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# Age, Condition, Environmental Risk, and Future Opportunity Continuously Reshape Reproductive Value in Insect Life-History Decisions

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**ABSTRACT**

Life-history decisions are often interpreted as responses to age, energetic condition, or mortality risk considered separately. Such treatment is problematic because the expected value of current reproduction depends simultaneously on survival prospects, physiological capacity, access to reproductive opportunities, and the likelihood that comparable opportunities will recur. This theoretical article develops a proposed dynamic reproductive-value framework for insects in which chronological age is only one contributor to residual reproductive value. Somatic condition determines what investment is physiologically feasible; environmental hazards alter survival expectations and may also impair decision processes; mates and reproductive resources modify the immediate return from investment; and future opportunity determines the cost of postponement. Evidence from beetles, crickets, flies, mosquitoes and other insects demonstrates heterogeneous responses that include terminal investment, reproductive restraint, altered mating effort, resource-sensitive oviposition, and changes in nutritional allocation. These outcomes cannot be reduced to a single monotonic age or risk effect. The proposed framework therefore treats reproductive value as a continuously updated state-dependent surface rather than a fixed age trajectory. It predicts that similar mortality cues may produce different allocation responses depending on condition and opportunity and that superficially similar reproductive changes may arise through different mechanisms. The framework is intended as an evidence-bounded basis for designing factorial and longitudinal tests rather than as an empirically validated universal rule.

**Keywords:** Reproductive value, Terminal investment, Life-history trade-offs, Somatic condition, Mortality risk, Reproductive allocation.

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## Introduction

Reproductive allocation is commonly described as a trade-off between current reproduction and retained capacity for future reproduction. In insects, however, the decision boundary separating these alternatives need not be fixed. Dynamic-state and terminal-investment models indicate that reproductive allocation can change with age, energetic state and expected future reproductive prospects, while broader life-history evidence cautions against assuming that negative trade-offs are expressed uniformly across traits, environments or biological scales [1–3].

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The important inferential problem is therefore not whether insects "invest now" or "save for later," but how the relative value of those alternatives is recalculated as internal state and ecological opportunity change.

Energetic constraints add a second complication. Reproduction can impose costs through resource depletion, altered survival probability or both, and these mechanisms need not yield the same optimal allocation schedule [4]. Consequently, chronological age alone is an incomplete proxy for residual reproductive value. Two insects of the same age may differ in stored reserves, developmental history, reproductive load, infection state, access to mates, quality of available oviposition substrates and the probability of obtaining future reproductive opportunities. Conversely, two insects with similar somatic condition may differ substantially in the opportunity cost of postponing reproduction.

This article therefore develops a proposed dynamic reproductive-value framework in which age, somatic condition, environmental mortality risk, mate and resource availability, and future reproductive opportunity remain analytically distinct but interact continuously. The framework is not presented as an empirically validated optimization model. Its purpose is to organize heterogeneous insect evidence while distinguishing increased current investment from reproductive restraint, senescence, physiological incapacity and environmentally induced decision impairment.

## Materials and Methods

*Dynamic-state variables*

The framework was constructed as synthesis of state-dependent relationships represented in the cited insect evidence base. No new dataset, parameter estimation, statistical model fitting or quantitative reproductive-value score was generated. Instead, variables were retained only where the literature provided a defensible biological distinction and an identifiable measurement boundary.

Somatic condition was treated as multidimensional rather than synonymous with body mass or stored energy. Nutritional-geometry experiments in Drosophila melanogaster show that protein-to-carbohydrate balance can differentially shape reproduction and lifespan according to sex and mating state [5]. Developmental nutrition can also alter adult reproductive performance without producing an equivalent change in survival following injury or infection [6]. Moreover, developmental diet can change the observed relationship between fecundity and longevity, demonstrating that the sign of an apparent life-history association may depend on prior nutritional environment [7]. These findings justify separating current energetic state, nutrient composition and developmental history within the proposed state description.

