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Mating History, Oogenesis, Condition, and Survival Jointly Determine the Timing of Reproductive Investment in Adult Insects

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ABSTRACT

Adult insects do not allocate reproductive effort according to a single clock. Mating-derived signals, ovarian maturation, nutritional and somatic state, and the expected opportunity for future reproduction can change at different rates and can generate similar reproductive outputs from different internal states. This article develops a proposed non-empirical state-space model in which reproductive timing emerges from the joint configuration of four variables: mating history, oogenic readiness, nutritional and somatic condition, and residual survival probability. The model treats these variables as conceptually distinct but biologically coupled. It therefore avoids equating mating with immediate egg production, chronological age with remaining reproductive opportunity, food intake with condition, or delayed reproduction with a single mechanism such as senescence or restraint. Evidence across Diptera, Lepidoptera, Hymenoptera, Orthoptera, Coleoptera, and Blattodea shows that mating can alter germline and somatic physiology, oogenesis has its own endocrine and cellular gates, nutritional effects depend on life stage and nutrient balance, and reproductive effort can increase, decline, or remain constrained under reduced future opportunity. The proposed model predicts multiple investment trajectories rather than one universal terminal-investment rule. Its purpose is to organize mechanistically plausible state combinations, identify where superficially similar phenotypes have different causes, and define measurements required for future longitudinal validation.

Keywords: Reproductive timing, Mating history, Oogenesis, Nutritional condition, Terminal investment, Life-history allocation.

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Introduction

Adult reproductive investment is often described using variables that are easy to observe—age, mating status, fecundity, body condition, or recent environmental stress—but these variables are not interchangeable with the physiological states that generate reproductive decisions. In *Drosophila melanogaster*, sexual behavior is modulated by internal and contextual state rather than operating as a fixed adult program [1]. Prior mating experience can also alter later reproductive performance and reproductive ageing, demonstrating that present reproductive capacity can depend on history rather than current mating status alone [2]. The central problem is therefore temporal and state-dependent: when should an adult convert available resources into current

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reproductive effort, and when should investment be delayed, restrained, redirected, or rendered impossible by physiological constraint?

Mating can directly alter reproductive machinery. In female *D. melanogaster*, mating-dependent signaling from the midgut promotes ovarian germline stem-cell proliferation, linking a mating-derived signal to a change in germline state [3]. Yet ejaculate effects are not fixed properties of males: seminal-fluid molecules and their consequences can be modulated by both sexes and vary with mating context [4]. Oogenesis itself is also independently regulated. Juvenile hormone participates in oogenic control, but its interactions with other endocrine and nutritional signals vary among insect systems [5]. Nutritional biology adds another layer because diet provides substrates for egg production while simultaneously altering endocrine and developmental regulation of reproduction [6].

These dimensions can dissociate. Age and starvation affect different components of reproductive performance in *D. melanogaster*, and acute energetic limitation cannot simply be treated as an intensified form of ageing [7]. Longitudinal evidence from wild crickets likewise shows that high early reproductive effort does not inevitably produce the straightforward later survival cost assumed by simple allocation models [8]. Such observations make a one-axis interpretation of reproductive timing inadequate.

This article therefore proposes that the timing of reproductive investment is better represented as an emergent property of four interacting state variables: mating history, oogenic readiness, nutritional and somatic condition, and residual survival probability. The first three can be anchored in observable physiological or behavioral measurements, although no single measure is universally sufficient. The fourth is more difficult: residual survival probability is treated here as a latent estimate of remaining reproductive opportunity, not as chronological age or a directly measured subjective probability. The model is intended as a theoretical organizing device, not as an empirically validated predictor. It separates state from outcome, permits multiple mechanisms to generate similar reproductive phenotypes, and preserves taxonomic and environmental limits when mechanisms differ among insects.

Reproductive state variables

A reproductive state variable should represent information that changes the feasible or expected timing of investment without being reducible to the reproductive output it helps generate. Ovarian ageing illustrates this distinction. Germline stem-cell function and the ovarian niche change with age in *D. melanogaster*, meaning that two females of similar chronological age can differ in cellular reproductive capacity [9]. Nutrient-responsive signaling adds a second source of variation because germline stem-cell activity is regulated through multiple local and systemic pathways, including nutrient-sensitive signaling networks [10]. Thus, ovarian state and nutritional state are coupled, but they are not conceptually identical.

