution against elevating one oxygen-based mechanism into a general explanation of insect body size. Experimental manipulation of temperature and oxygen partial pressure in larvae of the noctuid *Orthosia gothica* provided only partial support for the oxygen-dependent induction of moulting hypothesis [24]. This result is important precisely because it is not a clean confirmation. It indicates that oxygen-dependent processes can participate in developmental size regulation without establishing oxygen as the universal determinant of moulting or final body size.

Thermal resistance shows similar conditionality. A broad meta-analysis spanning more than one hundred insect species found acclimation-related plasticity in thermal limits to be widespread but weak on average, with substantial heterogeneity among taxa, life stages, methodological designs, and geographical coverage [25]. Stress resistance therefore should not be represented as a fully compensatory trait that can expand indefinitely when environmental temperature changes. Limits to plasticity may alter how much resource can profitably be diverted toward resistance instead of growth, reproduction, or maintenance.

Immune defence introduces another form of stress-related expenditure. Nutritional ecology studies show that infection, immune activation, nutrient composition, and feeding responses interact in ways that can produce different—and sometimes opposing—outcomes across host–pathogen combinations [26]. Greater nutrient availability does not automatically translate into stronger defence, because pathogens may also exploit host resources and because immune components differ in their nutritional requirements.

Accordingly, the proposed resource budget treats stress resistance as a family of context-dependent demands rather than a single reserve. Thermal tolerance, hypoxia resistance, starvation resistance, and immune defence may share some substrates or regulatory pathways, but they need not respond in parallel. Their opportunity costs should therefore be inferred only when competing allocation has been measured directly or when a specific mechanism supports the connection. This restriction prevents survival under one challenge from being interpreted automatically as generalized robustness or as evidence that reduced structural growth was adaptively redirected toward stress resistance.

maintenance and repair

Maintenance competes with reproduction and other demands most clearly when a specific limiting resource can be followed mechanistically. In adult female *Drosophila melanogaster*, the lifespan response to dietary protein-to-carbohydrate balance can depend strongly on cholesterol availability because reproduction draws sterols into egg production. Supplementing cholesterol changes the apparent reproduction–lifespan trade-off, showing that an observed macronutrient effect can arise through depletion of a limiting micronutrient rather than through a direct cost of protein itself [27]. Maintenance therefore cannot be represented solely as expenditure of generic energy.

The survival consequences of reduced reproductive investment are likewise conditional. Tests of dietary restriction in *D. melanogaster* across infection and injury contexts show that nutritional regimes associated with longer life under benign conditions do not confer identical benefits under challenge; low-protein diets can become detrimental during infection [28]. Longevity is consequently not an invariant measure of successful maintenance, and a diet that reallocates resources away from reproduction cannot automatically be characterized as beneficial.

Field evidence provides another boundary. In the biparental beetle *Lethrus apterus*, immune measures and reproductive investment vary with sex, body size, season and parasite context, rather than expressing a fixed reproduction–immunity trade-off [29]. These observations do not establish causal allocation among the measured traits, but they demonstrate why laboratory trade-offs should not be transferred to natural populations without accounting for state and season.

The proposed model therefore treats maintenance and repair as a heterogeneous demand encompassing resource preservation, immune function and processes sustaining adult performance, while avoiding the unsupported assumption that every molecular repair pathway draws from one measurable pool. The key triage problem is interpretive: a body-size difference may coexist with enhanced reserves, reproduction, defence or longevity, but none of those outcomes alone identifies where resources were diverted. **Figure 1** makes that discordance explicit before the integrated budget is constructed.