Physiological feasibility is additionally constrained by competing functions. In reproductively active female D. melanogaster, shared fat-body machinery can limit simultaneous investment in reproduction and antibacterial immunity [8]. This mechanism is not assumed to generalize unchanged across insect orders, but it demonstrates why declining future reproductive value cannot automatically generate greater current reproduction: an insect may lack the physiological capacity to translate an altered allocation incentive into additional reproductive output. Accordingly, the framework distinguishes reproductive value, which concerns the relative value of current and future opportunities, from feasible reproductive effort, which depends on organismal state.

Age, mortality risk, resource availability and future opportunity are therefore treated as separate theoretical coordinates. Their values are not converted into scores or universal thresholds. The framework instead asks whether a change in one coordinate should alter current investment after the remaining coordinates and their biological measurement boundaries are considered.

## Results and Discussion

*Age-dependent residual value*

Chronological age often changes the expected number of future reproductive opportunities, but insect evidence does not support a universal age-to-investment rule. In female Tenebrio molitor, age-specific responses to pathogenic threat were inconsistent with an obligatory terminal increase in fecundity and instead included reproductive restraint [9]. Male Teleogryllus oceanicus, by contrast, increased reproductive signaling with age even though an immune challenge did not itself trigger the predicted terminal-investment response [10]. These differences show why age and mortality cues should not be treated as interchangeable indicators of declining residual reproductive value.

Experimental manipulation of threat intensity in male crickets further indicates that the threshold for increased reproductive effort can depend on age [11]. Yet the relevant reproductive trait was calling effort, not lifetime reproductive success, and increased signaling cannot by itself establish an adaptive fitness benefit. Late-life experiments in T. molitor similarly indicate that terminal investment, reproductive restraint and senescence can generate partially overlapping phenotypes and therefore require explicit discrimination rather than retrospective classification from age-related fecundity alone [12].

Age effects are also conditional on sex and social context. Manipulated reproductive environments in T. molitor produced sex-specific patterns in reproductive costs and senescence [13]. In burying beetles, maternal, paternal and foster-parent ages can interact in determining reproductive and offspring outcomes, making focal-individual age an incomplete description of the reproductive environment [14]. These studies collectively support treating chronological age as a modifier of expected future opportunity rather than as residual reproductive value itself.

The proposed framework consequently defines an age-dependent residual-value component rather than an age rule. Its direction is expected to depend on remaining lifespan, reproductive capacity, opportunity recurrence and the cost of current reproduction. Older age can therefore move an individual toward greater current effort, restraint or apparent reproductive decline depending on where the other state variables place that individual.

*Somatic condition*

Somatic condition determines both the resources available for reproduction and the physiological cost of reallocating them. It cannot be represented adequately by a single proxy. In female Gryllus firmus, increasing age was associated with reduced fat stores while egg load increased, demonstrating that reproductive state and stored energetic reserves can move in opposite directions [15]. Thus, low reserve mass need not indicate low current reproductive investment, and high reproductive load need not indicate high residual capacity.

Nutrient composition provides another layer. Female Drosophila adjust macronutrient intake according to mating and reproductive state, with diets associated with high reproduction differing from those associated with longer lifespan [16]. Sterol availability can independently constrain production of viable eggs, showing that a nominally adequate caloric state may still be reproductively limiting when a specific essential nutrient is scarce [17]. Conversely, high dietary sugar can reduce fertility independently of an obesity-like phenotype, illustrating that nutritional exposure and generalized “body condition” are not interchangeable constructs [18].

Condition also modifies responses to mortality threat. Following infection in Drosophila, the reproductive component that increased depended on dietary context rather than following one invariant terminal-investment phenotype [19]. The proposed framework therefore treats somatic condition as a set of biologically separable constraints affecting both the feasibility and the marginal return of current reproduction.

Because these distinctions are difficult to recover from a single linear condition axis, the comparison below separates condition dimensions that would otherwise be conflated.