The proposed model uses four coordinates. Mating history represents more than virgin-versus-mated status; it includes the number, timing, and physiological consequences of previous matings and, where relevant, persistence of ejaculate-derived signals. Oogenic readiness describes the current ability of the ovary to progress through germline proliferation, vitellogenesis, maturation, retention, resorption, and oviposition-related transitions. Nutritional and somatic condition describes the substrate, energetic, micronutrient, tissue, and developmental state that can support or constrain reproduction. Residual survival probability represents expected future reproductive opportunity conditional on age, damage, stress, infection risk, and other mortality-relevant information.

These coordinates are not assumed to be statistically independent. Mating can modify feeding and metabolism; nutritional state can modify oogenesis; ovarian activity can change nutrient demand; and declining future opportunity can alter the value of current versus delayed reproduction. Their analytical separation is nevertheless useful because the same fecundity value can emerge from different combinations. A female may lay few eggs because she is unmated, because eggs are not mature, because nutritional state constrains egg production, or because reproductive allocation is restrained despite adequate physiological capacity. The state-space formulation is designed to preserve these alternatives rather than infer mechanism directly from output.

Mating history

Mating history is temporally cumulative and physiologically heterogeneous. In the parasitoid *Aphelinus asychis*, increased mating frequency increased the production of female progeny but shortened adult longevity, showing that repeated mating can simultaneously alter reproductive outcome and survival in a non-*Drosophila* system [11].

This does not imply that repeated mating universally raises fecundity or reduces lifespan, but it establishes that mating number can matter beyond the binary fact of insemination.

The consequences of mating can also extend into somatic physiology. In female *D. melanogaster*, Sex Peptide contributes to post-mating changes in midgut morphology and transcriptional state under the tested nutritional conditions [12]. In the lepidopteran *Helicoverpa armigera*, functional disruption of the Sex Peptide Receptor altered long-term receptivity and oviposition-related responses and was associated with increased longevity, demonstrating that mating-related signaling can couple behavior, egg release, and survival in a taxon outside Diptera [13]. These mechanisms should not be collapsed into a single conserved pathway; rather, they show that mating history can shift multiple physiological dimensions at once.

The state created by mating also depends on partner attributes. In *D. melanogaster*, male age and sexual history altered female post-mating aggression, feeding, and aspects of reproductive output, whereas different manipulations of male condition did not produce identical female responses [14]. A useful mating-history variable therefore cannot be interpreted as a simple scalar of "mate quality." It must allow different histories to have different physiological consequences even when mating frequency is the same.

Female physiology further modifies what mating means. Female reproductive-tract factors influence the association of Sex Peptide with stored sperm after transfer, helping determine persistence of long-term post-mating effects [15]. Female reproductive glands also contribute to mating-plug composition and the timing of sperm ejection [16]. These findings reject a passive model in which receipt of male material fully specifies the female state. Mating history is jointly produced by transferred signals, female processing, and the time elapsed since mating.

Time is especially important because the post-mating state is not static. Time-series transcriptomic analysis in *D. melanogaster* shows that early post-mating transcriptional changes are not entirely Sex-Peptide-dependent, whereas later metabolic and neuronal responses are more strongly maintained or diversified by that signal [17]. Across insects more broadly, seminal-fluid proteins, octopaminergic signaling, and other routes can contribute to post-mating responses, with substantial taxonomic heterogeneity [18]. The proposed model therefore treats mating history as a dynamic input whose physiological influence can persist, decay, or change in composition rather than as a permanent switch from "virgin" to "mated."

Oogenesis and egg maturation

Oogenesis is the conversion interface between reproductive intent and physically realizable egg production. Its importance becomes evident when nutrient demand is measured at different reproductive states. In field crickets, ovarian synthesis increases female nutrient requirements, and carbohydrate-biased dietary constraint can reduce ovarian synthesis in reproductive morphs [19]. Oogenic readiness therefore changes the marginal value of available nutrients: the same nutritional intake can have different reproductive consequences depending on whether ovarian tissue is actively synthesizing eggs.

