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Foraging, Risk Taking, and Habitat Choice Shift with Internal State Rather Than Reflecting Fixed Behavioral Strategies in Insects

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ABSTRACT

Insect behavior is often described with apparently stable categories such as bold, cautious, selective, persistent, or opportunistic. These labels can obscure within-individual changes produced by energetic, reproductive, developmental, and informational state. This behavioral theory integrates insect personality, neuroethology, nutritional ecology, reproductive behavior, and habitat-choice evidence to distinguish persistent between-individual variation from reversible state-dependent reweighting of cues and actions. The argument is not that stable behavioral types are absent, but that foraging, risk-taking, and habitat-choice phenotypes should not be treated as fixed strategies by default. Evidence supports state-dependent shifts in food seeking, sensory valence, aggression, courtship, oviposition choosiness, host seeking, and thermal preference. Important limits remain: some behavioral components are unchanged, mechanistic evidence is taxonomically concentrated, field associations do not identify causal state pathways, and behavioral change does not establish fitness consequences. The article therefore proposes a state-dependent decision surface in which individual baselines coexist with changing energetic, reproductive, developmental, and information states. Its ecological predictions require repeated-measures and field validation.

Keywords: Behavioral plasticity, Internal state, Foraging decisions, Risk taking, Habitat choice, Insect behavioral ecology

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Introduction

Repeatable between-individual differences occur in insects without demonstrating that behavioral consistency is necessarily immutable or constitutes an integrated life-history strategy [1, 2]. The central problem is therefore not whether insects can differ consistently, but whether a behavioral snapshot should be interpreted as a fixed strategy. Behavioral expression is condition dependent rather than invariant across environmental or physiological contexts [3, 4]. Between-individual consistency and within-individual plasticity consequently occupy different analytical levels. A population may contain different behavioral baselines while each individual still moves through state-dependent regimes. Treating these levels as alternatives risks assigning to "personality" variation that is partly state driven, or assigning to state differences that are actually persistent.

Direct neural evidence makes the distinction concrete. In *Drosophila*, flight state alters coupling between a visual sensory pathway and landing output [5]. The same class of sensory information therefore need not generate the same action in different behavioral states. This is an existence proof, not a universal insect circuit.

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This article proposes that energetic condition, reproductive status, developmental stage, information about current opportunities, and recent experience should be tested before observed foraging, risk taking, or habitat choice is labelled a fixed strategy. Stable individual differences remain possible as baselines or sensitivities. The contribution is to place those baselines inside a dynamic decision architecture and to specify the limits of that interpretation.

Theoretical methods and state variables

This is a behavioral theory constructed by comparative conceptual synthesis. No new observations, pooled estimates, fitted utility functions, or quantitative thresholds are introduced. Evidence is used to identify state variables when studies manipulate, measure, or mechanistically link those variables to behavior; broader reviews define boundaries across related systems. Because taxa, life stages, behavioral assays, and levels of analysis differ, the resulting architecture is qualitative.

Energetic state should not be represented automatically by body mass or stored reserves. In *Drosophila*, SIFamide-linked circuitry integrates hunger-related information into appetitive and feeding responses [6]. Hunger and satiety pathways also converge on mushroom-body outputs that bidirectionally regulate food seeking [7]. These findings justify treating energetic state as a regulated control variable that changes action valuation while leaving its best physiological proxy taxon dependent.

State effects can extend beyond feeding. Feeding status shifts temperature preference through insulin signaling in *Drosophila* warm-sensing neurons [8]. Nutritional change can therefore alter an abiotic preference relevant to microhabitat use, although laboratory thermotaxis is not equivalent to realized field occupancy.

Reproductive state is a separate axis. Female mosquito host seeking changes across the gonotrophic cycle, including suppression after a blood meal and later recovery [9]. Developmental state adds another: hormonal maturation gates motivational circuitry controlling male *Drosophila* sexual behavior [10]. These examples show why hunger, reproductive phase, and developmental readiness should not be collapsed into one generic motivation score.