**Table 1.** Somatic states that change the interpretation of current reproductive capacity without defining a single condition score

| | |
|---|---|
| **Reserve quantity and nutrient quality** | |
| **Low stored reserves with high reproductive load** | *Evidence-derived* |
| **Physiological setting** | Aging adult females |
| **Reserve mass and egg load move in opposite directions** | |
| **Observable condition evidence** | |
| **Current allocation may already be high despite depleted reserves** | Reserve mass is not equivalent to total physiological capacity |
| **Reproductive-value implication** | **Boundary** |
| **Discriminating experiment** | Measure reserves and reproductive load independently |
| **Macronutrient imbalance** | *Evidence-derived* |
| **Physiological setting** | Mated versus unmated adults |
| **Protein–carbohydrate intake and reproductive output** | |
| **Observable condition evidence** | |
| **Resource quantity alone may misclassify reproductive feasibility** | Laboratory diet choice may not equal field optimum |
| **Reproductive-value implication** | **Boundary** |
| **Discriminating experiment** | Manipulate nutrient composition separately from calories |
| **Specific limiting nutrient** | *Evidence-derived* |
| **Physiological setting** | Egg-producing females |

| | |
|---|---|
| **Egg viability changes with sterol availability** | |
| **Observable condition evidence** | |
| **A narrow biochemical constraint may dominate apparent energetic state** | Nutrient-specific effect |
| **Reproductive-value implication** | **Boundary** |
| **Discriminating experiment** | Quantify essential resource pools rather than bulk energy only |
| **Exposure and competing demand** | |
| **Adverse dietary exposure without matching condition phenotype** | *Evidence-derived* |
| **Physiological setting** | Adult females |
| **Fertility changes despite weak correspondence with obesity-like state** | |
| **Observable condition evidence** | |
| **External nutritional environment and internal condition should remain separate variables** | Metabolic effects are species- and diet-specific |
| **Reproductive-value implication** | **Boundary** |
| **Discriminating experiment** | Test exposure and physiological state factorially |
| **Competing physiological demand** | *Evidence-derived* |
| **Physiological setting** | Reproduction under immune challenge |
| **Shared tissue or translational capacity** | |
| **Observable condition evidence** | |
| **Declining future value may not increase reproduction when capacity is constrained** | Mechanism demonstrated in a limited taxonomic context |
| **Reproductive-value implication** | **Boundary** |
| **Discriminating experiment** | Measure physiological feasibility before inferring restraint |
| **Historical state** | |
| **Historical-state dependence** | *Proposed synthesis* |
| **Physiological setting** | Adults emerging from contrasting developmental diets |
| **Adult reproduction differs by developmental history** | |
| **Observable condition evidence** | |
| **Present condition may carry information about earlier environments** | Persistence varies across traits and ages |
| **Reproductive-value implication** | **Boundary** |
| **Discriminating experiment** | Include developmental history in longitudinal designs |

*Environmental mortality risk*

Mortality risk can reduce expected future reproductive opportunity, but the resulting allocation response depends on the type, timing and biological meaning of the threat. Simulated heat stress, anthropogenic light exposure and pathogen challenge have produced different reproductive and life-history responses in insects [20–22]. These differences make a single "environmental stress" axis inadequate: acute thermal stress, chronic environmental disturbance and infectious threat may alter survival prospects, physiology and information reliability through different pathways.

Risk can also operate through offspring environments rather than adult survival. Female herbivorous insects may alter oviposition when host quality and predator efficacy vary simultaneously, trading nutritional quality against enemy-free space [23]. This is a reproductive decision, but it should not be classified automatically as terminal investment because the proximate quantity being optimized concerns offspring placement rather than the parent's energetic expenditure.

The proposed framework therefore separates three components of environmental risk: risk to the reproducing adult, risk to reproductive output or offspring, and risk-induced impairment of the decision process itself. Only the first directly maps onto reduced expected adult survival. The second changes the expected return from a current reproductive opportunity, while the third can make observed behaviour diverge from the allocation that would be expected under intact information processing.

