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Egg Production, Mating Effort, Somatic Maintenance, and Future Opportunity Compete Dynamically During Insect Reproduction Under Uncertainty

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ABSTRACT

Reproduction in insects is commonly interpreted through pairwise trade-offs, particularly fecundity versus survival or current versus future reproduction. Such formulations are useful but can obscure how reproductive decisions are assembled from several biologically distinct demands whose relative costs and benefits change through time. Egg production requires nutrient-specific and physiological investment; mate acquisition and mating can consume time, expose individuals to thermal or pathogenic constraints, generate sexual conflict, and alter resource acquisition; somatic maintenance can impose delayed costs that are not visible in short-term reproductive measures; and future reproductive opportunity depends on age, condition, reproductive history, partner state, and environmental circumstances rather than chronological age alone. This article develops a proposed dynamic allocation theory that keeps these demands analytically separate while allowing them to interact. The model treats resource acquisition, physiological state, reproductive state, social opportunity, environmental information, and expected future reproductive value as changing inputs rather than fixed background conditions. Evidence from flies, crickets, beetles, bed bugs, dragonflies, and other insect systems shows that apparent trade-offs may be strengthened, masked, reversed, or partly uncoupled by nutrient identity, mating state, immune activation, thermal exposure, sex, developmental history, and partner characteristics. Accordingly, allocation is represented here not as movement along one universal reproduction–maintenance axis but as a conditional reweighting among competing reproductive and somatic demands. The theory generates stage- and sex-specific predictions while explicitly retaining alternative explanations, including senescence, resource acquisition effects, reproductive restraint, direct pathology, and methodological non-replication. Its principal value is therefore organizational and hypothesis-generating rather than claims of universal mechanism or validated predictive performance.

Keywords: Reproductive allocation, Life-history trade-offs, Residual reproductive value, Mating effort, Somatic maintenance, Environmental uncertainty

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Introduction

Life-history theory often represents reproduction as a competition between current investment and survival or future fecundity. That abstraction is valuable, but it becomes difficult to interpret when trait covariance is treated as allocation itself. Individuals that acquire more resources may simultaneously invest more in reproduction and maintenance, producing positive covariance even when physiological trade-offs remain present; conversely,

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negative covariance does not by itself identify the causal currency being allocated [1]. For insect reproduction, the inferential problem is especially acute because reproductive expenditure includes nutritionally distinct egg components, courtship and mate-search behavior, copulation, parental or postmating costs, and physiological consequences that may emerge only after the reproductive episode.

The terminal-investment literature illustrates why a fixed current-versus-future rule is insufficient. Across experimental studies, immune challenge does not produce a uniform increase in reproductive investment, and response magnitude varies with biological context [2]. Dynamic-threshold theory consequently predicts that increased current investment should occur only when a threat shifts expected future reproductive value beyond a state-dependent threshold [3]. This principle is useful, but it does not by itself specify which component of reproduction should increase, which component of somatic maintenance should be sacrificed, or how resource acquisition changes the location of that threshold.

Recent insect work makes those missing dimensions explicit. A dynamic state-variable model for burying beetles predicts strong age-dependent changes in optimal allocation regions while retaining effects of energetic state and environmental conditions [4]. In crickets, food and mate availability alter apparent allocation relationships, demonstrating that resource acquisition and reproductive opportunity can modify the phenotype from which a trade-off is inferred [5]. The central argument developed here is therefore that egg production, mating effort, somatic maintenance, and future reproductive opportunity should be represented as separate but interacting allocation demands. The resulting framework is proposed rather than empirically validated as a unified mechanism. Its purpose is to explain why the same broad reproductive challenge can yield increased investment, restraint, maintenance, or deferred reproduction under different combinations of state and uncertainty.

Materials and Methods

Dynamic allocation variables

This article uses a theory-building synthesis in which variables were retained only when the insect literature permits them to be distinguished biologically or experimentally. The first distinction is between total resource abundance and resource composition. Zinc limitation in *Drosophila melanogaster* can suppress reproduction while leaving maternal lifespan comparatively preserved, showing that a specific micronutrient can constrain reproductive output without acting as a simple proxy for total energetic scarcity [6]. Resource state is therefore treated as a vector of nutritionally and physiologically relevant components rather than a single scalar budget.