The proposed state representation is therefore vector-like. Energetic demand, reproductive condition, developmental status, current information, and recent experience may covary, but each can alter cue value or action priority differently. Observed behavior is treated as their conditional output interacting with external opportunities and individual-specific baselines.

Results and Discussion

Energetic state changes both resource valuation and the costs an insect will accept. *Drosophila* larvae alter food intake and food-choice trade-offs after crossing critical weight [11]. The same nutritional option therefore need not have the same value before and after a developmental transition.

Predation-risk evidence rejects a simple hunger-to-boldness rule. In Colorado potato beetle larvae, nutritional condition changes the balance between behavioral and physiological responses to predation risk rather than uniformly suppressing danger responsiveness [12]. “Risk taking” can thus be misclassified if only locomotor or avoidance behavior is measured.

At a proximal level, CCAP regulation of the NPF pathway alters adult *Drosophila* feeding and sugar responsiveness [13]. More strikingly, food deprivation can switch selected larval odors from repulsive to attractive, with corresponding changes evident in early olfactory processing [14]. Here the sign of a preference changes, making a stable preference label especially misleading.

Energetic stress can also increase costly social behavior. Food-deprived male *Drosophila* become more aggressive in laboratory resource competition [15]. This does not establish that hunger generally increases aggression; rather, it shows that low energetic state can raise the relative value of a contested resource enough to change behavior.

The evidence therefore supports state-dependent sensory valuation, redistribution among response modes, and context-dependent changes in resource defense. None requires denying stable individual differences. It requires measuring state before interpreting consistent behavior as a fixed foraging or risk strategy.

Reproductive state and risk acceptance

Reproduction creates competing priorities not captured by energetic state alone. Adult diet alters components of *Drosophila* mate preference and attractiveness, but not as one uniform reproductive shift [16]. Courtship rate, attractiveness, acceptance, and choosiness must therefore remain separate outputs.

Resource history makes this clearer. Food deprivation reduces *Drosophila* mating rate, yet a food-rich current environment can rapidly reverse that reduction while mate choice remains unchanged [17]. One reproductive component can thus reverse while another remains stable, arguing against a single strategy axis.

Cross-order evidence adds sex and timing dependence. In *Nicrophorus vespilloides*, nutrition during sexual maturation and at mating affects reproductive behavior differently in males and females [18]. In *Pieris rapae*, adult nutritional stress reduces oviposition choosiness and fecundity, while developmental and adult nutritional effects are not interchangeable [19]. Apparent host-use strategy can therefore change with both current condition and nutritional history.

Competing-drive studies provide a mechanistic basis. Nutritional status changes how male *Drosophila* balance sleep and courtship in a time- and context-dependent manner [20]. When deprived of both food and sexual opportunity, males can shift priority toward feeding through a defined neuronal mechanism that oppositely regulates feeding and courtship [21]. This supports arbitration among needs without establishing a universal common currency.

Reproductive risk acceptance should consequently be interpreted relatively. The value of mating, oviposition, or host acquisition changes with sex, reproductive phase, nutritional history, and available alternatives. The proposed theory therefore treats reproductive state as changing the rank order of actions rather than creating a permanently high- or low-risk phenotype.

Information state and habitat choice

Habitat choice depends on information, but cues do not have fixed meanings independent of the receiver. Gravid *Aedes aegypti* females are attracted to geosmin-associated oviposition sites [22]. The cue's positive value is therefore reproductive- and taxon-specific rather than a universal property of geosmin.

Mosquito nectar acquisition likewise depends on multimodal sensory information, resource availability, sex, species, and physiological context [23]. Here, "information state" denotes the interaction between what the environment makes detectable and what the insect is currently prepared to value, not an isolated internal information store.

Field evidence cautions against converting laboratory cue responses into habitat mechanisms. In New York *Aedes albopictus*, sugar-feeding patterns covary with saturation deficit, floral conditions, sex, and host-seeking status [24]. These associations establish ecological conditionality but do not identify whether weather changes sensory sampling, metabolic demand, resource access, or several processes together.