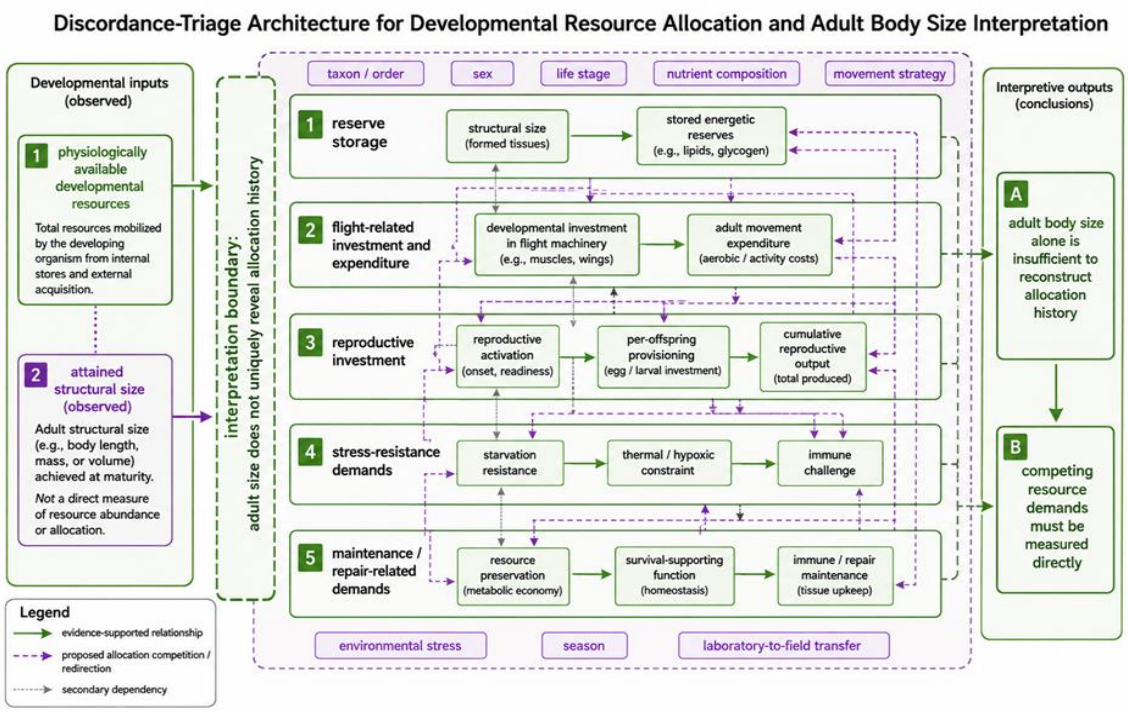


Figure 1. Discordant adult outcomes that prevent body size from identifying the destination of developmental resources

Integrated resource-budget model of body size

We propose that insect body size emerges from a resource budget with three analytically distinct operations: acquisition and physiological filtering, allocation among competing demands, and developmental termination. The available budget is compositionally heterogeneous; allocation sinks are therefore not assumed to exchange at a constant energetic rate. Structural growth, reserve storage, flight machinery, reproduction, stress resistance and maintenance may compete directly for some substrates while influencing one another indirectly through endocrine signaling, developmental timing or altered expenditure.

Allocation can also cross metamorphic boundaries. Experimental evolution under chronic larval malnutrition in *D. melanogaster* produced genomic and phenotypic responses associated with consequences for adult starvation resistance [30]. This supports the narrower premise that juvenile resource environments can generate adult opportunity costs; it does not establish that natural populations universally optimize the same trade-off. The model therefore allows developmental allocation history to modify adult state without treating every carry-over effect as adaptive.

Attained size is additionally an input to later ecology rather than merely the terminal output of development. Body size alters thermal coupling between insects and plant surfaces, so differently sized individuals can experience physical environments differently even at the same site [31]. This creates a reciprocal structure: environment influences development and allocation, while attained morphology changes subsequent exposure and performance conditions.

A critical implication is that apparently similar adult sizes may conceal different developmental histories. One individual may achieve a given size by rapid structural growth with low reserves, another by prolonged development with greater storage, and another under substantial investment in locomotor or defensive capacity. These alternatives are not interchangeable model states. The same adult size therefore does not imply the same

allocation history, physiological resilience or future reproductive capacity, and discrimination among them requires measurements targeted to the hypothesized competing demand rather than morphology alone.

The model consequently rejects a single body-size optimum. It instead proposes conditional optima generated where the marginal benefits of additional structure are balanced against resource composition, developmental time, alternative allocation demands and the ecological consequences of size. These optima are hypotheses, not fitted estimates. **Table 2** converts the model into qualitative predictions that can be falsified without inventing thresholds.