The second distinction is between resource availability and resource acquisition behavior. In *D. melanogaster*, mating changes dietary preference through sex-specific physiological and neural processes, meaning that reproductive state can alter what resources are acquired rather than merely determining how a fixed pool is spent [7]. This creates a reciprocal relationship: acquisition constrains allocation, but allocation state can also alter subsequent acquisition.

Nutritional studies further show why fecundity and maintenance should not be forced onto one obligatory axis. Micronutrient limitation, methionine restriction, and sterol availability can differentially affect reproductive output, egg viability, and lifespan, with some manipulations partly uncoupling reproductive decline from longevity [6, 8, 9]. Accordingly, the model distinguishes egg number, egg quality or viability, and somatic persistence rather than treating “reproduction” as a single outcome.

Sex and developmental history are additional state variables. In black soldier flies, mating reduced male longevity but increased female longevity, demonstrating that the direction of a mating-associated survival effect can differ between sexes within the same species [10]. Developmental diet can also alter adult lifespan through later physiological consequences, so adult allocation cannot always be interpreted independently of earlier nutritional history [11]. Finally, experiments in burying beetles show that resource acquisition and maintenance during a reproductive episode can mask detectable costs across successive breeding attempts [12]. The conceptual method used here therefore separates six classes of inputs: acquired resources, physiological condition, sex and developmental history, current reproductive state, social opportunity, and environmental information. None is assumed to represent fitness or reproductive value directly.

Results and Discussion

Egg production is not treated here as an indivisible energetic expenditure. It comprises sequential processes—oogenesis, vitellogenesis, provisioning, maturation, oviposition, and the production of viable offspring—that can interact differently with other physiological systems. In female *D. melanogaster*, experiments arresting oogenesis at different stages indicate that progression through vitellogenesis contributes to postmating suppression of antibacterial defense, while residual immune changes remain even when yolk-related processes are disrupted [13]. Thus, egg provisioning can contribute to an immune cost without accounting for the entire postmating physiological state.

The reverse direction is also biologically important. Infection can impair reproduction, while reproductive activity can worsen aspects of infection outcome, creating reciprocal rather than strictly one-way costs [14]. Such reciprocity cautions against describing every decline in fecundity during infection as deliberate allocation away from reproduction. Direct pathology, inflammatory damage, altered feeding, and reproductive physiology may coexist.

The shape of the cost function may also be nonlinear. In *Tribolium castaneum*, graded dysregulation of Toll signaling altered resistance together with reproductive and somatic traits, with increasing immune activation producing disproportionate fitness-related costs rather than a simple linear exchange [15]. This result supports treating immune defense as a state-dependent constraint but does not establish a universal immune–fecundity curve under natural infection.

Genetic context adds another layer of contingency. Natural variation in the antimicrobial peptide Metchnikowin can alter immune and life-history phenotypes in ways that depend on sex, pathogen, and allele [16]. The proposed theory therefore represents egg-production cost as a conditional surface rather than a fixed debit: nutrient identity, immune state, genetic background, and the particular stage of egg production can each alter both the magnitude and biological meaning of reduced reproductive output.

Mate acquisition and mating effort

Mating effort creates allocation problems that are partly independent of egg production. In male *Gryllus bimaculatus*, severe experimental heat reduced reproductive success while courtship effort increased and measured lifespan did not decline [17]. The pattern shows that reproductive effort and reproductive return can diverge under thermal stress; it does not demonstrate that males consciously sacrifice soma or that unchanged lifespan means somatic physiology was unaffected.

Field observations in the dragonfly *Celithemis elisa* reveal a different solution to high temperature: males spend less time mating and more time thermoregulating as thermal conditions become more demanding [18]. Here the relevant currency is partly behavioral time rather than stored nutrient alone. The comparison with crickets is important because superficially similar thermal challenge can be associated with increased mating effort in one system and reduced mating activity in another.