Temporal structure is also critical. A brief threat cue may justify different behavior from a persistent hazard, and unreliable cues may generate responses that are costly under natural environmental variation. The present evidence does not justify universal numerical thresholds. Instead, risk is represented as a temporally updated signal whose meaning depends on condition, opportunity and the biological target of the threat.

The distinction between these pathways is sufficiently central that it should be visible rather than confined to prose.

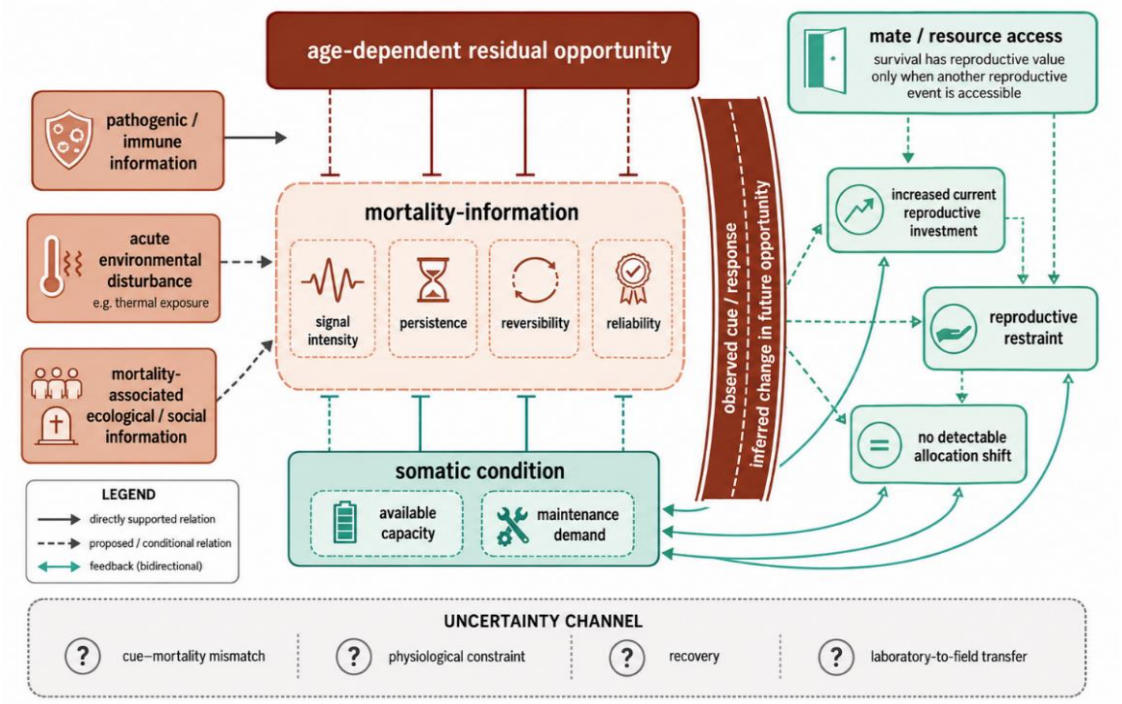



**Figure 1.** Mortality signals alter reproductive decisions through survival, offspring-return, and impairment pathways that need not converge

*Mate and resource availability*

The value of current reproduction depends not only on an individual's capacity to reproduce but also on whether a useful reproductive opportunity is presently available. In Aedes aegypti, resource availability and predation risk interact in determining oviposition behavior, illustrating that reproductive resources have value only within their environmental context [24]. A resource-rich site can therefore remain unattractive when offspring risk is high, while a lower-resource site may have greater expected reproductive return under safer conditions.

Current adult resources can also change mating effort rapidly. In D. melanogaster, past and present food availability affected mating rate, but the influence of earlier deprivation could be modified when current food became available; mate choice itself did not change in the same way [25]. This distinction matters because resource state may alter willingness or ability to mate without changing the relative ranking of prospective mates.

