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Predator Avoidance in Insects Reflects Dynamic Trade-Offs Among Vigilance, Feeding, Reproduction, and Immediate Survival

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ABSTRACT

Predator avoidance in insects is commonly described through conspicuous defensive outcomes such as vigilance, freezing, escape, hiding, reduced feeding, or altered reproductive behavior. Yet these responses do not represent a single interchangeable cost. Their expression depends on what information an insect detects, its physiological and developmental state, the opportunities displaced by defense, and when the consequences become manifest. Existing evidence establishes substantial context dependence but does not establish fixed exchange rates among vigilance, resource acquisition, reproduction, and survival. Similar predator information can therefore produce different behaviors, while similar observed behaviors can arise from different organismal states or ecological constraints. This article develops a proposed dynamic trade-off theory in which antipredator decisions are interpreted through four interacting dimensions: threat information, organismal state, foregone opportunity, and temporal consequence. Predator detection is separated from defensive execution; feeding and reproductive costs are treated as distinct opportunity losses; and immediate encounter survival is distinguished from consequences expressed later in development, physiology, reproduction, dispersal, or population performance. The resulting trade-off surface is qualitative rather than a parameterized fitness landscape. The theory predicts that predator avoidance should vary across predator regimes because cue reliability, exposure persistence, internal state, and available feeding or reproductive opportunities jointly alter the consequences of defensive allocation. These predictions require direct comparative and longitudinal validation and should not be interpreted as established optimality rules.

Keywords: Predation risk, Antipredator behavior, Vigilance, Foraging trade-offs, Reproductive opportunity costs, State-dependent behaviour

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Introduction

Predator effects on insects extend beyond individuals that are captured and consumed. Predation-risk terminology therefore requires a distinction between a prey response induced by perceived danger and the subsequent ecological or demographic consequences of that response [1]. This distinction is especially important when an insect reduces activity, delays feeding, changes habitat, interrupts courtship, or modifies oviposition without being

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killed. Such behaviors can influence later performance, but the behavioral change itself is not equivalent to a measured fitness consequence. The inferential problem addressed here is consequently not whether insects respond to predators, but how defensive responses should be interpreted when vigilance, feeding, reproduction, and survival impose potentially conflicting demands.

Across insect and arthropod systems, non-consumptive predator effects are widespread but markedly heterogeneous, with their expression depending on organismal characteristics, environmental context, experimental scale, and the response variable being measured [2, 3]. This heterogeneity argues against treating "fear" as a unitary biological currency. A chemical cue, approaching predator, looming visual stimulus, or disturbed substrate can each alter behavior, yet the resulting allocation need not have the same energetic, reproductive, or survival meaning. The central theoretical requirement is therefore to preserve conditionality rather than reduce predator avoidance to a monotonic relationship in which increasing risk automatically produces increasing vigilance and equivalent losses elsewhere.

A second boundary concerns biological scale. Evidence that predation risk changes behavior, physiology, development, or reproductive output at the individual level does not by itself establish a reduction in population size. Direct demonstrations linking non-consumptive predator effects to population-level outcomes remain comparatively sparse [4]. Compensation through density dependence, altered resource availability, survival of different phenotypes, or subsequent reproduction can intervene between a short-term behavioral response and population dynamics. Accordingly, this article treats behavioral allocation, individual consequences, and higher-level outcomes as related but analytically separate quantities.

Natural-field attribution creates an additional constraint. Much of the predation-risk literature has relied on experiments or manipulations, whereas comparatively few studies directly establish how strongly risk-induced effects explain patterns observed under natural field conditions [5]. Predator cues in controlled settings can reveal response capacity without reproducing predator density, encounter history, alternative stressors, resource heterogeneity, or the informational ambiguity experienced in nature. The contribution developed here is therefore a proposed state-dependent allocation theory, not a claim that one experimentally derived rule governs insect antipredator behavior universally.

Theoretical decision variables

The first proposed decision variable is resource state. Threat effects in *Aedes triseriatus* depend on resource conditions, demonstrating that the consequences of predator exposure cannot be interpreted independently of the resources available for development and life-history performance [6]. Resource limitation can make foregone acquisition more consequential, whereas abundant resources may alter the cost of temporary withdrawal from feeding. The proposed theory therefore treats resource availability as a modifier of defensive allocation rather than assigning a constant energetic price to vigilance or avoidance.

A second distinction separates information about danger from the cost of executing defense. Experiments in female *Gryllus texensis* that differentiated predator-cue exposure from activation of fight-or-flight behavior produced different reproductive and longevity consequences [7]. Perceiving risk and performing escape are consequently not interchangeable treatments. In theoretical terms, an insect may receive information that changes subsequent behavior without paying the same immediate locomotor or physiological cost as an individual that repeatedly runs, flies, or otherwise executes an escape response.

Internal state must also be interpreted through ontogeny. In the holometabolous sawfly *Athalia rosae*, experimentally altered nutritional state affected behavioral traits differently between larval and adult stages [8]. A state variable such as hunger therefore cannot be assigned a stage-invariant behavioral coefficient. Larvae and adults differ in morphology, resource targets, mobility, vulnerability, and future reproductive value, so equivalent energetic states can have different behavioral implications. Ontogenetic position is consequently retained as a boundary on any proposed decision rule.