Egg maturation can also be gated. In *D. melanogaster*, a somatostatin-like pathway participates in controlling vitellogenesis during reproductive maturation, and mating modifies this gating through post-mating neural-endocrine signaling [20]. The specific pathway is taxon-specific, but the broader point is general enough for the theoretical model: mating information and oogenic state need not be simultaneous, and physiological readiness may limit whether a mating-derived signal becomes immediate reproductive output.

Oogenic state is also more complex than the number of developing oocytes. In *Schistocerca gregaria*, differences in oogenesis duration and oosorption accompany shifts toward fewer, larger eggs, illustrating that egg maturation, resorption, and allocation form can change together [21]. In speckled cockroaches, ovarian apoptosis responds strongly to carbohydrate intake rather than to protein intake alone, and cellular ovarian responses do not map perfectly onto whole-organism reproductive measures [22]. Consequently, a low egg count may indicate resource limitation, altered allocation among eggs, oocyte resorption, cellular loss, or a temporary maturational state.

Reproductive delay can additionally preserve future reproductive capacity under specialized conditions. During *Drosophila* diapause, suppressed germline stem-cell activity is associated with reduced damage and improved recovery of germline function when reproduction resumes [23]. This is not evidence that ordinary reproductive delay is generally beneficial, because diapause is a specialized physiological state. It nevertheless demonstrates that low current reproductive activity can reflect a state transition that changes future ovarian capacity rather than simple reproductive failure.

Finally, oogenic condition includes resource classes beyond gross calories or macronutrient ratios. Metal ions and metal-dependent proteins participate in reproductive physiology and can intersect with immune function, although the evidence is uneven among insect taxa [24]. The model therefore treats oogenic readiness as a multidimensional physiological state. No universal threshold, hormone concentration, or egg-stage index is assumed.

Nutritional and somatic condition

Condition is often used as if it were a single quantity, but adult reproductive capacity can retain information from both earlier development and current adult nutrition. In *Aedes aegypti*, larval and adult nutritional conditions have differential effects on adult size, fecundity, and survival [25]. Adult feeding status therefore cannot by itself reconstruct the condition that an adult carries into reproduction.

Nutritional history can also alter later reproductive performance without producing a simple irreversible cost. In *D. melanogaster*, early dietary restriction followed by refeeding increased later reproductive and mating performance without the expected refeeding-associated survival penalty, and total fecundity could be maintained under the tested regime [26]. This finding does not establish dietary restriction as universally adaptive; instead, it shows that current condition can depend on the path by which it was reached.

Mating can further change how nutrients are used. In female *D. melanogaster*, receipt of Sex Peptide altered macronutrient utilization and reproductive output depending on dietary intake, but it did not shift the optimal yeast-to-sugar ratio and did not generate a simple fecundity-versus-lifespan mirror image [27]. Thus, mating history and nutritional state can interact without collapsing into a single additive effect.

For the proposed model, nutritional and somatic condition therefore includes at least four distinguishable dimensions: current substrate availability, developmental carry-over, tissue or cellular integrity, and physiological demand imposed by the current reproductive state. These dimensions can reinforce one another, but they can also diverge. A large adult may be nutritionally constrained, a recently refed adult may differ from one continuously maintained on the same current diet, and a mated female may convert the same intake differently from a virgin female. Condition should therefore be treated as a structured state, not a score.

The analytical problem is not to rank insects from "poor" to "good" condition, but to identify which component of condition limits or redirects reproductive timing. The distinctions are compacted in **Table 1** because their measurement implications, taxonomic boundaries, and validation needs are easier to compare in parallel than in sequential prose.