Mate quality creates a related but separate dimension. Male Drosophila can allocate more to a high-quality current mating in ways that reduce later postcopulatory performance, demonstrating that a valuable present opportunity may increase current investment while simultaneously lowering future reproductive capacity [26]. Yet body size, when used as a condition proxy, does not necessarily modify the strength of mate choice [27]. Condition, mate value and opportunity availability should therefore remain independent coordinates until evidence demonstrates otherwise.

Within the proposed framework, the immediate value of reproduction is highest when a suitable mate or reproductive substrate is available, expected current return is high, and investment remains physiologically feasible. Scarce or low-quality opportunities can instead favor restraint even in an older individual if postponement has a realistic chance of producing a better opportunity. This is a theoretical prediction, not an established universal response.

The prediction-and-test ledger below separates opportunity states that superficially look similar but imply different experimental tests.

**Table 2.** Mate and resource states that distinguish present reproductive opportunity from general somatic condition

| Present opportunity | | | Context | Temporal adjudication | | |
|---|---|---|---|---|---|---|
| **Opportunity signal** | **Observed basis** | **Current-investment implication** | **Biological context** | **Discriminating test** | **Alternative explanation** | **Standing** |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Resource restoration** | | | | | | |
| **Resource restored after prior deprivation** | Mating rate changes after current food becomes available | Current opportunity can update behavior rapidly despite poor recent history | Adult mating context | Manipulate present and historical resources factorially | Increased activity or condition may mediate the response | Evidence-derived |
| **Mate value** | | | | | | |
| **High-value current mate** | Increased investment in one mating followed by reduced later performance | High present return can justify greater current expenditure while creating future cost | Sequential mating | Measure both present investment and later reproductive performance | Mechanism may be postcopulatory rather than whole-organism allocation | Evidence-derived |
| **Condition proxy unchanged but mate preference persists** | Preference strength independent of body-size treatment | Mate valuation and somatic-condition proxy need not covary | Adult mate choice | Compare multiple condition indices | Body size may inadequately represent physiological condition | Evidence-derived |
| **Resource–offspring-risk trade-off** | | | | | | |
| **Resource-rich but offspring-risky reproductive site** | Resource abundance and predator cues jointly shape site use | Present resources must be discounted by expected offspring return | Oviposition context | Manipulate resource quality and offspring risk independently | Oviposition choice does not directly measure parental energetic investment | Evidence-derived |
| **Present versus future access** | | | | | | |
| **High current opportunity with low future opportunity** | Requires simultaneous information on present and expected future access | Greater current investment is predicted when postponement has high opportunity cost | General state-space prediction | Experimentally restrict later mate or resource access | Future opportunity is rarely measured directly | Proposed |
| **Low current opportunity with recoverable future access** | Present mate/resource scarcity plus credible later availability | Restraint may preserve capacity for later reproduction | General state-space prediction | Separate feasibility from opportunity in longitudinal designs | Delay may reflect incapacity rather than strategic allocation | Proposed |

*Future reproductive opportunity*

Future reproductive opportunity is not reducible to remaining lifespan. An insect may survive for considerable time yet encounter few suitable mates, hosts, oviposition substrates, or reproductive resources. Conversely, a short-lived individual can experience repeated high-value opportunities during a brief interval. Experimental restriction of early oviposition in Callosobruchus maculatus altered subsequent fecundity and longevity, demonstrating that temporarily unavailable reproductive resources can redirect later life-history trajectories [28]. Reproductive state also changes how resources relevant to future reproduction are acquired. In D. melanogaster, mating produces sex-specific switches in protein-rich food preference through identified neural circuitry [29]. Developmental and adult diets likewise have different age-dependent effects on female reproductive ageing: developmental nutrition contributes strongly to early reproductive performance, whereas adult diet becomes more influential later [30]. Thus, future opportunity depends partly on whether condition can be renewed as well as on whether an individual remains alive.