Morphological state can restructure the same problem within a life stage or population. Winged and wingless *Myzus persicae* differ in behavioral, fecundity, and transgenerational responses to predator risk [9]. Such endpoint-specific differences are important because morphology can alter both the possibilities available to an insect and the opportunity costs attached to using them. The proposed framework therefore treats morph as a modifier of allocation rather than assuming that all individuals exposed to the same predator information occupy an equivalent decision state.

Finally, predator exposure can influence consequences expressed after the original exposure period. Larval exposure in *Anopheles coluzzii* and *Anopheles gambiae* was associated with adult life-history and physiological effects that differed by species, sex, and measured trait [10]. These differences do not demonstrate universally adaptive reallocation, but they do establish that contemporaneous defensive behavior can be an incomplete representation of downstream cost. The resulting theoretical variable is temporal consequence: an allocation made under present danger may affect immediate survival, yet its costs or compensations may appear later through body condition, physiological reserves, reproductive output, or other life-history traits.

Together, these observations motivate four analytically distinct quantities in the proposed theory: threat information, organismal state, foregone opportunity, and temporal consequence. They are not measured currencies and are not assumed to combine additively. Their role is to prevent biologically different situations from being assigned the same interpretation simply because the observed insect appears more or less active.

Predator detection and vigilance

Predator avoidance begins with information, but information quality varies. Insect alarm pheromones and other chemically mediated warning systems demonstrate that chemical risk information depends on taxon, ecological context, signal properties, and concentration rather than operating through a single invariant alarm mechanism [11]. A detected chemical signal should therefore be interpreted as evidence available to the insect, not as a direct measurement of objective predation probability. Reliability, persistence, spatial structure, and prior exposure can all affect what defensive allocation would follow from the same nominal cue.

Predator identity further complicates detection. In aphid–ladybird interactions, avoidance differs among predator identities, indicating that prey do not necessarily treat all potential enemies as equivalent [12]. Failure to respond strongly to one predator cue cannot consequently be read simply as absence of vigilance, nor does recognition establish the objective danger posed by that predator. The relevant theoretical quantity is the threat estimate generated from available information, which may be incomplete or predator-specific.

Detection rules can also change across ontogeny. Cross-stage experiments in mosquitoes show that responses to predation cues at one stage do not necessarily predict responses at another and that the degree of linkage can differ among species [13]. This weakens any assumption that antipredator responsiveness forms a single behavioral syndrome carried unchanged through development. Stage-specific sensory systems, habitat use, locomotion, and sources of mortality can instead reorganize the relationship between information and response.

Mechanistic work in adult *Drosophila* provides a finer-scale demonstration that even an acute visual threat is not processed as a binary switch. Looming-related features are integrated so that escape behavior is probabilistic and depends on combinations of visual information [14]. Such results give mechanistic support to a multi-feature threat estimate, but their circuit-level specificity prevents extrapolation to all insects. They establish a principle of conditional sensory integration within a model system, not an insect-wide vigilance mechanism.

Current locomotor state can further change which defense is expressed. In walking *Drosophila melanogaster*, locomotor speed influences the selection between freezing and fleeing in response to looming threat [15]. Thus, identical external information can be associated with different defensive outputs depending on what the insect is already doing. This is critical for interpreting vigilance because immobility and escape are alternative responses rather than points on one universal scale of defensive intensity.

Evasive behavior also contains an action-execution layer distinct from threat recognition. Identified visuomotor circuitry contributes to evasive flight turns in *Drosophila* [16]. Such mechanistic resolution demonstrates that sensory detection can be transformed into organized motor output through identifiable neural components, while leaving open how other insect orders, cue modalities, and ecological settings accomplish equivalent functions. The proposed theory therefore separates information acquisition, defensive selection, and motor execution rather than collapsing all three into “vigilance.”

Predator exposure may additionally engage physiological stress processes, although evidence and mechanisms are uneven across insect systems [17]. Physiological activation can influence reserves or later performance without establishing that the response is beneficial or adaptive. Vigilance is therefore treated here as one part of a wider defensive state: detecting danger, freezing, fleeing, hiding, altering activity, and physiological mobilization can covary, but none should be used automatically as a proxy for all the others.

Feeding opportunity costs

Antipredator allocation becomes costly when defensive behavior competes with resource acquisition, but even this conflict is state dependent. In bumblebee workers, body size modifies antipredator responses during foraging,

demonstrating that phenotype can alter the balance between access to resources and perceived danger [18]. The direction of that size effect should not be generalized beyond the tested context; its theoretical importance is that individuals differing in phenotype need not attach the same consequence to abandoning or continuing a feeding opportunity.

Feeding suppression is also separable from locomotor avoidance. Ladybird odors can reduce feeding by *Myzus persicae* and alter population abundance without producing a corresponding increase in movement between plants [19]. An insect can therefore remain spatially associated with a resource while changing how intensively it exploits that resource. Treating movement alone as the index of avoidance would miss this cost, whereas assuming that reduced feeding necessarily causes dispersal would add a response that was not observed.

Resource-acquisition changes can propagate beyond the individual prey. In a grasshopper mesocosm system, predator risk altered herbivore consumption and growth with downstream consequences for soil microbial functioning [20]. Such cross-level effects demonstrate that feeding-mediated responses can reach ecosystem processes, but the direction and magnitude remain food-web specific. They do not justify a generic prediction that predator-induced feeding suppression will produce the same ecosystem response in other insect communities.