Table 1. Nutritional and somatic condition states that alter interpretation of reproductive timing without forming a single condition score

	Developmental history and current substrate		
Condition-vector coordinate	**Developmental carry-over**	**Current substrate limitation**	**Nutritional-path dependence**
Observed condition evidence	Adult size, stored resources, survival, fecundity, larval nutritional history	Food intake, nutrient balance, ovarian or tissue synthesis	Diet history, refeeding trajectory, subsequent mating and fecundity
Effect on reproductive timing	Current adult intake may not represent resources available for reproduction	Immediate egg production may be constrained even when mating-derived signals favor reproduction	Similar present intake can correspond to different future reproductive capacities
Taxonomic/physiological context	Mosquito and other insects in which juvenile nutrition affects adult phenotype	Reproductive females with active ovarian synthesis	Adults reaching similar current diets through different prior regimes
Research implication	Measure juvenile and adult nutritional histories separately	Couple diet measurements with direct ovarian-state measures	Compare matched current diets with different nutritional histories
Measurement boundary	Magnitude and persistence are species- and environment-dependent	The limiting nutrient can differ among taxa and physiological states	Effects depend on duration, severity, and timing of restriction

Standing	Evidence-supported distinction	Evidence-supported distinction	Evidence-supported distinction

Mating, tissue integrity, and demand				
Condition-vector coordinate	**Mating-conditioned resource use**	**Tissue or cellular reproductive integrity**	**Demand-state mismatch**	**Structured condition vector**
Observed condition evidence	Reproductive output across nutrient mixtures and mating-derived signal status	Ovarian cell state, stem-cell function, resorption, or apoptosis	Reproductive morph, ovarian synthesis, intake pattern	Joint observation of current resources, developmental history, tissue state, and reproductive demand
Effect on reproductive timing	Mating can alter utilization of available resources without shifting all dietary optima	Adequate intake may not translate into immediate investment if reproductive tissue is constrained	The reproductive value of a nutrient depends on current oogenic demand	Reproductive timing should be interpreted from component states rather than one body-condition score
Taxonomic/physiological context	Mated versus unmated females under matched nutrient environments	Ovarian systems showing apoptosis, stem-cell ageing, or diapause-related preservation	Females whose ovarian activity changes nutrient requirement	Cross-taxon theoretical application
Research implication	Test mating-by-diet interactions rather than main effects alone	Validate tissue markers against longitudinal egg-production trajectories	Estimate nutrient demand conditional on ovarian state	Test whether multidimensional condition improves longitudinal prediction over single proxies
Measurement boundary	Mechanisms are especially well resolved in Drosophila	Cellular markers are not interchangeable with organismal fecundity	Strongly context-dependent across life histories	No validated universal composite scale exists
Standing	Evidence-supported distinction	Evidence-supported distinction	Evidence-supported distinction	Proposed synthesis

Residual survival probability

Residual survival probability is the most inferential of the four proposed state variables. Chronological age can correlate with future reproductive opportunity, but it also changes reproductive physiology. In female *Tenebrio molitor*, fecundity declined with age and early reproductive effort accelerated reproductive senescence, yet neither a terminal increase in late reproduction nor a simple longevity cost was detected [28]. Late-life reproductive decline therefore cannot automatically be interpreted as terminal investment.

Age can likewise affect different reproductive components unequally. In *Bactrocera tryoni*, female fecundity declined with age, whereas fertility also depended on the age combination of the mating pair [29]. Age thus provides information about reproductive capacity but does not itself specify the probability that future reproduction remains available.

Mortality-associated cues are equally ambiguous. In *T. molitor*, experimentally mimicked pathogenic threat did not increase reproduction or reduce survival; early challenge instead reduced fecundity [30]. Conversely, a simulated heat wave in female *Gryllus lineaticeps* shifted relative investment toward ovarian tissue, whereas herbicide exposure did not produce the same allocation response [31]. “Stress” therefore cannot serve as a unitary proxy for low residual survival.

The proposed model consequently defines residual survival probability as a latent estimate of remaining reproductive opportunity, informed by age, physiological damage, environmental hazard, infection-related state, and other mortality-relevant information but equated with none of them. Low future opportunity may favor greater present allocation, restraint may dominate when nutritional or ovarian capacity is poor, and senescence may reduce what can physically be invested. The variable therefore represents an inference about opportunity rather than a directly observed physiological measurement.

Figure 1 separates observable survival-related cues from inferred future opportunity and, critically, to show why the reproductive consequence of that inference changes with mating history, oogenic readiness, and nutritional or somatic constraint.