Development can also remap abiotic information. *Drosophila* larvae shift temperature preference across development through changes involving ionotropic-receptor-dependent cool-sensing cells [25]. Preference plasticity is therefore demonstrable, but corresponding field habitat relocation is not.

The central interpretive question is whether detection becomes attraction, avoidance, persistence, or switching under a particular state. A conditionality matrix is needed because the principal failure modes arise at different levels—cue valuation, physiological state, ecological context, and inference—rather than along one continuum.

Table 1. State-contingent meanings of environmental information in insect habitat choice

Biological setting · State-contingent interpretation	Evidence · Failure mode if treated as	Discriminating test · Evidential standing
Reproductive-phase cue gating		
Mosquito host seeking or oviposition **Cue priority changes with reproductive state**	Responsiveness changes across reproductive phases Species-level "preference" hides within-female switching	Repeat matched assays across gonotrophic phases Evidence-supported
Nutritional remapping of abiotic preference		
Fed versus deprived flies **Energetic state changes habitat-relevant valuation**	Preferred temperature shifts Laboratory preference is mistaken for a fixed habitat optimum	Link state manipulation to repeated choice and field use Evidence-supported
Cue-valence reversal		

Fed versus deprived larvae **State changes cue value, not only response strength**	Selected odor responses change sign Opposite responses are averaged into a misleading mean	Test the same cue across defined state transitions Evidence-supported
Multimodal resource interpretation		
Nectar-seeking mosquitoes **External information is filtered by current need**	Several cue classes and resource conditions contribute One modality is assigned context-free control	Cross cue combinations with physiological state Evidence-supported
Field context decoupling		
Free-ranging mosquitoes **Realized use reflects coupled ecological contexts**	Sugar status covaries with weather, flowers, and host seeking Association is read as a direct hunger mechanism	Pair field observation with state measurement and perturbation Evidence-supported
Developmental thermal remapping		
Larvae across development **Development changes the value of a shared thermal landscape**	Stage-dependent thermal preference One preferred temperature is generalized across stages	Combine stage-resolved choice with field exposure Evidence-supported
State–information interaction		
Cross-context theoretical construct **Proposed — habitat choice reflects state × cue availability × individual sensitivity**	Convergent pattern across the preceding configurations State or environment alone is treated as sufficient	Fit repeated-measures interaction models Proposed synthesis

These cross-level relationships are difficult to recover from a single behavioral endpoint. The visual architecture therefore needs to separate internal state, environmental information, sensory valuation, behavioral selection, and realized habitat use while retaining the boundaries between laboratory mechanism, field choice, and fitness inference.