The competition between defense and feeding is especially explicit when behaviors are mutually exclusive. Larval *Ischnura elegans* exposed to chemical cues associated with cannibalism shifted toward hiding and away from hunting [21]. This directly supports the idea of a foregone feeding opportunity, while leaving the survival benefit of that behavioral displacement unmeasured in that experiment. Concealment may reduce exposure, but its value cannot be inferred without connecting the behavior to actual encounter and survival outcomes.

Feeding-related behavioral changes may also alter functions that cannot be reduced to the insect's energetic balance. Predator and alarm information can modify behavior of an aphid vector and consequently alter plant-virus transmission outcomes [22]. The finding is pathosystem specific and does not imply that risk consistently raises or lowers transmission across vectors. It instead shows why feeding opportunity must be treated as a multidimensional behavioral domain: changing how, when, or where an insect feeds can affect individual acquisition and wider ecological interactions through different pathways.

Reproductive opportunity costs

Reproductive opportunity is not a single endpoint that can simply be subtracted from vigilance. Predator presence can reorganize the behavioral sequence leading from host selection through feeding to reproduction even when the exposed adult stage is comparatively difficult for the predator to consume [23]. Differences between greenhouse and field responses further caution against assuming that a response expressed under one setting will have equal strength under another. In the proposed theory, reproductive cost therefore includes disruption or postponement of the behavioral sequence required to reach reproduction, not only a measured decrease in final egg production.

Sex can change both the behavior at risk and the alternative opportunities lost when defense is expressed. Male and female tree crickets alter reproductive tactics differently under spider risk [24]. A reduction in calling, changes in mate-search behavior, or altered female tactics cannot therefore be assigned one sex-independent cost. The relevant opportunity depends on which reproductive behavior the individual would otherwise perform, how that behavior exposes it to predators, and what alternatives remain available under the same ecological conditions.

Sexual signalling illustrates an additional form of discordance. A meta-analysis of predator and other natural-enemy exploitation of sexual signals found substantial heterogeneity among signal modalities and contexts rather than an invariant signalling penalty [25]. In particular, visual signalling did not display the same average pattern reported for some acoustic or olfactory signals. Because the evidence base includes different enemy classes, predator-specific inference must remain more restricted than a general statement about eavesdropping. Signal production is therefore best treated as a conditional exposure pathway, not as evidence that conspicuous reproduction always carries a fixed predation cost.

Reproductive avoidance may instead be expressed through offspring placement. Females of two closely related malaria-vector species differ in larval-habitat selection when presented with predator-associated information [26]. The contrast demonstrates that predator cues do not universally deter mosquito oviposition. Species-specific sensory ecology, habitat evaluation, and the consequences of placing offspring in alternative sites can produce different choices even when the broad reproductive task is comparable. This makes offspring-habitat risk a distinct component of reproductive opportunity rather than a simple extension of adult escape.

Internal resource state can intersect with reproductive and predatory contexts as well. In *Menochilus sexmaculatus*, hunger and predator cues jointly alter cannibalistic behavior [27]. Cannibalism in this system should not be treated as a generic surrogate for feeding or reproduction, but the factorial interaction provides a useful boundary condition: predator information does not operate independently of internal reserves. Reproductive opportunity costs therefore emerge from combinations of behavioral sequence, sex, signalling mode, offspring-placement decisions, and resource state rather than from one universal suppression pathway.

These distinctions are difficult to recover from a single prose continuum because identical labels such as "reduced reproduction" can arise through biologically different routes. The cross-scale grid below separates the reproductive decision states, the evidence through which they are observed, and the boundary conditions that would need to be retained when testing the proposed theory.

Table 1. Reproductive opportunity costs arise through distinct decision states rather than a single suppression pathway

Interpretive consequence · Limits and uncertainty	Research or test · Biological setting	Evidential standing · Evidence
Host-use → reproduction sequence reorganization		
Risk can alter access to reproduction by reorganizing preceding behaviors, even where direct vulnerability of the adult stage is limited **Expression differs between controlled and field settings; disturbance and other environmental differences remain possible**	Measure sequential behaviors and final reproductive endpoints in the same individuals or populations Adult herbivorous beetle in predator-present host environments	Evidence-derived distinction Changes across colonization, feeding, and oviposition behaviors
Sex-specific reproductive tactic displacement		
The opportunity foregone under defense depends on the sex-specific behavior that would otherwise be performed **One species and predator context; sex differences cannot be generalized across insects**	Manipulate comparable risk while quantifying sex-specific mating opportunities, exposure, and subsequent reproduction Male and female tree crickets exposed to spider risk	Evidence-derived distinction Sex-dependent changes in reproductive tactics
Signal-eavesdropping exposure		
Signalling can alter exposure, but the cost is conditional rather than a fixed penalty attached to reproduction **High heterogeneity; enemy classes and sensory modalities must remain separated**	Test predator-specific exposure while manipulating signal modality without assuming equivalent costs Sexual signallers across multiple taxa, modalities, predators and other natural enemies	Evidence-derived distinction Differential natural-enemy exploitation associated with signal modality and context
Offspring-habitat risk allocation		
Reproductive defense can be expressed as where offspring are placed rather than as reduced adult reproductive effort **Closely related species need not respond alike; cue interpretation and habitat quality may covary**	Measure cue perception, alternative habitat quality, oviposition choice, and offspring consequences jointly Female malaria-vector mosquitoes selecting larval habitat	Evidence-derived distinction Species-divergent oviposition choices in response to predator-associated information
Hunger-conditioned reproductive/resource conflict		
Internal reserves can modify behavior within a reproductive/resource context, preventing a risk-only interpretation **Cannibalism ecology is not interchangeable with ordinary foraging or mating behavior**	Factorially manipulate resource state and predator information while retaining behavior-specific endpoints Cannibalistic ladybird under predator information and manipulated hunger	Evidence-derived boundary; integration into the broader opportunity-cost theory is proposed Interaction between internal resource state and predator-cue treatment