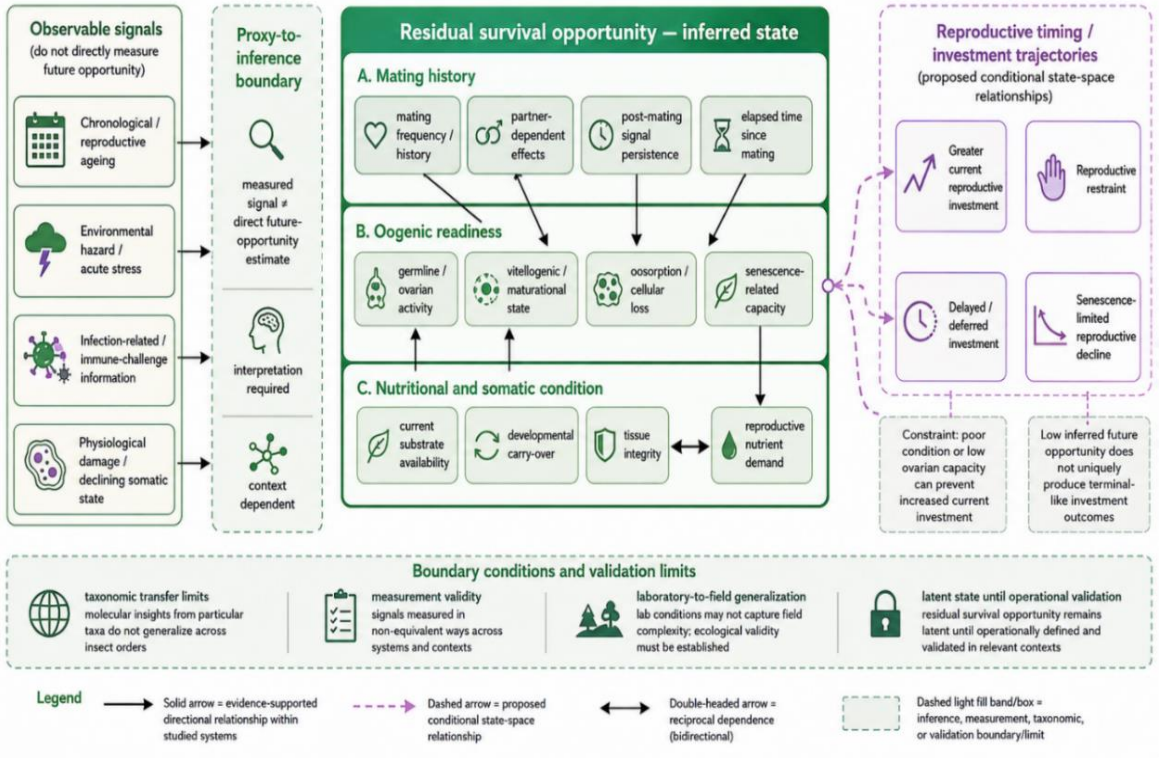


Figure 1. Survival opportunity is inferred through a conditional reproductive-state field rather than read directly from age or stress

State-space model of reproductive timing

The proposed state vector can be written conceptually as ($S(t) = \{M(t), O(t), C(t), R(t)\}$), where (M) is mating history, (O) is oogenic readiness, (C) is nutritional and somatic condition, and (R) is residual survival probability at time (t). The notation is organizational rather than quantitative: no common units, weights, thresholds, transition coefficients, or empirically fitted response surface are assumed.

Reproductive timing arises from the configuration and trajectory of these variables rather than from their isolated values. Mating-derived signals can alter female somatic physiology [12], but their realized reproductive consequence depends partly on ovarian state and available resources. Active ovarian synthesis can itself increase nutrient demand [19], so condition is not merely an upstream cause of reproduction. Likewise, experimentally reduced future opportunity does not justify a monotonic rule in which current reproductive effort must increase, because restraint or declining fecundity can occur instead [30].

The model distinguishes four proposed interpretive states. A permissive state combines sufficient mating-derived stimulation, oogenic readiness, and condition for current investment to be expressed. A constrained state occurs when one or more physiological components prevent realization of reproduction despite mating-derived or opportunity-related cues. A restrained state denotes comparatively low current allocation despite retained capacity. A senescence-limited state occurs when deterioration of reproductive machinery reduces attainable investment. These are theoretical analytical categories, not validated natural classes.