The proposed framework consequently defines future reproductive opportunity as the expected accessibility and reproductive return of later events, conditional on survival and future feasible condition. This quantity should remain distinct from present mate quality, current resource abundance, and chronological age. Its direct measurement is difficult, making experimental manipulation of later access to mates, hosts, food, or oviposition substrates especially important for testing the framework.

*Dynamic reproductive-value surface*

The evidence assembled above argues against representing reproductive value as a one-dimensional decline with age. Trade-offs differ across biological scales, overwintering and breeding contexts alter the relation between survival and reproduction, and spatial resource distributions modify reproductive-site decisions [31–33]. These observations motivate a proposed dynamic reproductive-value surface.

The surface represents the relative value of investing in a current reproductive event versus retaining capacity for future events. Age changes the temporal horizon; somatic condition constrains feasible investment; adult mortality risk alters expected persistence; current mate or resource availability changes immediate return; and future opportunity changes the cost of postponement. None is assigned a universal weight. Interactions are essential because the same shift in one variable can imply different responses depending on the others. High mortality risk, for example, can favor greater current investment when condition and opportunity are adequate, but can coincide with restraint when physiological capacity is poor or when the threat disrupts decision processes.

A second boundary separates the latent reproductive-value inference from its observable proxies. Calling effort, mating duration, egg number, oviposition-site choice, nutrient preference and offspring viability describe different components of reproductive behavior or performance. They should not be converted automatically into equivalent units of "investment." Likewise, a relationship observed within individuals cannot be assumed to explain differences among species. The surface is therefore an organizing hypothesis whose coordinates must be operationalized for each taxon and reproductive mode.

**Table 3** is needed to distinguish regions that could generate superficially similar reproductive phenotypes while implying different biological explanations and validation tests.

**Table 3.** Distinguishing reproductive-value states from look-alike allocation outcomes on the proposed dynamic surface

| | **Present-value dominant** | |
|---|---|---|
| **Dynamic-surface coordinate** | **Low future opportunity, adequate condition, valuable present opportunity** | **Low future opportunity, poor condition** |
| **State combination** | Short future horizon plus feasible reproduction | Reduced future horizon plus physiological constraint |
| **Observable allocation pattern** | Increased current effort | Stable or reduced reproduction |
| **Reproductive-value reading** | Current reproduction has high relative value | Incentive to reproduce may exceed feasible capacity |
| **Validation test** | Measure later opportunity and lifetime reproductive consequences | Measure reserves, reproductive machinery, and recovery potential |
| **Look-alike explanation** | Stress-induced hyperactivity or trait-specific response | Senescence or pathology |
| **Standing** | Proposed | Proposed |
| | | |
| | **Future-value or jointly favorable** | |
| **Dynamic-surface coordinate** | **High future opportunity, poor present opportunity** | **High present and future opportunity** |
| **State combination** | Future access likely but present return low | Repeated favorable events |
| **Observable allocation pattern** | Reproductive restraint or delay | Sustained rather than terminal investment |
| **Reproductive-value reading** | Capacity is retained for later opportunity | Current reproduction need not exhaust future value |
| **Validation test** | Manipulate future access while holding condition constant | Track repeated events and condition trajectories |
| **Look-alike explanation** | Failure to encounter a suitable mate or substrate | Abundant resources may mask allocation costs |
| **Standing** | Proposed | Proposed |
| | | |
| | **Discordant allocation outcomes** | |
| **Dynamic-surface coordinate** | **Altered reproductive-site choice without increased output** | **Cross-scale trade-off mismatch** |
| **State combination** | Offspring risk or resource configuration changes | Individual and species patterns differ |
| **Observable allocation pattern** | Redistribution of oviposition | Trade-off evident at one scale but absent at another |

| | | |
|---|---|---|
| **Reproductive-value reading** | Expected return changes without necessarily changing total effort | Scale changes permissible inference |
| **Validation test** | Measure both allocation quantity and offspring return | Test within-individual, population, and species levels separately |
| **Look-alike explanation** | Sensory bias or stress-impaired decision | Independent evolutionary divergence |
| **Standing** | Evidence-bounded synthesis | Evidence-derived |

The surface also requires an explicit validation boundary, because evidence supporting individual coordinates is stronger than evidence for their joint topology. **Figure 2** therefore separates observed state information from the proposed inference and from the tests required to establish whether predicted state transitions occur.