Reproductive decisions can also become discordant because information about danger, exposure created by reproductive behavior, and the value of the opportunity at stake need not change together. **Figure 1** therefore uses a triage architecture to distinguish empirically supported sources of reproductive-risk discordance from the proposed theoretical step of deciding which opportunity-cost pathway should be prioritized for testing.

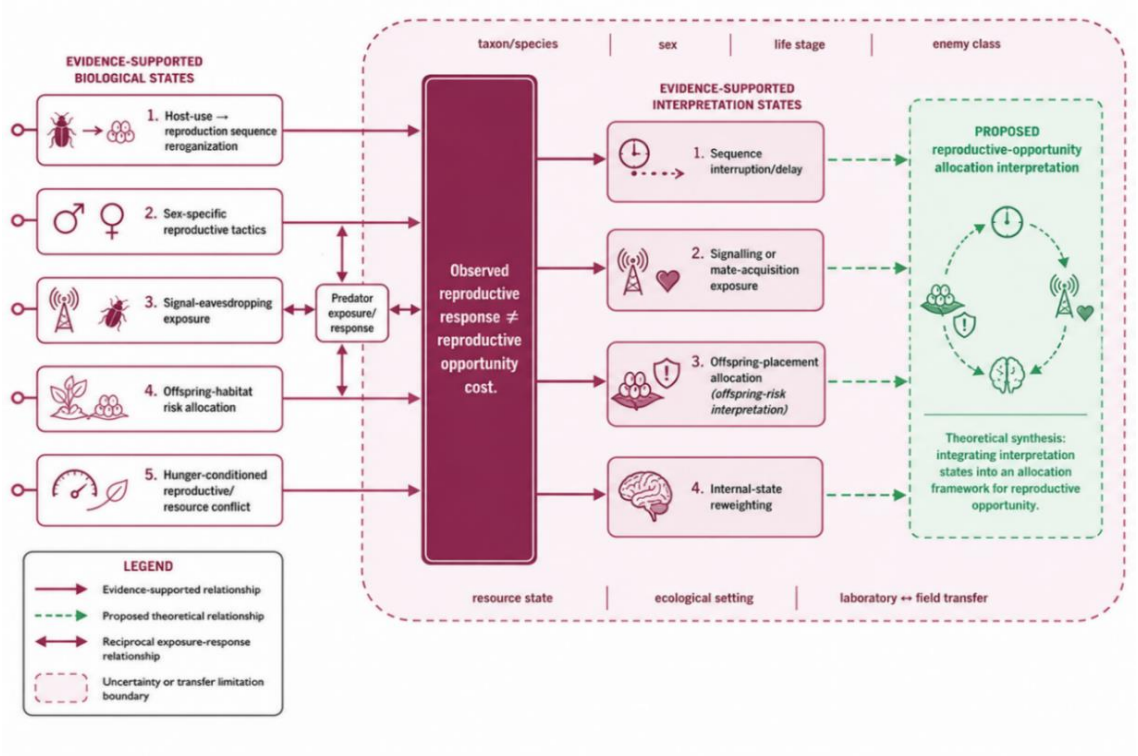


Figure 1. Discordant routes by which predator information can alter insect reproductive opportunity

Immediate versus deferred survival

The survival consequences of predator avoidance operate on more than one timescale. Field observations of *Bombus terrestris* exposed to the invasive hornet *Vespa velutina* associate predator pressure with colony-level consequences, showing that effects of predator presence can extend beyond an individual worker's momentary escape response [28]. Those colony outcomes cannot be attributed solely to non-consumptive fear because direct mortality, disturbance, and other exposure-related processes may coexist. The important theoretical distinction is temporal: avoiding an encounter now and maintaining colony performance over a season are different biological endpoints.

Mosquito evidence similarly argues against collapsing immediate mortality and deferred phenotype into one response. Quantitative synthesis indicates that predators can influence mosquito systems through both consumptive and non-consumptive pathways, with survival and body-size effects not necessarily accompanied by equivalent changes in development time [29]. Endpoint discordance is therefore informative rather than anomalous. An insect can experience a substantial survival effect without every developmental trait changing in parallel, or can survive while carrying altered physiological or life-history consequences forward.

Comparisons among predator regimes add a population-level perspective but require stricter causal limits. In *Leucorrhinia pectoralis*, predator regimes are associated with differences in means and variances of some antipredator traits, while other trait means remain comparatively unchanged [30]. Such distributions are consistent with regime-dependent ecological histories, but observational contrasts cannot by themselves establish predator-driven selection. Habitat covariance, developmental environment, and other ecological differences remain plausible contributors.