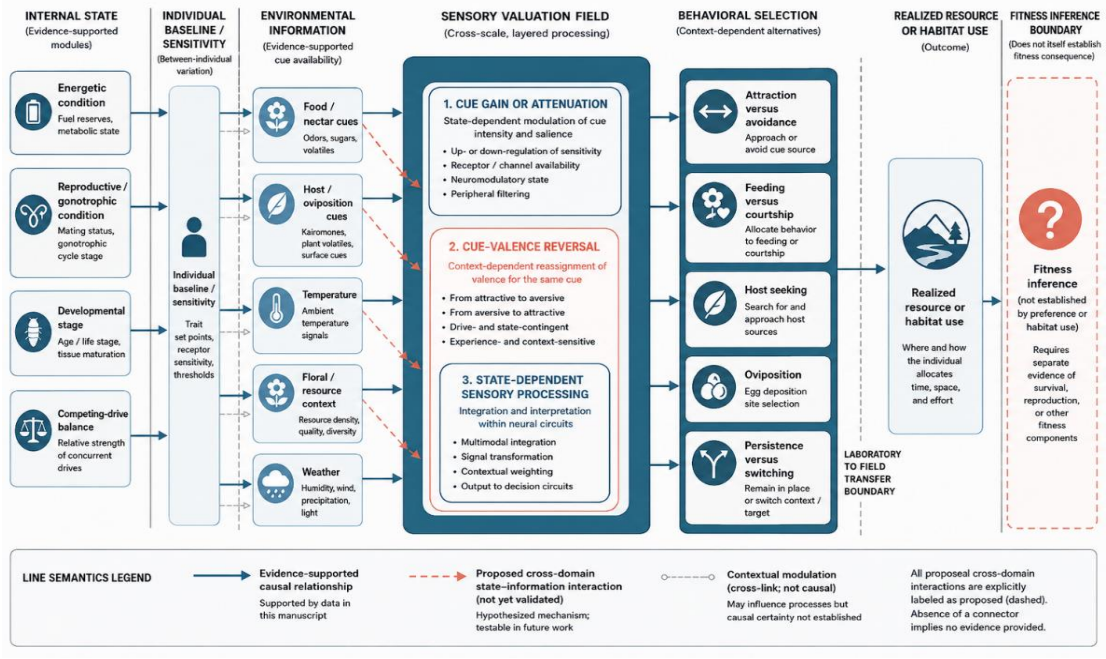


Figure 1. State-gated cue meaning across the path from sensory information to insect habitat use

State transitions and behavioral reversals

A state-dependent theory must explain apparent reversals as well as gradual modulation. First, the relevant latent state may differ from the proxy used to measure it. In *Aedes albopictus*, sugar feeding delays host seeking, but host-seeking variation tracks fat-body vitellogenin expression more closely than simple energy-reserve levels,

with RNAi evidence supporting a regulatory role [26]. Body condition alone can therefore miss the physiological variable governing behavior.

Reproductive transitions can also be coordinated molecularly. In *Drosophila* females, disruption of a defined miRNA-associated regulatory program makes virgins express elements of a post-mated behavioral state [27]. This shows that a coordinated behavioral state can switch without implying that the same molecular mechanism operates across insects.

State is also represented within sensory-value systems. Dopaminergic population activity in the *Drosophila* mushroom body jointly reflects stimulus valence and physiological or behavioral state [28]. Such coding supports state × information interaction, but not a universal scalar utility signal.

Behavioral change must remain separate from downstream performance. In *Nicrophorus vespilloides*, maternal food deprivation changes egg laying and care without a corresponding detectable reduction in the measured offspring-performance endpoints [29]. A state-dependent behavioral response is therefore not automatically adaptive, maladaptive, or fitness neutral.

Acute plasticity must likewise remain distinct from evolutionary change. Experimental starvation-selection history alters courtship-related behavior in *Drosophila* [30]. These evolved baseline shifts are not equivalent to an individual's reversible response to current deprivation.

Finally, stable-like profiles and experience effects can coexist. In male *Gryllus bimaculatus*, some differences between eventual winners and losers are detectable before fighting and become stronger after contest experience [31]. Pre-contest differences resist an all-state explanation; post-contest changes resist an immutable-strategy explanation.

Behavioral reversal is therefore defined here as a change in the mapping from cue or opportunity to action following a physiologically, developmentally, reproductively, or experientially meaningful transition. The strongest inference is not that insects switch among universal discrete strategies, but that strategy stability is an empirical question. Repeated measurements across identified state transitions are required before a fixed-strategy interpretation is preferred.

Unified state-dependent decision surface

The preceding evidence supports a proposed state-dependent decision surface rather than a single behavioral axis. Hunger and satiety can bidirectionally regulate food seeking [7]. Food deprivation can reverse the valence of particular olfactory cues [14]. Competing food and sexual needs can also change behavioral priority [21]. Together, these findings justify a conceptual surface in which the relative value of available actions varies with current state, while the exact mathematical form remains unspecified.

Stable individual differences are incorporated as baselines or sensitivities rather than treated as incompatible with state dependence. Persistence across developmental transitions can occur [1]. Repeatable risk-related differences can exist without an integrated behavioral syndrome or demonstrated resource-acquisition payoff [2]. Cricket aggression profiles likewise contain pre-existing differences that are further modified by contest experience [31]. The proposed surface therefore permits individuals to occupy different starting positions or respond with different sensitivities while still changing behavior as state changes.