Disease can modify still different components. Fungal infection in male house flies progressively reduces sexual motivation, attractiveness or female acceptance, and sperm performance [19]. These changes demonstrate that "mating effort" cannot be represented only as courtship intensity. Mate acquisition, persistence, mating success, and gamete performance may fail at different rates and for different proximate reasons.

Costs can also arise from the mating interaction itself. In bed bugs, frequent traumatic insemination imposes substantial female reproductive and longevity costs, while female avoidance and male mate choice alter realized exposure to those costs [20]. In *D. melanogaster*, two matings cause more copulatory wounding than one, establishing a physical consequence of repeated mating even though the study does not by itself demonstrate a corresponding lifetime-fitness reduction [21]. Mating duration can additionally generate sexual conflict: longer copulation may improve components of male reproductive success while reducing female fecundity, so male and female optima need not coincide [22].

Social information modifies these costs through time. In bushcrickets, perceived competition alters reproductive allocation in an age-dependent manner, with younger and older males responding differently to acoustic cues from rivals [23]. The proposed model therefore treats mate availability and competition as uncertain opportunity signals rather than fixed environmental constants. Mating effort can rise, fall, or be redirected depending on expected return, condition, age, thermal constraints, disease, and the costs imposed on either sex.

Somatic maintenance

Somatic maintenance differs from reproduction not only in function but also in temporal observability. Some maintenance costs emerge long after the reproductive or physiological event that created them. In *D. melanogaster*, an early-adult surge in protein translation contributes to later proteostatic decline and aging through juvenile-hormone and germline-associated signaling [24]. This establishes that early physiological activity can generate delayed somatic consequences, although it does not prove that the entire effect represents a direct cost of reproductive effort. A theory based only on simultaneous fecundity and lifespan measurements can therefore miss temporally displaced maintenance costs.

Mechanistic caution is equally important. A reported single-gene explanation for a male fecundity–lifespan trade-off in *Drosophila* was not reproduced in a later CRISPR-based re-test [25]. The null result does not invalidate life-history trade-offs; it demonstrates that a specific proposed mechanism may fail replication and that gene-level explanations should not be elevated to universal allocation rules without independent validation.

Environmental challenge also exposes the danger of treating "stress" as one maintenance demand. In *Gryllus texensis*, predator cues and the physical performance of repeated fight-or-flight behavior had different, even opposing, reproductive consequences [26]. A cue indicating danger, the physiological interpretation of that cue, and the energetic or mechanical act of responding to danger are therefore analytically distinct. Under the proposed theory, somatic maintenance includes immediate defense, repair, proteostasis, body-condition preservation, and delayed functional integrity, but no single measurement is assumed to capture all of them.

Because these distinctions are difficult to compare in prose alone, **Table 1** organizes the somatic-maintenance patterns by what can actually be observed, what they permit us to infer, and which experiment would discriminate a true allocation shift from pathology, acquisition effects, or delayed physiological cost.

Table 1. Distinguishing somatic-maintenance signals from apparent reproductive trade-offs in insect allocation studies

Maintenance pattern	Biological context	Observable allocation evidence	Permitted reading and competing explanation	Discriminator and evidence state
Temporal displacement and acquisition masking				
Temporally displaced maintenance cost	Early-adult physiological activity followed by later decline	Later proteostatic or survival deterioration after an earlier physiological state	Current reproduction and later soma need not covary synchronously Developmental or aging programs may produce the same timing pattern	Measure reproductive activity and somatic function repeatedly across adulthood Evidence-supported distinction
Maintenance preserved despite reduced reproduction	Nutrient-specific limitation or dietary manipulation	Reproductive output falls while lifespan or selected maintenance outcomes remain comparatively preserved	Reproductive limitation need not imply proportional somatic deterioration Different tissues may compete for different nutrients	Manipulate nutrient identity while measuring reproduction, condition, and survival separately Evidence-supported distinction
Acquisition-masked maintenance cost	Resource-rich reproductive episode	High reproductive output co-occurs with maintained condition	Absence of a negative phenotypic correlation does not exclude allocation cost High-resource individuals may simply acquire more	Standardize or model acquisition before inferring allocation Evidence-supported distinction
Defense, threat-information, and enacted-response demand				
Defense-associated maintenance demand	Infection or immune activation	Increased defense accompanies reduced reproductive or somatic performance	Defense can constrain reproduction under some physiological states Pathology or immune dysregulation may cause the loss directly	Separate natural infection, immune activation, pathology, and resource intake experimentally Evidence-supported distinction
Threat-information effect	Predator or environmental cue without equivalent physical response	Reproduction changes after perceived risk	Information can alter reproductive behavior before large physical expenditure occurs	Cross cue-only, response-only, and combined treatments