Predator risk can also be relatively weak when embedded among other environmental forces. In *Ischnura elegans*, warming and predation risk produced only limited effects on some size-mediated priority outcomes [31]. This negative or weak evidence is essential for the present theory because it prevents risk from becoming an assumed dominant variable. The proposed immediate-versus-deferred distinction therefore permits regions in which

predator information has low behavioral weight because temperature, competitive asymmetry, nutritional condition, or other constraints dominate the current decision state.

Dynamic trade-off surface

Natural insect behavior is generated by simultaneous drivers rather than by predator information alone. Multi-year field analysis of pea-aphid dispersal morph production shows that alate occurrence covaries with several environmental and population factors and that predator-related variables need not dominate those relationships [32]. Consequently, dispersal or activity state in nature cannot be treated as a direct readout of predation risk. Any theory that uses observable behavior to infer defensive allocation must therefore include competing environmental explanations.

The inferred predator regime also depends partly on how predation is measured. Comparisons using live and artificial insect prey can yield different patterns of estimated predation risk [33]. A methodological proxy is therefore not equivalent to the biological process it attempts to represent. This creates an observation boundary around the proposed theory: the latent combination of perceived danger, state, and opportunity cannot be recovered perfectly from any single assay of predator activity or prey response.

Cue identity and biological endpoint can produce further discordance. In *Spodoptera exigua*, auditory cues from predatory wasps affected survival and herbivory, whereas nonpredatory mosquito sounds did not produce equivalent effects; among survivors, some developmental endpoints showed little or no detectable change [34]. The result demonstrates that recognition is cue-specific and that behavioral, survival, and developmental responses need not move together. It does not establish a universal auditory-defense pathway.

These observations support a proposed dynamic trade-off surface in which insect defensive allocation occupies qualitatively different regions according to four interacting dimensions: available threat information, organismal state, the feeding or reproductive opportunity that would be foregone, and whether the relevant consequence is immediate or deferred. The surface is not a quantitative fitness landscape. It has no empirically estimated coordinates, slopes, optima, thresholds, or universal exchange rates. Instead, it represents conditional relationships: high-quality threat information can favor withdrawal in one state yet produce a different response when locomotor condition, morph, sex, hunger, or opportunity structure changes. Equivalent observed inactivity may likewise arise from concealment, energetic limitation, or developmental constraint rather than equivalent perceived danger.

Because those conditionalities can fail for different reasons, a matrix is more informative than a single risk gradient. The following table separates biologically meaningful surface states from the principal conditions under which interpreting them as predator-driven allocation would fail.

Table 2. Conditions that reshape or invalidate inference from positions on the dynamic trade-off surface

Dynamic trade-off surface state	Foundational dimensions	Interpretive and testing dimensions	
	Status · Biological or analytical context · Evidential standing · Biological or analytical setting	**Evidence basis · Interpretation or consequence · Evidence · Interpretive consequence**	**Failure mode or boundary · Research or test · Failure mode or boundary condition**
Predator-weighted allocation	Proposed state, evidence-informed Systems in which predator information is salient relative to competing drivers	Coordinated change in defensive behavior or opportunity use after predator-associated information Defensive allocation may dominate immediate behavior	Cue exposure may not represent realized attack probability Pair cue manipulations with encounter or predation measurements
Opportunity-dominated allocation	Proposed state, evidence-informed High feeding or reproductive value, strong resource limitation, or restricted alternatives	Continued exploitation despite detectable danger Foregone opportunity may outweigh withdrawal in the current state	Continued activity can also reflect poor detection Measure perception and opportunity value separately
State-constrained allocation	Proposed state, evidence-informed Stage, sex, morph, locomotor condition, hunger, or physiological limitation	Different responses to comparable information among organismal states Same external risk can occupy different behavioral regions	State variables may covary with habitat or prior experience Factorially manipulate state and predator information

Deferred-cost region	Proposed state, evidence-informed Cross-stage or longer-term exposure histories	Weak immediate change paired with later physiological, life-history, or reproductive differences Present behavior may underestimate downstream cost	Deferred endpoints may arise from density, stress, or development rather than defense itself Use longitudinal designs linking exposure, behavior, and later phenotype
Multicausal field state	Evidence-derived boundary Natural environments with temperature, resource, density, host, and enemy variation	Behavior or morphology explained by several simultaneous environmental variables Predator-related allocation is only one contributor	Environmental covariation can mimic predator effects Combine experimental manipulation with repeated field measurements
Observation-discordant state	Evidence-derived boundary Predation or risk quantified by different assay types	Live-prey and proxy methods yield different apparent patterns The measured regime may not faithfully represent biological risk	Proxy-specific artefacts alter inference Validate multiple risk measures against biologically relevant prey responses
Cue–endpoint discordance	Evidence-derived boundary Sensory systems in which predator and nonpredator stimuli or downstream endpoints differ	Specific cues change some behavioral or survival endpoints while others remain unchanged Response architecture is multidimensional	A single endpoint can conceal null or opposite responses elsewhere Measure cue discrimination and multiple outcome classes together

The topology of the proposed surface is best understood as a set of parallel decision lanes separated by explicit observation and inference boundaries rather than as a single continuum. **Figure 2** compresses those conditional pathways while preserving where evidence ends and the article's theoretical synthesis begins.