No single physiological variable should define location on the surface. Feeding state can alter thermal preference through insulin-dependent sensory regulation [8], whereas mosquito host seeking can depend on vitellogenin-related regulation not captured by bulk energy reserves [26]. Dopaminergic populations can jointly represent stimulus valence and aspects of physiological or behavioral state [28]. These mechanisms are not assumed to be homologous or interchangeable. The proposed model is consequently multidimensional and mechanism-agnostic at the cross-taxonomic level.

The surface is not intended as a hidden common-currency scale. Its coordinates represent distinct biological conditions whose relevance may differ among decisions and taxa. A state variable may strongly affect feeding yet weakly affect mate choice, or alter sensory gain without changing the final action when another need dominates. Validation should therefore estimate state-specific reaction norms or transition responses rather than force all behaviors onto one latent score.

Ecological predictions

The first prediction is that within-individual reversals should be most detectable near identifiable state transitions rather than when individuals are sampled repeatedly within a narrow state range. Cue-valence reversal under food

deprivation supports this expectation [14]. Mating rate can recover rapidly when current food conditions improve [17]. Developmental switching in thermal preference provides another transition-dependent example [25]. The prediction itself remains unvalidated outside the systems in which these changes were observed.

Second, realized resource and habitat use should depend jointly on internal state and the distribution of informative environmental cues. Mosquito host seeking changes across reproductive state [9]. Gravid females can use geosmin as an oviposition cue [22]. Field sugar-feeding patterns also covary with weather, floral conditions, and host-seeking status [24]. Similar environments may therefore produce different choices when physiological state differs, while similar states may produce different choices when available information differs.

Third, population-level repeatability may coexist with state-dependent shifts in mean behavior or covariance. Environmental exposure can alter behavioral expression while repeatability remains detectable [3]. Cricket profiles similarly combine antecedent individual differences with experience-dependent change [31]. Repeated-measures studies should consequently estimate both between-individual variation and within-individual state responsiveness.

Fourth, behavioral plasticity should not be used as a proxy for fitness consequence. Repeatable behavioral variation in a parasitoid wasp did not yield a clear life-history payoff [2]. Food-deprived burying beetle mothers altered parental behavior without corresponding detectable reductions in the measured offspring-performance endpoints [29]. Validation must therefore proceed from state to behavior, ecological encounter, performance, and ultimately fitness rather than assuming those links.

Prediction tests should also sample state transitions at ecologically meaningful temporal resolution. Measurements separated too widely may miss short-lived reversals, whereas measurements confined to one state may exaggerate apparent consistency. Sampling should therefore be aligned with independently justified physiological, developmental, reproductive, or experiential transitions.

These predictions differ in the observable trait, the process being inferred, and the downstream consequence that requires independent testing. A trait–process–consequence map makes those inferential separations explicit.

Table 2. Ecological predictions that separate state-sensitive traits from processes and downstream consequences

Proposed prediction	Evidential standing · Observable trait or comparison	Process to test	Required validation	Ecological consequence that cannot be · Principal limit
Transition-zone reversal	Proposed prediction Same individual before and after a defined state transition	State-dependent change in cue or action valuation	Repeated within-individual measurements spanning the transition	Persistent change in resource use Transition may be cue-, stage-, or behavior-specific
State × information dependence	Proposed prediction Same cue landscape under different physiological states	Conditional weighting of environmental information	Crossed state and cue manipulation with field follow-up	Realized habitat redistribution Laboratory preference may not predict field occupancy
Repeatability with plasticity	Proposed prediction Individuals repeatedly measured across changing contexts	Different baselines plus different state sensitivities	Repeated-measures estimation of individual state responsiveness	Permanently discrete behavioral strategies Repeatability can persist despite shifted means or covariance
Risk-response reallocation	Proposed prediction Behavioral and physiological responses measured together	State-dependent allocation among response channels	Multimodal response measurement under controlled risk	Higher or lower mortality risk One behavioral endpoint may misclassify total risk response
Reproductive-priority switching	Proposed prediction Feeding, mating, host-seeking, or oviposition decisions across reproductive states	Re-ranking of competing actions	State-resolved reproductive and ecological performance measures	Increased reproductive success Sex, stage, and reproductive phase constrain transfer