Similar reproductive outputs can therefore occupy different positions in state space. Low egg production may arise from absent mating stimulation, incomplete maturation, nutrient limitation, ovarian cellular loss, restraint, or age-related deterioration. The selective effect of carbohydrate intake on ovarian apoptosis illustrates why cellular reproductive condition need not be inferred from bulk food intake or egg number alone [22]. Mechanistic interpretation therefore requires repeated joint observations rather than a single reproductive output.

Path dependence is also expected. Two adults with apparently similar current condition and ovarian state may differ in reproductive timing because one has recently emerged from nutritional restriction or mating-associated

activation while the other has remained stable. Refeeding experiments demonstrate that present diet does not erase prior nutritional history immediately [26]. The model therefore treats both present state and recent direction of change as potentially informative where physiological carry-over occurs.

Table 2 adjudicates among superficially similar reproductive states by pairing each state-space interpretation with its main competing explanation and the minimum observation needed to discriminate them.

Table 2. Distinguishing superficially similar reproductive-timing states within the proposed four-variable state space

Coordinates observed		Allocation inference		Adjudication	
State-space scenario	**Observable basis**	**Current-investment reading**	**Competing explanation**	**Boundary or discriminator**	**Standing**
Mating, oogenesis, and condition					
Mating-enabled, oogenesis-ready, condition-sufficient	Persistent mating-related state, active egg maturation, adequate resources	Current investment is physiologically permissive	Hidden somatic damage or environmental limitation	Repeated joint measurement of mating, ovarian, condition, and output states	Proposed synthesis
Mating-enabled, condition-constrained	Post-mating state with limited resources or tissue condition	Reproductive stimulation cannot be fully realized	Low oogenic readiness	Manipulate resources while measuring ovarian state	Proposed synthesis
Oogenesis-ready, mating-limited	Mature or maturing eggs with weak or absent mating-derived stimulation	Egg availability does not guarantee immediate reproductive deployment	Weak mating dependence in the focal taxon	Compare matched ovarian states across mating histories	Proposed synthesis
Future opportunity and senescence					
Low future opportunity, high physiological capacity	Mortality-relevant cue with adequate ovarian and somatic state	Greater current investment is possible but not obligatory	Restraint or incorrect interpretation of the cue	Manipulate cue identity while holding reproductive capacity comparable	Proposed synthesis
Low future opportunity, poor condition	Mortality-relevant cue plus resource or tissue limitation	Low output may reflect constraint rather than strategic delay	Senescence, pathology, or other physiological damage	Measure attainable capacity separately from realized output	Proposed synthesis
Senescence-limited state	Age-related decline in reproductive machinery	Maximum attainable output is reduced	Reversible nutritional limitation	Longitudinally distinguish ageing-related capacity loss from resource constraint	Proposed synthesis

Predicted investment trajectories

The model predicts trajectories rather than fixed strategies. When mating-derived stimulation, oogenic readiness, and condition increase together, reproductive investment should tend to occur earlier or at greater current intensity. This prediction is consistent with evidence that mating can stimulate germline activity [3] and that reproductive ovarian synthesis creates distinct nutritional requirements [19], but the joint trajectory itself is proposed rather than empirically established.

When mating stimulation is present but nutritional or ovarian state is limiting, realization should instead be delayed or reduced until the constraining coordinate changes. Nutrient-dependent ovarian apoptosis shows that an apparently reproductive adult can retain an internal physiological constraint not captured by mating status alone [22]. A single measurement of fecundity would therefore be insufficient to distinguish failure of stimulation from failure of realization.

A second prediction is equifinality: similar egg output can arise from different internal states. Low reproduction caused by senescence, restraint, nutritional limitation, and incomplete oogenesis should not be interpreted equivalently. Age-related decline in reproductive potential in *B. tryoni* demonstrates that reproductive components themselves can diverge with age [29]. Repeated state measurements should consequently be more informative than a single fecundity observation.