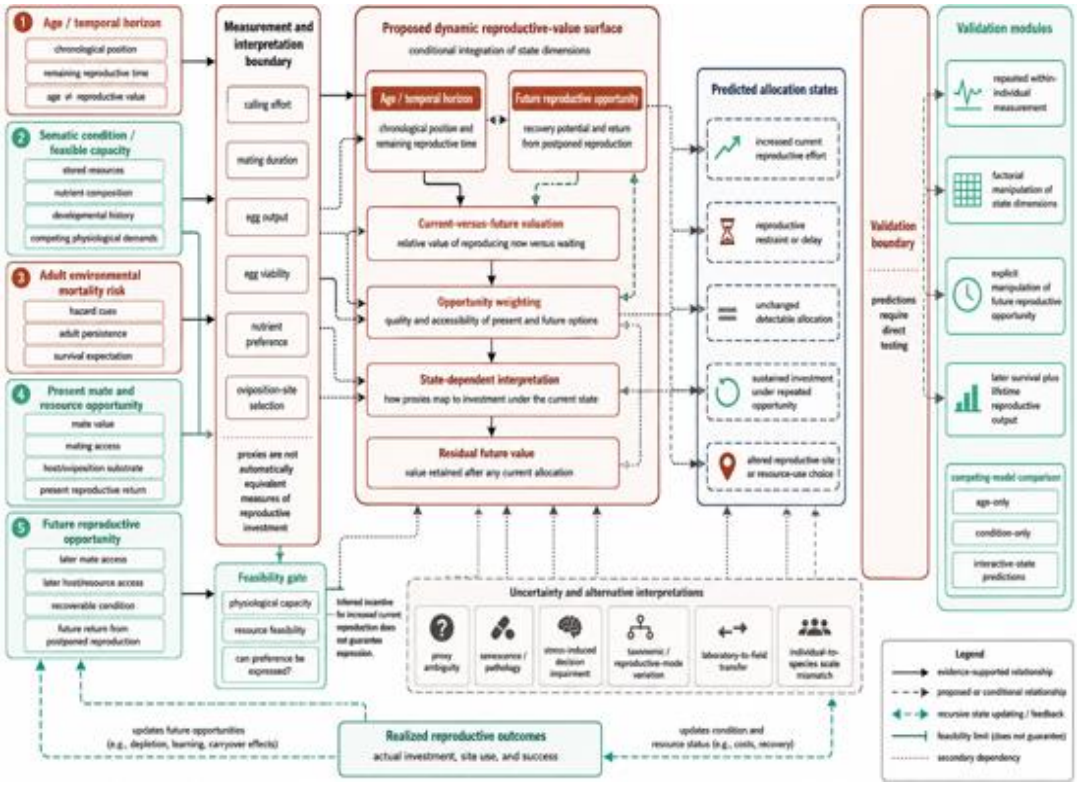



**Figure 2.** Observable state signals cannot identify reproductive value without crossing explicit inference and validation boundaries

*Predicted shifts in current investment*

The framework predicts directions of change only conditionally. Reduced future opportunity should increase current effort when a valuable reproductive opportunity exists and the individual retains sufficient physiological capacity. If capacity is limiting, the same decline in future value can yield restraint or no detectable increase. Infection experiments in which diet changes the reproductive component expressed after challenge illustrate why a single endpoint cannot diagnose the underlying allocation rule [19].

