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Sensory Uncertainty, Exploration, and Behavioral Errors Generate Decision Noise With Ecological Consequences for Insects

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ABSTRACT

Insect decisions are often evaluated as if behavioral variation around an apparently optimal response were measurement error, sensory failure, or imprecision. Yet natural decisions are made with incomplete and fluctuating sensory evidence, under changing reward structures and internal states, and through motor systems that can deliberately or intrinsically generate variable actions. This non-empirical behavioral theory separates decision noise by its point of entry into perception–decision–action sequences. It distinguishes sensory noise, environmental ambiguity, exploration, internal-state variability, and behavioral error, while treating ecological consequence and adaptive value as separate inferential questions. Decision variance can arise when the same external state generates different sensory samples, when different external states produce similar cues, when animals sample alternatives, when physiological or social state changes cue weighting, or when action selection departs from the current best-supported option. These sources are not interchangeable. Apparent error can therefore reflect limited evidence, context-inappropriate control, state-dependent valuation, or stochastic search rather than deficient sensory processing. Conversely, variability is not inherently beneficial: its value depends on uncertainty structure, costs of mistakes, temporal autocorrelation, and consequences for resource acquisition, predation, reproduction, and social information. The article proposes source-resolved decision noise as an analytical framework for insect behavior. The framework predicts that ecological interpretation improves when variance is decomposed before being labelled error, plasticity, exploration, or adaptation, and when laboratory choice metrics are linked cautiously to field-scale consequences.

Keywords: Insect decision-making, Sensory uncertainty, Behavioral variability, Exploration–exploitation, Internal state, Ecological consequences

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Introduction

Insects routinely decide with information that is partial, self-generated, intermittent, or confounded by movement. Sensory input is therefore not a passive readout of an external world: locomotion changes which stimuli are encountered and can create sensory activation that must be distinguished from externally caused change [1]. This matters because the same observed choice variance can originate at different stages. A bee may hesitate because

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evidence quality is low, a fly may turn stochastically in a turbulent plume, and a mosquito may rank hosts differently because odor mixtures differ. Calling all three outcomes "error" removes the biological mechanism that produced the variance.

Decision quality also cannot be inferred from response variability alone. Honey bees adjust acceptance and rejection according to evidence quality and reward likelihood, and their speed–accuracy relations differ between these response classes [2]. Thus, a variable response distribution may contain structured evidence weighting rather than random failure. At larger spatial scales, female *Anopheles gambiae* use human odor together with carbon dioxide and heat during host seeking, while attractiveness differs among human odor profiles [3]. Variance in mosquito landing decisions can consequently reflect both the insect's processing and genuine heterogeneity among targets.

Environmental change can also convert an otherwise functional control rule into conspicuous behavioral failure. Three-dimensional laboratory and field recordings showed that insects near artificial lights orient their dorsum toward the light rather than simply steering toward it; a response that normally supports attitude control can thereby generate trapping trajectories around an artificial source [4]. The ecological meaning of "mistake" is therefore relational: it depends on whether the cue–action mapping still corresponds to the environment in which the control rule is operating.

This article develops a proposed source-resolved account of insect decision noise. Decision noise is defined here as repeatable or stochastic variance in behavioral output that remains after specifying the decision context, without presuming that the variance is maladaptive. The central distinction is among uncertainty in sensory samples, ambiguity in what those samples mean, exploration among alternatives, state-dependent changes in weighting or valuation, and action-level error. Ecological consequence is treated separately from origin: identical behavioral variance can have different consequences depending on resource distribution, risk, life stage, sex, social context, and spatial scale.

Theoretical methods

This is an original non-empirical behavioral theory constructed by comparative conceptual synthesis of recent insect behavioral, sensory, neurobiological, and ecological evidence. Evidence was organized according to where variation enters a perception–decision–action sequence: stimulus acquisition, interpretation, option sampling, internal-state modulation, action selection, and ecological propagation. The synthesis did not treat variance itself as evidence of error or adaptation. Instead, an interpretation was considered stronger when the underlying study distinguished alternative explanations experimentally, mechanistically, or by explicit modeling.