			Fear-like or endocrine effects may mediate the response	Evidence-supported distinction
Enacted-response cost	Repeated escape, thermoregulation, or other defensive behavior	Reproductive change follows physical response rather than cue alone	Behavioral expenditure should be modeled separately from environmental information Activity may alter feeding or exposure simultaneously	Quantify activity, acquisition, and reproductive output in the same individuals **Proposed allocation classification**
Molecular evidence boundary				
Unreplicated molecular trade-off	Candidate gene linked to fecundity and longevity	Later targeted replication fails to reproduce the reported relation	Mechanistic confidence should remain provisional Allelic design, background, or incomplete loss of function may matter	Independent alleles, backgrounds, and preregistered replication Evidence-supported validation boundary

Residual reproductive value

Residual reproductive value is often approximated by age, but chronological age is only an imperfect indicator of future reproductive opportunity. In male *Teleogryllus oceanicus*, older individuals increased some reproductive traits, including spermatophore investment, whereas immune challenge produced little consistent terminal-investment response across measured components [27]. The important result is not that age universally increases current reproduction, but that reproductive traits can change at different rates even within the same individual and experimental context.

Future opportunity may also depend on the state of social partners. In *Nicrophorus orbicollis*, both an individual's age and its partner's age influence biparental care and reproductive outcome, and some age combinations perform differently from what either parent's age would predict alone [28]. For biparental species, residual reproductive value therefore cannot be represented exclusively as an intrinsic property of one organism. Partner quality, compatibility, and the probability of obtaining future mates can change the expected return from present investment.

Experimental terminal investment provides only conditional support for age-based predictions. Older challenged male burying beetles can increase current reproductive investment while gaining less body mass, whereas younger challenged males do not necessarily show the same response [29]. Such patterns are compatible with a decline in future opportunity, but age may also covary with experience, condition, and accumulated reproductive history.

Late-life reproduction further requires explicit alternative explanations. In female *Tenebrio molitor*, age-related reproductive change has been evaluated against terminal investment, reproductive restraint, and senescence rather than treated as evidence for one mechanism by default [30]. Pathogenic threat in the same broader system can reduce rather than increase fecundity under some age conditions, supporting reproductive restraint instead of obligatory terminal investment [31].

The proposed theory therefore defines residual reproductive value as a state-dependent expectation of future reproductive opportunity, not as age itself. Age can contribute information about declining survival prospects, but condition, prior reproductive expenditure, partner state, disease, seasonal opportunity, and environmental predictability may shift the expected value of conserving resources for later reproduction. This definition deliberately remains conceptual: most available experiments manipulate proxies for future opportunity rather than directly measuring an insect's complete expected lifetime reproductive value.

Environmental uncertainty

Environmental uncertainty enters reproduction as information, not simply as damage. A simulated heatwave altered relative reproductive and somatic investment in female *Gryllus lineaticeps*, whereas herbicide exposure in the same experimental framework did not produce the same allocation pattern [32]. This stressor specificity argues against a generic “adversity” variable. Temperature, pathogens, predators, mate availability, and seasonal signals differ in predictability, immediacy, physiological cost, and what they imply about future opportunity.