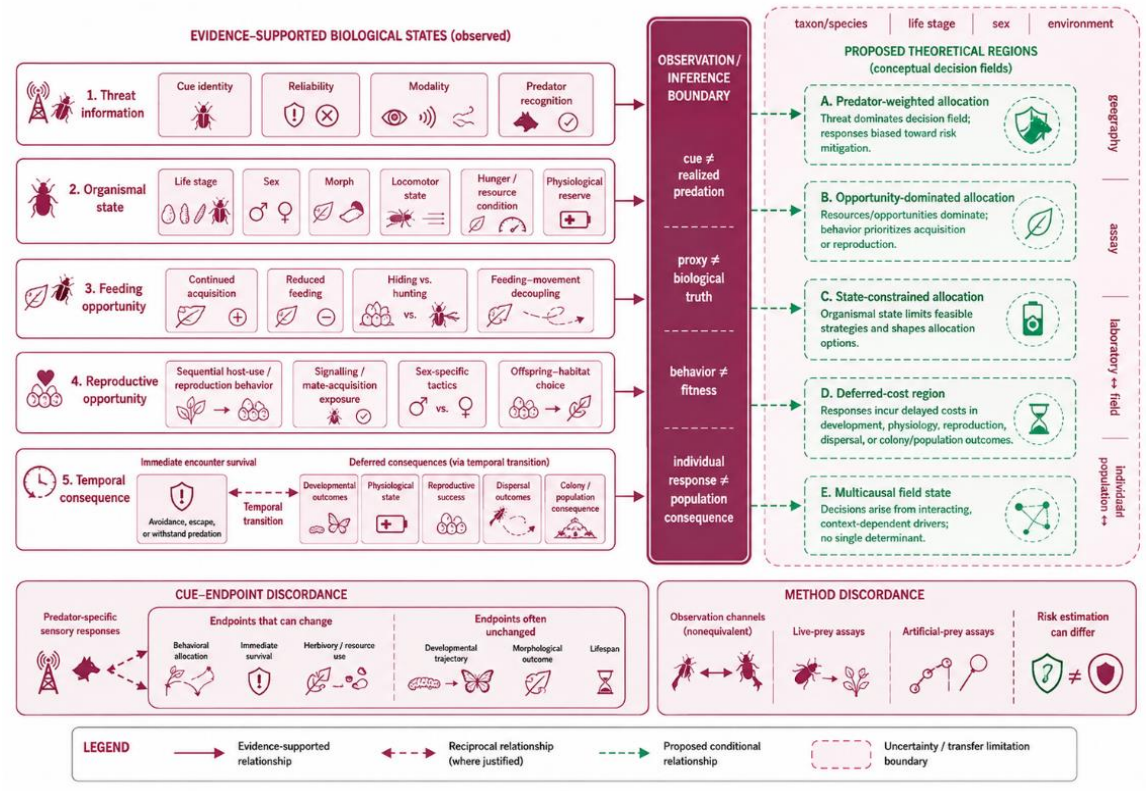


Figure 2. Parallel decision lanes defining where predator information does—and does not—dominate insect allocation

Predictions across predator regimes

Predator regimes need not generate linear or monotonic trait responses. Formal theory examining interactions between predation and sexually selected traits demonstrates that nonlinear and potentially complex eco-evolutionary dynamics can arise under different parameter regimes [35]. That model is not an empirical validation of the present insect framework, but it establishes that predation need not translate into a simple gradient of increasingly defensive phenotypes.

The proposed theory therefore predicts that persistent, reliable risk should more often shift allocation toward predator-weighted regions when the cues available to the insect repeatedly correspond to consequential encounters. This prediction remains conditional: predator identity can alter recognition, and continuing to hide rather than hunt may be favored only where the opportunity lost through reduced feeding does not become overriding. The prediction is falsified if manipulating risk persistence while holding resource and organismal state constant produces no systematic change in the relevant defensive allocation.

Under intermittent or ambiguous risk, greater switching among behavioral alternatives is predicted because information reliability is lower and the cost of repeatedly abandoning feeding or reproductive opportunities can accumulate. This does not require increased "boldness"; it predicts weaker dominance of predator information over other variables. Where environmental forces rival or exceed predator effects, the theory predicts particularly weak regime separation, consistent with experimental evidence that predation risk can produce limited effects in some multi-driver contexts [31]. Natural-field tests should also expect multicausality rather than treating predator abundance as the sole explanation for dispersal or state variation [32].

Cue modality should further change regime-specific predictions. Chemical, visual, and auditory information differ in persistence, spatial structure, and biological meaning. Consequently, predator regimes defined only by predator density may predict behavior poorly if the information actually available to insects differs among environments. The proposed predictions are therefore about perceived and state-filtered regimes, not predator counts alone.

Results and Discussion

The central contribution of this article is a shift from interpreting insect predator avoidance as a single continuum of defensive intensity toward interpreting it as conditional allocation among competing biological opportunities. Existing terminology already requires separation between risk-induced responses and their downstream consequences [1]. The additional step proposed here is to organize those responses through threat information, organismal state, foregone opportunity, and temporal consequence without assigning fixed exchange rates among them.

Heterogeneity is not merely statistical noise around an assumed universal response. Life stage can alter state dependence, closely related mosquito species and sexes can differ in deferred responses, and reproductive tactics can diverge between sexes within one species. These boundaries argue against transferring a decision rule from one insect taxon, stage, or sex to another without direct testing. The theory therefore predicts conditional equivalence rather than behavioral uniformity: different mechanisms may generate similar apparent inactivity, and similar predator information may generate different actions.