A third prediction concerns future opportunity. Lower residual survival probability should not generate a universal terminal-investment response. A mortality-associated challenge can be accompanied by reduced rather than increased fecundity [30], whereas heat stress can shift relative allocation toward ovarian tissue under another experimental context [31]. The model therefore predicts that increased present allocation is most plausible when reproductive machinery and condition can support it; restraint or decline remain plausible when they cannot.

Finally, trajectories should be path-dependent. Adults occupying comparable instantaneous condition states may differ if one has recently transitioned from restriction, reproductive arrest, or mating-associated activation. The direction and persistence of recent state change should therefore improve interpretation where physiological carry-over is important, although this proposition requires direct longitudinal testing.

Results and Discussion

The proposed model reframes reproductive timing as a joint-state problem. Its primary contribution is not a new molecular pathway but an analytical separation of mating history, ovarian readiness, nutritional and somatic condition, and future reproductive opportunity while preserving biologically justified interactions among them.

Mating history contains information discarded by a virgin-versus-mated variable. Partner condition or sexual history can alter the female post-mating phenotype [14], and female reproductive physiology can modify the persistence or processing of ejaculate-derived signals [15]. Time since mating matters as well because post-mating transcriptional responses change during the hours following mating [17]. These observations make a static binary mating variable biologically incomplete.

Oogenesis likewise cannot be represented by egg count alone. Changes in oogenesis duration and oosorption can alter how reproductive resources are expressed [21], while ovarian apoptosis can respond differently to specific macronutrients [22]. The relevant state is therefore reproductive capacity and maturation, not merely the number of eggs already produced.

Condition is multidimensional and path-dependent. Larval and adult nutrition can make different contributions to adult fecundity, survival, and body size [25], while mating-associated signaling can change macronutrient utilization without simply changing every dietary optimum [27]. Current food consumption or body size should therefore not be assumed to identify the resource state relevant to reproduction.

Residual survival probability is still less directly observable. Age, thermal stress, immune challenge, and other mortality-relevant events may provide information about future opportunity, but the selected evidence shows that these cues do not map to one invariant allocation response. A key validation problem is therefore measurement: egg counts index realized output rather than oogenic readiness, chronological age is not residual survival probability, and recorded food intake is not synonymous with stored or physiologically usable condition.

These distinctions constrain evolutionary interpretation. Greater present reproductive investment after a mortality-associated cue is not, by itself, evidence of adaptive terminal investment. Reduced reproductive effort is likewise not necessarily adaptive restraint, and delayed reproduction can arise from constraint, specialized reproductive arrest, or declining capacity. Demonstrating adaptation would require direct fitness evidence and designs capable of separating plastic response from evolved allocation strategy.

Taxonomic transfer is another boundary. Several molecular mechanisms are resolved most clearly in *Drosophila*, whereas the broader evidence includes parasitoid wasps, moths, mosquitoes, crickets, locusts, mealworms, and cockroaches. The proposed state variables are therefore higher-level analytical categories, not claims that identical endocrine, neural, seminal-fluid, or nutrient-sensing mechanisms operate across orders.

Validation should be longitudinal and taxonomically explicit. Studies should repeatedly measure mating history, ovarian state, nutritional and somatic condition, mortality-relevant cues, and realized reproductive output within the same individuals, ideally across controlled and field contexts. Alternative operationalizations of each coordinate should be compared rather than assuming that one convenient proxy identifies the theoretical state. Only such tests could determine whether joint-state information explains reproductive timing better than age, mating status, or condition alone and whether quantitative transition rules are justified.

Conclusion

The timing of reproductive investment in adult insects cannot be inferred reliably from mating status, chronological age, condition, or current fecundity in isolation. Mating history can alter reproductive and somatic

physiology, oogenesis has maturational and cellular constraints, condition retains current and historical information, and reduced future opportunity can coexist with increased allocation, restraint, or senescence-limited decline.

The proposed state-space model organizes these dimensions without treating them as universally measured, mechanistically identical, or empirically validated coordinates. Its principal prediction is conditionality: reproductive timing should reflect the joint configuration and recent trajectory of mating history, oogenic readiness, nutritional and somatic condition, and residual survival opportunity. Testing that proposition requires longitudinal measurements that separate reproductive capacity from realized output and observable mortality cues from inferred future opportunity.

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