A general decision representation is useful because observable choices can combine sensory and non-sensory factors. Logistic classification provides one formal description in which weighted factors jointly determine choice probability and can include sensory evidence, priors, motivation, expected value, and recent actions [5]. This article uses that logic heuristically rather than claiming that all insect decisions implement one algorithm. For plume navigation, the empirical requirement is different: walking *Drosophila* in unpredictable odor plumes make stochastic turns whose direction is biased by the timing of previous odor encounters, while walk–stop transitions also depend on encounter timing [6]. Randomness can therefore be part of a structured navigation policy.

The analysis further distinguishes information content from the sensory channel carrying it. *Drosophila* can extract directional information from odor motion through temporal correlations across the antennae, adding information not available from airflow alone [7]. Temporal processing also changes with odor statistics: freely walking flies combine offset responses, frequency-dependent novelty responses, and integration across different timescales instead of switching categorically between fixed strategies [8]. These findings motivate three guardrails used throughout: behavioral variance must be localized before interpretation; a laboratory mechanism should not be assumed to scale automatically to field fitness; and an apparently stochastic action should not be classified as error when its probability is systematically conditioned on informative history.

Sensory noise

Sensory noise is defined here as variability in the sampled or encoded evidence available to a decision system, not as uncertainty about which external state generated that evidence. This distinction is essential because insect sensory systems actively reject misleading information. In *Drosophila*, stationary retinal patterns provide counterevidence against self-rotation and suppress inappropriate stabilizing turning even when motion detectors

are also activated [9]. An observed correction therefore depends on the joint pattern of confirming and disconfirming evidence, not merely on the strength of one cue.

Multisensory interactions further make "input noise" context dependent. In female *Aedes aegypti*, carbon dioxide modulates behavioral and neural responses to discrete visual stimuli, whereas the reported cross-modal modulation was asymmetric rather than a simple reciprocal enhancement [10]. Sensory channels should therefore not be treated as independent noisy measurements that are merely averaged. Their weights can depend on behavioral context and on the architecture by which modalities interact.

Olfactory navigation illustrates why temporal structure must also be retained. Turbulent plumes transform odor into intermittent encounters, and insects can extract spatially useful information from temporal odor patterns rather than relying only on instantaneous concentration or wind direction [11]. The same physical plume can consequently yield different evidence sequences as an insect moves through it. Some variance in turning is then generated by sampling geometry, not by instability of the choice rule.

Finally, reflexive control can impose limits on error correction. In augmented-reality flight, *Drosophila* did not compensate for persistent errors introduced by altered visual feedback in the yaw optomotor response; the response behaved approximately as an autonomous, linear, time-invariant lower-level controller within that assay [12]. Sensory noise must therefore be analyzed together with control hierarchy. A discrepancy may persist not because it is undetected, but because the relevant control layer is insufficiently flexible to recalibrate it on the tested timescale.

Environmental ambiguity

Environmental ambiguity occurs when sensory evidence is reliable as a measurement yet compatible with more than one biologically relevant interpretation. Foraging decisions demonstrate that ambiguity often concerns value rather than detection. Bumblebees choosing artificial flowers traded nectar sucrose concentration against biomechanical handling difficulty, and their choices were consistent with maximizing the rate of energetic return rather than minimizing energetic expenditure [13]. A flower cannot therefore be labelled simply "good" or "bad" from one trait; its value depends on the joint configuration of reward and handling cost.

Visual structure likewise changes what a cue means. *Drosophila melanogaster* and desert-associated *Drosophila* lineages use different object-tracking strategies in visually cluttered versus sparse landscape analogues, with differences aligned to their visual ecologies [14]. A response classified as inaccurate under one background geometry may be appropriate under another. This is a boundary on generalization, not evidence that every species-specific strategy is adaptively optimal.