The most important limitation is evidence transfer. Individual behavioral or physiological change does not establish a population consequence [4], and natural-field demonstrations linking risk-induced responses to observed ecological patterns remain comparatively uncommon [5]. Validation should therefore measure multiple levels sequentially: information available to the insect, defensive behavior, displaced feeding or reproduction, immediate survival, deferred phenotype, and—where appropriate—population consequences. Field designs should also quantify competing environmental drivers rather than attributing residual variation to predation.

Measurement choice represents another validation problem. If live and artificial prey produce different apparent risk patterns [33], then tests of the proposed surface should avoid treating a single predation proxy as ground truth. Likewise, observation of reduced activity alone cannot distinguish concealment from low energetic state, developmental constraint, or other environmental limitation. Strong tests will require factorial manipulation of predator information and organismal state combined with longitudinal outcome measurement.

The dynamic trade-off surface should therefore be treated as falsifiable theoretical organization rather than a validated predictive model. Its useful tests are not demonstrations that every insect becomes more vigilant as risk rises. More discriminating tests ask whether changes in cue reliability, resource condition, life stage, sex, morph, or locomotor state alter the relationship between defensive behavior and the opportunities that are forgone. Failure

of those conditional relationships would require revision of the framework rather than reinterpretation of every null result as hidden antipredator behavior.

Conclusion

Predator avoidance in insects cannot be reduced to a fixed exchange between vigilance and fitness. Detection, defensive execution, feeding, reproduction, immediate survival, and deferred consequences are biologically separable, and their relationships vary with organismal state and ecological context. The proposed dynamic trade-off theory organizes this heterogeneity through threat information, state, foregone opportunity, and temporal consequence while preserving explicit boundaries between observed behavior and inferred biological cost.
Its principal implication is qualitative rather than quantitative: the same predator information need not produce the same behavior, and the same behavior need not indicate the same underlying trade-off. Predator avoidance should therefore be evaluated as conditional allocation across competing opportunities rather than as a universal increase in defensive effort. Empirical progress will depend on experiments and field studies that manipulate state and risk jointly, measure multiple behavioral and life-history endpoints across time, and test when predator information actually dominates other environmental drivers.

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References

1. Peacor SD, Barton BT, Kimbro DL, Sih A, Sheriff MJ. A framework and standardized terminology to facilitate the study of predation-risk effects. Ecology. 2020;101(12). doi:10.1002/ecy.3152
2. Hermann SL, Landis DA. Scaling up our understanding of non-consumptive effects in insect systems. Curr Opin Insect Sci. 2017;20:54-60. doi:10.1016/j.cois.2017.03.010
3. Buchanan AL, Hermann SL, Lund M, Szendrei Z. A meta-analysis of non-consumptive predator effects in arthropods: Influence of organismal and environmental characteristics. Oikos. 2017;126(9):1233-40. doi:10.1111/oik.04384
4. Sheriff MJ, Peacor SD, Hawlena D, Thaker M. Non-consumptive predator effects on prey population size: A dearth of evidence. J Anim Ecol. 2020;89(6):1302-16. doi:10.1111/1365-2656.13213
5. Peacor SD, Dorn NJ, Smith JA, Peckham NE, Cherry MJ, Sheriff MJ, et al. A skewed literature: Few studies evaluate the contribution of predation-risk effects to natural field patterns. Ecol Lett. 2022;25(9):2048-61. doi:10.1111/ele.14075
6. Ower GD, Juliano SA. The demographic and life-history costs of fear: Trait-mediated effects of threat of predation on Aedes triseriatus. Ecol Evol. 2019;9(7):3794-806. doi:10.1002/ece3.5003
7. Adamo SA, McKee R. Differential effects of predator cues versus activation of fight-or-flight behaviour on reproduction in the cricket Gryllus texensis. Anim Behav. 2017;134:1-8. doi:10.1016/j.anbehav.2017.09.027
8. Singh P, Wolthaus J, Schielzeth H, Müller C. State dependency of behavioural traits is a function of the life stage in a holometabolous insect. Anim Behav. 2023;203:29-39. doi:10.1016/j.anbehav.2023.06.013
9. Hermann SL, Bird SA, Ellis DR, Landis DA. Predation risk differentially affects aphid morphotypes: Impacts on prey behavior, fecundity and transgenerational dispersal morphology. Oecologia. 2021;197(2):411-9. doi:10.1007/s00442-021-05037-z
10. Roux O, Renault D, Mouline K, Diabaté A, Simard F. Living with predators at the larval stage has differential long-lasting effects on adult life history and physiological traits in two anopheline mosquito species. J Insect Physiol. 2021;131:104234. doi:10.1016/j.jinsphys.2021.104234