Behavior–performance decoupling	Proposed prediction Behavioral change paired with offspring or life-history outcome	Whether plasticity changes downstream performance	Longitudinal performance and fitness-component measurement	Fitness benefit or cost Measured performance is not lifetime fitness
Plasticity–selection separation	Proposed prediction Acute deprivation contrasted with selected or historically stressed populations	Reversible state response versus evolved baseline difference	Acute-state manipulation plus common-garden or selection-history comparison	Adaptation to resource stress Similar phenotypes may arise through different processes

The temporal logic of these predictions matters because the same insect can enter, leave, and re-enter biologically distinct states. **Figure 2** therefore retains successive state updates, individual baselines, and inferential boundaries rather than reducing behavior to movement along a permanent category.

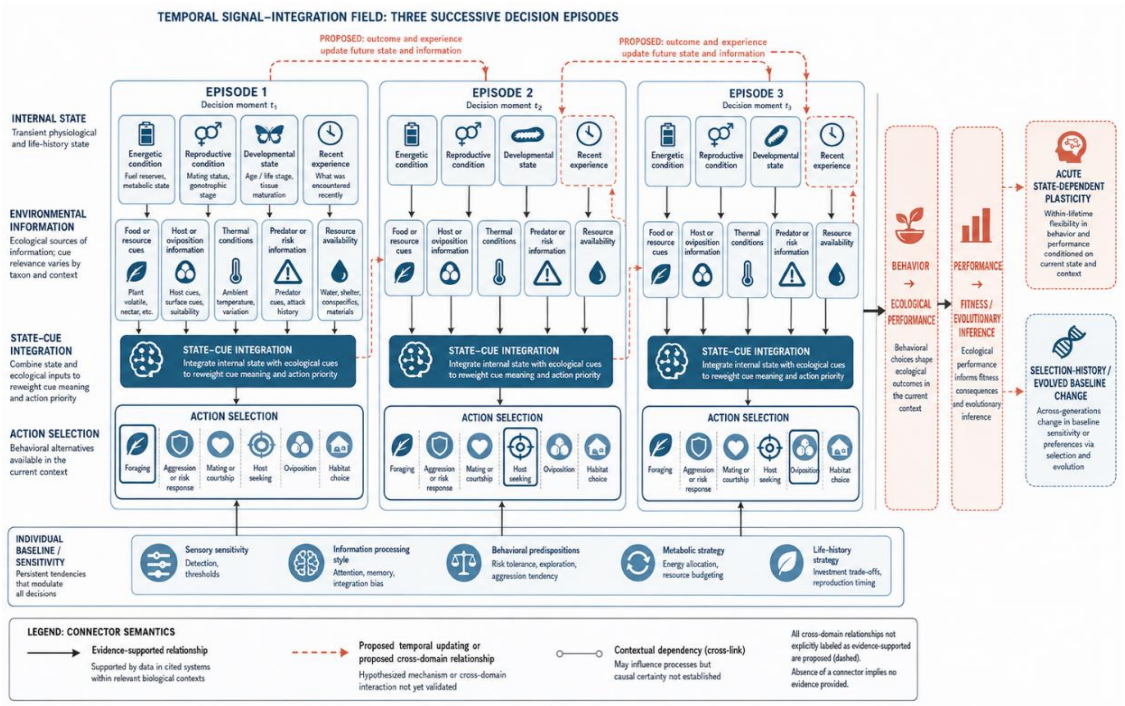


Figure 2. Temporal updating of insect decisions across changing internal state, environmental information, and inference boundaries

The evidence supports a narrower but stronger claim than generalized behavioral fluidity. Mechanistic resolution is concentrated in *Drosophila* and mosquitoes, as reflected in syntheses of state-dependent neural plasticity [4]. Mosquito reproductive state provides a particularly clear ecological example of changing host-seeking motivation [9]. Competing-drive arbitration has been resolved mechanistically in male *Drosophila* [21]. Vitellogenin-associated host-seeking regulation further shows that the behaviorally relevant physiological state may not be captured by simple energetic proxies [26]. Cross-taxonomic transfer should therefore concern the logic of conditional decision making, not presumed conservation of pathways.