Ambiguity also arises because ecologically relevant targets vary. Across African *Aedes aegypti* populations, preference for human versus animal odor differs geographically and is associated with dry-season intensity, urbanization, and human-specialist ancestry [15]. Such population structure cautions against treating a host-choice distribution measured in one population as the species-wide decision rule.

At the sensory-system level, similar odors need not carry identical behavioral valence across species. Comparative work in five drosophilids found species-specific odor preferences and differences across olfactory receptors, antennal-lobe organization, coding, and behavior; variation could not be reduced to a single processing level [16]. The proposed framework therefore treats environmental ambiguity as an ecological mapping problem: what matters is not only whether a cue is detected, but whether its meaning is stable across habitats, taxa, and decision objectives.

Exploration–exploitation trade-offs

Exploration introduces variance because information sometimes has to be acquired through action. It should therefore be separated from both sensory failure and undirected motor noise. Repeated interactions with initially unfamiliar spherical objects cause *Drosophila* to develop a preference for immobile over mobile objects despite similar appearance, with specific fan-shaped-body neurons influencing both interaction motifs and fidelity to visual guidance [17]. The crucial feature is that object properties become discriminable through interaction. Variable contact behaviors can thus function as information gathering even when they temporarily diverge from a fixed goal-directed trajectory.

Exploration is also embedded within motor architecture. Spontaneous *Drosophila* flight turns are regulated by identified descending circuitry containing excitatory and inhibitory components, and such turns are suppressed in behavioral contexts favoring straighter flight [18]. This organization argues against treating every spontaneous

saccade as unstructured execution error. Whether a turn is exploratory depends on context, its regulation, and what information or spatial coverage it enables.

Individuality creates an additional layer. Genetically matched *Drosophila* reared under similar conditions show high-dimensional intragenotypic behavioral variation rather than a small set of stereotyped personality types, and components of this variation relate to gene expression and neural manipulation [19]. Persistent individual differences can therefore alter apparent exploration rates even when animals face the same assay. They should not automatically be interpreted as optimized diversification.

The proposed distinction is consequently functional rather than descriptive. Exploration is variance that changes sampling of options or environments; exploitation favors currently valued options. A behavior becomes evidence for an exploration–exploitation trade-off only when the competing functions can be identified. Increased path tortuosity, latency, switching, or choice entropy alone is insufficient, because the same patterns can arise from weak sensory evidence, motor instability, stress, or persistent individuality.

Internal-state variability

The external stimulus does not uniquely determine an insect decision because internal conditions alter how evidence is weighted and translated into action. In *Drosophila*, metabolic state modifies sensorimotor processing broadly during nutrient choice, whereas reproductive state acts more locally on the transformation of sensory information into feeding motor output; together these states alter protein-directed food choice [20]. Decision variance measured across animals or times can therefore arise even when stimulus statistics are held constant.

Social state can modify sensory processing itself. During female *Drosophila* aggression, visual information about fly-sized objects is altered through multiple circuit motifs, including convergent state and sensory input, dendritic disinhibition, and switching between visual-feature pathways; related switching features also operate during male courtship pursuit [21]. Internal state is thus not merely an additive motivational variable applied after perception. It can reconfigure which sensory features reach downstream decision circuits.

State dependence also complicates interpretation of ambiguous choices. In an active-choice judgement-bias assay, physically stressed bumblebees were less likely to choose the location associated with high reward when presented with ambiguous colors, and modeling supported a shift in estimated reward expectation [22]. The experiment was explicitly designed to reduce alternative explanations associated with go/no-go tests, yet the inference remains tied to the assay and should not be generalized into a universal emotional mechanism for insects.

Environmental state can interact with internal valuation at longer temporal scales. Honey-bee foragers became more persistent at risky resources and less likely to produce inhibitory stop signals during late-season resource scarcity [23]. This pattern shows that risk sensitivity and social communication can shift with seasonal resource conditions rather than remaining fixed individual traits.