The distinction between information and response is equally important. Predator cues can suppress egg laying while repeated escape behavior can shift reproduction differently [26]. Thermal evidence also shows that exposure need not map onto a single response: male crickets may maintain or increase courtship under severe heat while reproductive success falls [17], whereas male dragonflies reduce mating activity as thermoregulatory demands rise [18]. Social cues are similarly filtered through age, because competitive acoustic information changes

reproductive investment differently across the adult lifespan [23]. Pathogenic threat can even favor restraint rather than increased current reproduction [31]. The proposed theory therefore treats uncertainty as state-dependent updating: a cue modifies allocation only through its interaction with condition, sex, reproductive history, expected persistence of the disturbance, and the likely availability of future reproductive opportunities.

Deferred reproduction provides an important boundary case. During *Drosophila* diapause, reproductive arrest is accompanied by preservation of germline stem-cell capacity, demonstrating that reduced immediate reproduction can coexist with maintenance of later reproductive potential [33]. This does not imply anticipatory cognition or prove adaptive optimization in every diapause system. It shows that preserving future reproductive machinery can be biologically distinct from both current egg production and general somatic survival.

Because uncertainty acts through several non-equivalent channels, the article's central environmental logic is compressed in **Figure 1** rather than represented as a single stress-response arrow.

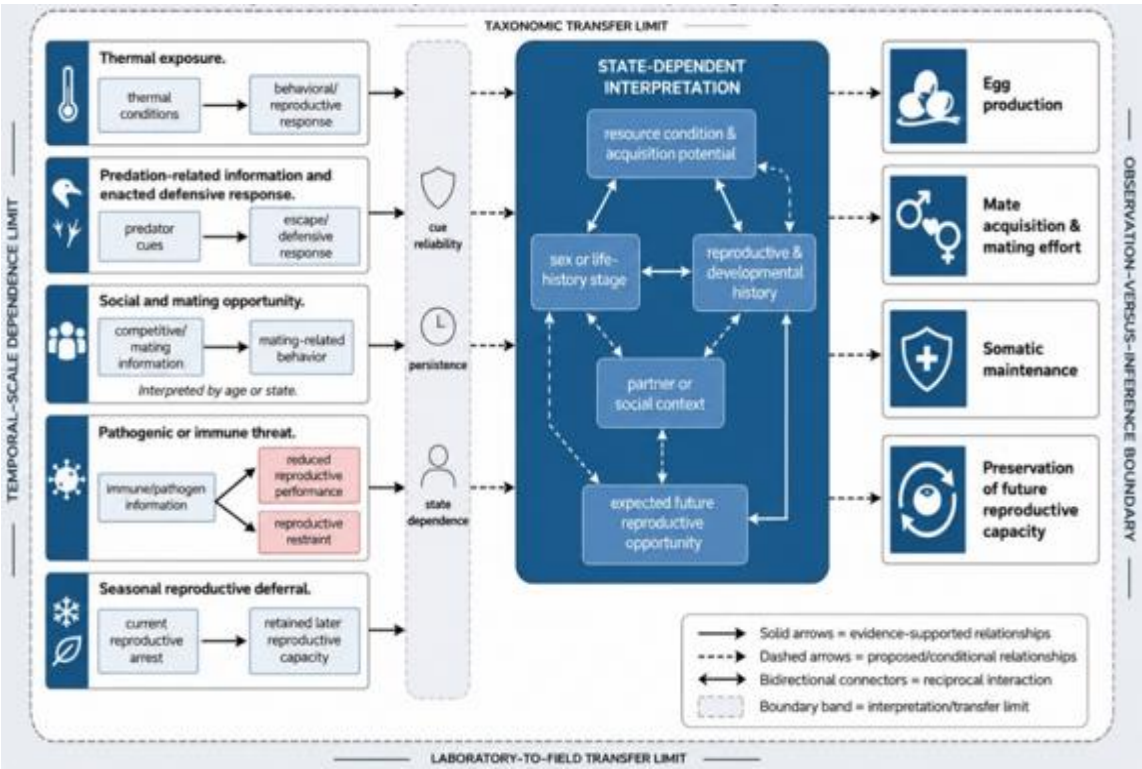


Figure 1. Environmental signals alter reproductive allocation only after state-dependent interpretation across competing reproductive demands

Dynamic allocation solutions

The evidence does not support one optimal response to deteriorating conditions. The proposed theory instead defines an allocation solution as a temporary state in which the relative priority of the four focal demands changes. Resource acquisition can move an individual between such states without any intrinsic change in allocation rule; burying-beetle experiments show that acquisition and maintenance can mask detectable costs across reproductive attempts [12]. Mating can itself change acquisition behavior [7], making the system recursively coupled rather than a one-way division of a fixed budget.