Evidence outside Diptera broadens ecological plausibility without eliminating heterogeneity. Nutritional condition changes predation-risk responses in a beetle [12]. Nutritional timing alters mating behavior in a burying beetle [18]. Adult nutritional stress changes oviposition choosiness in a butterfly [19]. Cricket aggression combines pre-existing variation with experience effects [31]. These studies differ in life stage, sex, ecological task, and measurement. Their commonality is conditional behavioral expression rather than a demonstrated shared mechanism.

Acute plasticity must also remain distinct from evolutionary adaptation. Food deprivation can acutely increase aggression [15]. Experimental starvation-selection history can alter mating behavior across generations [30]. Similar outward phenotypes arising at different temporal scales therefore require different explanations, and the presence of state-dependent plasticity is not evidence that the response itself is adaptive.

Validation priorities follow directly. Repeated measurements are needed to distinguish individual baselines from state responsiveness, as context-dependent personality studies demonstrate [3]. Field work remains indispensable because realized resource use covaries with multiple environmental and behavioral factors [24]. Mechanistic experiments, repeated-measures behavioral ecology, and field validation should therefore be complementary rather than substitutable. Particularly important are designs that measure state independently of the focal behavior, expose the same individuals to informative transitions, and retain null behavioral components rather than combining them into composite strategy categories.

The principal limitation is evidential asymmetry. Fine mechanistic evidence is concentrated in tractable dipteran systems, whereas cross-order examples more often establish ecological conditionality without resolving homologous molecular or neural mechanisms. The proposed decision surface should consequently be tested taxon by taxon and behavior by behavior rather than treated as an insect-wide mechanistic law.

Broader behavioral-ecology implications

A state-aware interpretation changes what a behavioral phenotype means without eliminating individual differences. Personality can persist across developmental transitions in some systems [1], while environmental context can alter behavioral expression [3]. The relevant question becomes whether an observed phenotype reflects a persistent baseline, current state, sensitivity to state, or some combination.

This distinction is consequential for vector ecology. Mosquito host seeking varies with reproductive condition [9]. Nectar acquisition is strongly context dependent [23]. Physiological regulation can alter host-seeking propensity independently of a simple reserve measure [26]. These relationships may help explain behavioral heterogeneity among vectors, but they do not establish that manipulating state will produce effective population control.

The same logic applies to behavioral-ecology inference more broadly. Repeatable behavior may lack a demonstrated performance payoff [2]. State-induced parental behavior can change without a corresponding effect on measured offspring performance [29]. The article therefore proposes the hierarchy state signal → behavioral expression → ecological encounter → performance → fitness or population consequence. Each transition requires separate evidence, and failure to validate one link should not be concealed by evidence at another level.

Under this view, apparently inconsistent insect behavior is not automatically noise and repeatability is not automatically strategy. Both may emerge when different individuals are observed at different positions on a changing state-dependent decision surface. Distinguishing these alternatives requires measurements that preserve identity, state, context, and time simultaneously.

Conclusion

Foraging, risk taking, and habitat choice in insects should not be interpreted as fixed behavioral strategies solely because observations are repeatable or individually distinctive. The evidence instead supports coexistence between persistent individual variation and state-dependent changes in sensory valuation, behavioral priority, reproductive decisions, and habitat-relevant preference. The proposed decision surface formalizes that coexistence without claiming a universal mechanism or fitted predictive model. Its central empirical requirement is repeated observation across meaningful state transitions, with laboratory mechanisms, field behavior, performance, fitness consequences, and evolutionary interpretation kept analytically separate.

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