11. Basu S, Clark RE, Fu Z, Lee BW, Crowder DW. Insect alarm pheromones in response to predators: Ecological trade-offs and molecular mechanisms. Insect Biochem Mol Biol. 2021;128:103514. doi:10.1016/j.ibmb.2020.103514
12. Bertleff D, Diekmann J, Brand S, Ünlü AG, Bucher R. Predation and avoidance behaviour in aphid-ladybird interactions of native and invasive ladybirds in Europe. Ecol Entomol. 2021;46(1):41-7. doi:10.1111/een.12938
13. Andrade MR, Albeny-Simões D, Breaux JA, Juliano SA, Lima E. Are behavioural responses to predation cues linked across life cycle stages? Ecol Entomol. 2017;42(1):77-85. doi:10.1111/een.12358
14. von Reyn CR, Nern A, Williamson WR, Breads P, Wu M, Namiki S, et al. Feature integration drives probabilistic behavior in the Drosophila escape response. Neuron. 2017;94(6):1190-204.e6. doi:10.1016/j.neuron.2017.05.036
15. Zacarias R, Namiki S, Card GM, Vasconcelos ML, Moita MA. Speed dependent descending control of freezing behavior in Drosophila melanogaster. Nat Commun. 2018;9(1):3697. doi:10.1038/s41467-018-05875-1
16. Kim H, Park H, Lee J, Kim AJ. A visuomotor circuit for evasive flight turns in Drosophila. Curr Biol. 2023;33(2):321-35.e6. doi:10.1016/j.cub.2022.12.014
17. Cinel SD, Hahn DA, Kawahara AY. Predator-induced stress responses in insects: A review. J Insect Physiol. 2020;122:104039. doi:10.1016/j.jinsphys.2020.104039
18. Gavini SS, Quintero C, Tadey M. Intraspecific variation in body size of bumblebee workers influences anti-predator behaviour. J Anim Ecol. 2020;89(2):658-69. doi:10.1111/1365-2656.13135
19. Kansman JT, Nersten CE, Hermann SL. Smelling danger: Lady beetle odors affect aphid population abundance and feeding, but not movement between plants. Basic Appl Ecol. 2023;71:1-8. doi:10.1016/j.baae.2023.05.004
20. Tian W, Hawlena D, Pagès JF, Zhong Z, Wang D. Fear of predators alters herbivore regulation of soil microbial community function. Ecol Evol. 2023;13(7). doi:10.1002/ece3.10207
21. Sysiak M, Pietrzak B, Kubiak M, Bednarska A, Mikulski A. Chemical cannibalistic cues make damselfly larvae hide rather than hunt. Sci Rep. 2023;13(1):13556. doi:10.1038/s41598-023-40732-2
22. Lee BW, Basu S, Bera S, Casteel CL, Crowder DW. Responses to predation risk cues and alarm pheromones affect plant virus transmission by an aphid vector. Oecologia. 2021;196(4):1005-15. doi:10.1007/s00442-021-04989-6
23. Hermann SL, Thaler JS. The effect of predator presence on the behavioral sequence from host selection to reproduction in an invulnerable stage of insect prey. Oecologia. 2018;188(4):945-52. doi:10.1007/s00442-018-4202-7
24. Torsekar VR, Balakrishnan R. Sex differences in alternative reproductive tactics in response to predation risk in tree crickets. Funct Ecol. 2020;34(11):2326-37. doi:10.1111/1365-2435.13652
25. White TE, Latty T, Umbers KDL. The exploitation of sexual signals by predators: A meta-analysis. Proc Biol Sci. 2022;289(1976):20220444. doi:10.1098/rspb.2022.0444
26. Sougué E, Dabiré RK, Roux O. Larval habitat selection by females of two malaria vectors in response to predation risk. Acta Trop. 2021;221:106016. doi:10.1016/j.actatropica.2021.106016
27. Yadav T, Omkar, Mishra G. Effect of the presence of predatory cues and hunger on cannibalistic behaviour of ladybird beetle, Menochilus sexmaculatus Fabricius (Coleoptera: Coccinellidae). Ecol Entomol. 2023;48(1):1-10. doi:10.1111/een.13196
28. O'Shea-Wheller TA, Curtis RJ, Kennedy PJ, Groom EKJ, Poidatz J, Raffle DS, et al. Quantifying the impact of an invasive hornet on Bombus terrestris colonies. Commun Biol. 2023;6(1):990. doi:10.1038/s42003-023-05329-5
29. Russell MC, Herzog CM, Gajewski Z, Ramsay C, El Moustaid F, Evans MV, et al. Both consumptive and non-consumptive effects of predators impact mosquito populations and have implications for disease transmission. Elife. 2022;11. doi:10.7554/eLife.71503
30. Jiang B, Zhang Y, Mauersberger R, Schiel FJ, Mikolajewski DJ. Predation promotes diversification in the mean and variance of antipredator traits. Ecol Entomol. 2022;47(4):679-88. doi:10.1111/een.13152
31. Raczyński M, Stoks R, Sniegula S. Warming and predation risk only weakly shape size-mediated priority effects in a cannibalistic damselfly. Sci Rep. 2022;12(1):17324. doi:10.1038/s41598-022-22110-6

32. Bosch MJ, Ives AR. Identifying environmental factors affecting the production of pea aphid dispersal morphs in field populations. Ecol Entomol. 2023;48(5):597-609. doi:10.1111/een.13257
33. Zvereva EL, Kozlov MV. Predation risk estimated on live and artificial insect prey follows different patterns. Ecology. 2023;104(3). doi:10.1002/ecy.3943
34. Lee ZA, Cohen CB, Baranowski AK, Berry KN, McGuire MR, Pelletier TS, et al. Auditory predator cues decrease herbivore survival and plant damage. Ecology. 2023;104(4). doi:10.1002/ecy.4007
35. Lerch BA, Servedio MR. Predation drives complex eco-evolutionary dynamics in sexually selected traits. PLoS Biol. 2023;21(4). doi:10.1371/journal.pbio.3002059