A second prediction is that age effects should be strongest when aging actually changes future opportunity. Restricting early reproduction can alter later investment [28], so chronological age and opportunity history should be manipulated independently wherever possible. Present mate value should also matter: greater allocation to a high-quality current mate can reduce later postcopulatory performance [26], creating a direct route by which current opportunity changes the future state.

Finally, changes in behavior need not represent successful reproductive-value recalibration. Physiological stress in parasitoids can impair chemosensory processing, learning, or memory during oviposition decisions [34]. The framework therefore predicts a diagnostic divergence: state-dependent allocation should change reproductive behavior coherently with experimentally manipulated opportunity, whereas impairment should weaken information use or produce mismatches between behavior and reproductive return.

The central contribution of this article is a proposed shift from categorical explanations toward continuous state-dependent inference. Terminal investment and reproductive restraint remain useful descriptions, but neither should be treated as a universal response to age or mortality threat. Empirical contrasts among crickets, mealworms, flies, beetles and ovipositing insects indicate that the direction and even the measured component of reproductive change depend on condition, cue type, sex, reproductive mode and opportunity structure.

This interpretation is consistent with broader quantitative evidence showing heterogeneous reproductive responses to immune challenge and stronger mean terminal-investment responses in older individuals, while also revealing increased between-individual variation rather than a single deterministic reaction [35]. Such evidence supports conditionality, not the exact multidimensional surface proposed here. The surface should therefore be regarded as a hypothesis-generating architecture that makes otherwise hidden assumptions explicit.

Several boundaries are especially important. First, reproductive effort is not synonymous with reproductive success. Calling, courtship, mating duration, egg production, egg viability and offspring placement capture different processes. Second, somatic condition is measurement dependent: fat stores, body size, nutrient balance and organ-level capacity cannot be substituted without validation. Third, mortality cues can alter expected survival, alter offspring return, or impair the machinery of decision-making. These pathways may produce similar outward changes but imply different life-history interpretations.

Taxonomic transfer is another limitation. Much of the mechanistic and nutritional evidence comes from Drosophila, whereas terminal-investment tests include orthopterans and coleopterans and opportunity decisions include mosquitoes, herbivores and parasitoids. Reproductive modes differ profoundly among these taxa. Capital versus income breeding, diapause, parental care, host dependence, mating systems and the spatial distribution of reproductive substrates can all change the meaning of future opportunity. Field conditions also contain correlated hazards and opportunities that laboratory experiments intentionally separate.

Validation therefore requires designs that measure several coordinates simultaneously rather than manipulating a single “stress” variable. Repeated within-individual observations could distinguish state change from selective disappearance. Factorial experiments should manipulate condition, mortality information, present opportunity and later opportunity independently where biology permits. Competing models should compare age-only, condition-only and interactive predictions. Studies should follow reproductive effort to later survival and lifetime reproductive output before describing a response as fitness maximizing.

The framework is useful precisely because it permits failure. If future-opportunity manipulations add no explanatory power beyond age and condition, that coordinate can be simplified. If responses cluster into discrete strategies rather than continuous regions, the surface assumption should be rejected. If state effects are taxon specific, cross-order generalization should be restricted. The objective is not to force insect reproduction onto one topology, but to provide explicit variables and boundaries with which alternative explanations can be tested.

## Conclusion

Insect reproductive value should not be inferred from age, condition, mortality risk, or current opportunity in isolation. Each changes a different part of the current-versus-future reproductive problem, and their effects can reinforce, oppose, or constrain one another. The proposed dynamic reproductive-value surface organizes these interactions while preserving distinctions among reproductive incentive, physiological feasibility, environmental return, and decision impairment. It therefore predicts conditional shifts among increased current effort, restraint, delay, unchanged allocation, and altered reproductive-site choice rather than a universal terminal response. The framework remains theoretical: its value depends on factorial, longitudinal, taxon-aware tests that measure future opportunity and lifetime consequences directly. Such tests can determine whether reproductive decisions are better understood as continuously updated state-dependent valuations or whether simpler, taxon-specific rules provide a more accurate account.

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