Three consequences follow. First, increased current reproduction is only one possible solution. Older or experienced individuals may increase current investment under particular threats [29], but pathogenic threat can instead be associated with reproductive restraint [31]. Second, maintenance can be buffered while reproduction falls when a limiting nutrient constrains reproductive physiology more strongly than measured survival [6]. Third, reproductive deferral can preserve future reproductive machinery, as illustrated by diapause-associated germline maintenance [33]. These alternatives are not claimed to share one proximate mechanism.

The proposed model therefore distinguishes allocation states by the combination of current reproductive return, maintenance requirement, acquisition potential, and expected future opportunity. **Table 2** is needed to separate

these theoretically distinct solutions and, crucially, to specify observations that could falsify an allocation interpretation rather than merely redescribe a phenotype.

Table 2. Decision matrix for distinguishing dynamic reproductive-allocation solutions under changing current and future opportunity

Current-output escalation versus restraint		
Dynamic comparison dimension	**Current-output escalation**	**Reproductive restraint**
State signature	Future opportunity falls while current reproduction remains feasible	Current threat makes immediate reproduction disproportionately costly
Dominant demand or reweighting	Egg or mating investment gains priority	Maintenance or retained capacity gains priority
Compatible observable pattern	Increased reproductive component despite threat or age	Fecundity or mating effort declines without assuming irreversible failure
Boundary and discriminating test	Senescence or condition differences may mimic age effects Manipulate future-opportunity cues independently of condition Proposed synthesis	Pathology can directly suppress reproduction Separate reversible allocation from physiological incapacity Proposed synthesis
Acquisition compensation versus maintenance buffering		
Dynamic comparison dimension	**Acquisition compensation**	**Maintenance buffering**
State signature	Greater intake obscures underlying allocation competition	A reproductive substrate becomes limiting before measured somatic persistence
Dominant demand or reweighting	Acquisition expands the usable resource pool	Somatic function is comparatively preserved
Compatible observable pattern	High reproduction and maintained soma coexist	Reproduction falls more strongly than lifespan or condition
Boundary and discriminating test	Positive covariance does not demonstrate absence of trade-off Measure acquisition and allocation simultaneously Evidence-grounded proposed category	Different maintenance traits may remain unmeasured Manipulate nutrient identity and assay multiple somatic functions Evidence-grounded proposed category
Mating reorientation versus future-capacity preservation		
Dynamic comparison dimension	**Mating-effort reorientation**	**Future-capacity preservation**
State signature	Opportunity or environmental cost changes behavioral return	Current reproduction is suspended while later reproductive machinery remains functional
Dominant demand or reweighting	Time and effort move among courtship, mating, and protective behavior	Future opportunity receives greater weight
Compatible observable pattern	Mating effort increases, decreases, or changes form with context	Reproductive arrest with retained germline potential
Boundary and discriminating test	Effort and reproductive success are not interchangeable Measure behavior, mating success, gamete performance, and survival separately Proposed synthesis	Dormancy physiology is not evidence of conscious forecasting Compare recovery and later reproduction after controlled deferral Evidence-grounded proposed category

Stage- and sex-specific predictions

The theory predicts differences in allocation surfaces rather than one directional sex effect. Mating can change resource choice differently in males and females [7], and mating-associated longevity can reverse direction between sexes within a species [10]. Where mating imposes sexually asymmetric injury or conflict, the same copulation may therefore increase expected return for one sex while increasing maintenance or future costs for the other [20]. A valid test must measure sex-specific reproductive components rather than infer a shared optimum.