Table 2. Qualitative tests that distinguish competing explanations within the proposed insect resource-budget model

Resource-budget tension	Diagnostic pattern	Model implication	Boundary experiment
Structure–reserve decoupling	Structural dimensions and stored fuels change independently	Adult size is not a sufficient proxy for energetic state. Evidence-grounded prediction.	Sex, stage and diet composition. Measure structural size and reserves simultaneously across controlled diets
Flight-allocation conflict	Investment in flight phenotype or realized movement covaries with reproductive or storage traits	Mobility demand may alter allocation opportunity. Proposed model test.	Movement strategy and taxon. Separate developmental flight morphology from adult flight expenditure
Reproduction–maintenance competition	Reproductive output changes with survival or maintenance-related traits under limitation	Shared limiting resources may generate opportunity costs. Evidence-grounded prediction.	Nutrient identity and challenge environment. Manipulate the candidate limiting nutrient while measuring both outcomes
Cross-stage carry-over	Juvenile resource treatment changes adult allocation phenotype after controlling adult diet	Developmental history contributes to the adult budget. Proposed model test.	Metamorphic strategy and adult feeding. Cross larval and adult nutritional environments factorially
Size–environment feedback	Individuals differing in size experience different operative conditions	Size changes later ecological exposure. Evidence-grounded prediction.	Microhabitat and physical setting. Pair morphology with individual-scale microclimate measurements

Predicted size optima across ecological contexts

Temperature-sensitive development makes any predicted size optimum environment dependent. Developmental reaction norms can shift phenology and size-related outcomes, yet translating laboratory temperature responses to field conditions remains difficult because insects experience fluctuating microclimates, behavioral thermoregulation and seasonally changing resources [32]. The proposed model therefore predicts not a temperature-defined size, but a change in the relative value of structural growth versus competing demands as thermal opportunity and developmental time change.

Reproductive context can shift the balance independently. Temperature affects multiple behavioral components of insect reproduction, including interactions involved in mate location, signaling and mating [33]. A size that performs well under one reproductive thermal environment may therefore lose advantage when behavioral opportunity, movement cost or reproductive timing changes. This is a conditional prediction, not evidence for a measured optimum.

More generally, size optima should differ among migrants and local dispersers, between sexes with different nutritional reaction norms, across habitats with different thermal coupling, and between environments dominated by starvation, immune or reproductive demands. Crucially, the model also predicts cases in which greater resource acquisition does not produce larger adults because additional resources are stored, committed to reproduction or used to sustain other functions. Testing these predictions requires joint measurement of the competing sinks rather than retrospective explanation from adult size alone.

Results and Discussion

The proposed framework changes the inferential status of insect body size. Size remains an informative phenotype, but it is not a universal currency for developmental quality. Direct evidence that structural size can diverge from lipid storage [13], comparative evidence that migration and dispersal associate differently with morphology and reproduction [17], and nutrient-specific reproduction–lifespan effects [27] all show why allocation cannot be reconstructed from size alone. Experimental evolution further indicates that developmental resource regimes can have adult consequences [30], but these independent premises do not amount to validation of the integrated model.

Taxonomic coverage is a major limitation. Mechanistic endocrine and nutritional evidence is disproportionately derived from *Drosophila*, whereas bees, butterflies, beetles, thrips and other systems contribute narrower tests of particular links. Meta-analytic thermal evidence also remains heterogeneous across stages and taxa [25]. The framework should therefore be treated as a set of separable hypotheses whose topology can differ among insect lineages, not as a universal allocation diagram.

Competing explanations must remain viable. Oxygen-based growth mechanisms receive conditional rather than complete support [24]; body size does not impose one monotonic flight cost [18]; nutritional effects on immunity vary among challenges [26]; and dietary restriction changes meaning under infection [28]. A useful validation program would manipulate resource quantity and composition factorially, measure growth rate and developmental duration, quantify structure and reserves separately, and record at least one competing adult demand. Replication across sexes, life stages and orders would test transferability. Field validation would then be needed because attained size itself modifies microenvironmental coupling [31] and laboratory developmental responses do not automatically predict field phenology [32].

The strongest use of the model is therefore diagnostic rather than predictive: it identifies what must be measured before a body-size difference can be assigned a resource-allocation explanation. Its predictions become stronger only when the relevant resource, allocation sink, regulatory mechanism and ecological boundary are specified in advance.

Conclusion

Insect body size is better interpreted as one product of a conditional developmental resource budget than as a direct index of resource abundance or organismal quality. Structural growth can diverge from reserve storage, locomotor and reproductive demands are multidimensional, and stress resistance and maintenance vary with physiological and environmental context. The proposed model integrates these distinctions while preserving differences between direct competition, regulatory mediation, developmental timing and ecological feedback. It does not specify a universal optimum or validated allocation equation. Its practical value is to make body-size explanations testable: claims about why an insect became larger or smaller should identify the competing resource demand, measure the relevant allocation components, and demonstrate the boundary conditions under which the inferred trade-off occurs.

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