Age predictions are likewise component specific. Competitive social information changes male investment differently across life stages [23], while older crickets can increase spermatophore investment without uniformly increasing every reproductive trait [27]. In biparental beetles, partner age also modifies care and reproductive outcome [28]. The proposed prediction is thus that chronological age will shift different components at different thresholds, with partner state becoming an additional axis in social or parental systems.

Developmental history should further modify adult allocation under otherwise similar current conditions because early diet can alter later physiological state [11]. Finally, environmental effects should depend on cue identity and buffering capacity: severe heat, predator information, pathogenic threat, and seasonal reproductive arrest need not generate responses of the same direction. These predictions require longitudinal, multicomponent measurements before they can be considered prospectively validated.

The proposed theory replaces a single reproduction–survival axis with a conditional competition among egg production, mating effort, somatic maintenance, and future opportunity. Its central interpretive rule is that allocation cannot be diagnosed from trait covariance without considering acquisition [1]. Nutrient-specific effects, delayed maintenance costs, mating-state changes in feeding, sexual conflict, and environmental information all demonstrate why the relevant currencies and time scales can differ among reproductive components.

The strongest evidence against a fixed rule comes from heterogeneity itself. Age-associated terminal investment, late-life alternatives, and pathogenic-threat restraint occur across closely related life-history questions [27, 30, 31]. These patterns make residual reproductive value useful as a theoretical expectation but warn against equating it with age. Similarly, the failure to reproduce a specific gene-level fecundity–lifespan effect shows that even plausible mechanisms require independent validation [25].

Taxonomic transfer is another critical boundary. Much of the mechanistic evidence comes from *Drosophila*, whereas parental-care, terminal-investment, thermal, and traumatic-mating evidence comes from beetles, crickets, dragonflies, bed bugs, and other systems with different reproductive ecologies. The framework therefore predicts shared decision dimensions more cautiously than shared mechanisms. A resource or environmental cue should be expected to influence allocation only when it changes a biologically relevant constraint or opportunity in the focal species. This distinction is particularly important for insects with capital versus income breeding, prolonged parental care versus no care, repeated versus brief mating opportunities, or reproductive dormancy. Cross-order validation should consequently test whether the same conceptual state variables improve explanation while allowing the proximate mechanisms and direction of trait change to differ. Failure of a predicted direction in one taxon would not automatically falsify the full framework, but repeated failure of the proposed state variables to improve discrimination among competing explanations would.

The framework therefore makes deliberately limited claims. It does not assert that every observed reproductive decline is strategic, that all insects solve an optimization problem through the same mechanism, or that laboratory responses transfer directly to field populations. Resource acquisition, pathology, senescence, developmental constraint, sexual conflict, and measurement timing can all generate patterns resembling allocation. The proposed architecture is useful only if experiments discriminate among these alternatives.

A decisive test would follow individuals across reproductive episodes while measuring acquisition, egg production or male reproductive output, mating effort, multiple somatic-maintenance traits, and subsequent reproductive opportunity. Experimental manipulations should alter cue reliability, resource composition, partner opportunity, or mortality risk independently wherever possible. Such designs could determine whether the proposed allocation states predict transitions better than simpler pairwise trade-off models without assuming in advance that any transition is adaptive.

Conclusion

Insect reproduction cannot be represented reliably as a fixed transfer of resources between fecundity and survival. Egg production, mating effort, somatic maintenance, and future reproductive opportunity are biologically separable demands whose apparent relationships change with acquisition, nutrient identity, sex, age, reproductive history, partner state, and environmental information. The proposed dynamic allocation theory organizes these dimensions without treating observed covariance as mechanism or chronological age as future reproductive value. Its principal prediction is conditionality: increased current investment, restraint, maintenance buffering, altered mating effort, acquisition compensation, and reproductive deferral should occur in different state combinations rather than as universal responses. Testing that proposition requires longitudinal, acquisition-aware and sex- or

stage-resolved experiments that distinguish allocation from pathology, senescence, constraint, and measurement artefact.

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