Within the proposed source-resolved framework, internal-state variability therefore means variance generated when physiological, reproductive, social, stress-related, or resource-dependent states change the mapping from evidence to action. It is analytically distinct from sensory noise because identical evidence can be treated differently, and from environmental ambiguity because the relevant uncertainty can reside in valuation rather than cue meaning. The practical implication is that repeated-choice variance should be partitioned by measurable state whenever possible before residual variation is labelled behavioral error.

Behavioral error

Behavioral error should be reserved for an action that is mismatched to the organism's current information, state, or task, rather than used as a synonym for unexplained variance. Even apparently random locomotor structure can be generated by specific control constraints. In freely walking *Drosophila*, locomotor statistics can be explained by inhibitory control acting on transitions between behavioral states, indicating that pauses, bouts, and movement timing need not be treated as independent execution failures [24]. The relevant question is therefore whether a deviation arises from the control policy itself or from failure to implement that policy.

Developmental individuality complicates this diagnosis. Neurodevelopmental variation in the *Drosophila* visual system can generate stable differences in object-orientation behavior among genetically identical individuals [25]. A response that appears erroneous relative to the population mean may consequently be internally consistent for one individual. Population averaging can conceal this structure and make lawful individual policies look noisy.

Decision-related neural activity also warns against locating error too early in the sequence. Mushroom-body output neurons encode behavioral decisions during sensory–motor transformation, linking sensory representations

to the action ultimately selected [26]. This does not imply that every choice error is generated in the mushroom body; rather, it demonstrates that transformation stages between evidence and movement are experimentally separable and can contribute distinct variance.

Behavioral sequences add another failure mode. *Drosophila* egg laying contains transition points whose expression is flexibly controlled by descending pathways, so a sequence can be modified at particular transitions without requiring failure of the entire motor program [27]. Error can therefore concern timing, ordering, or inappropriate persistence at a transition, not only selection of the wrong endpoint.

Defensive behavior shows why an apparently excessive response may still be evidence-conditioned. Mechanosensory bristles trigger sustained local motor activity that supports avoidance in *Drosophila*, linking localized stimulation to persistent movement [28]. Persistence after a trigger may be costly in some contexts, but the existence of a sustained response does not by itself establish maladaptive overshoot.

The proposed adjudication rule is thus source-first: classify a deviation only after asking whether sensory sampling, cue interpretation, internal valuation, sequence control, or motor execution better explains it. Behavioral error is the residual category for context-inappropriate action after these alternatives have been considered, not a default label for variance.

Because the same outward deviation can originate from different control levels, **Table 1** separates the principal error states by what must be observed before a mechanistic or ecological interpretation is warranted.

Table 1. Adjudicating apparent behavioral error by its point of origin in insect decision sequences

Behavioral-error state	Biological context	Observable basis	Interpretation consequence	Boundary or uncertainty	Research/test implication	Status
Control-policy variability	Locomotor state transitions	Structured bout, pause, or transition statistics	Variance may be generated by inhibitory or transition control rather than failed execution	Assay-specific control architecture may not generalize across taxa or tasks	Manipulate transition control while holding sensory evidence constant	Evidence-supported distinction
Persistent individual policy	Neurodevelopmentally variable individuals	Stable within-individual response differences around a population mean	Population-level "error" can mask internally consistent behavior	Developmental origin does not establish ecological benefit	Repeated-measures designs should separate within- from among-individual variance	Evidence-supported distinction
Decision-transformation divergence	Sensory-to-action circuitry	Different actions arising after comparable sensory representation	Error may enter between evidence encoding and motor command	Neural correlates do not by themselves prove causal origin	Perturb transformation stages while preserving stimulus statistics	Evidence-supported distinction
Sequence-transition mismatch	Multi-step behaviors such as oviposition	Inappropriate timing, ordering, or persistence at a behavioral transition	A local transition error need not imply failure of the whole behavioral program	Correct sequence depends on task and environmental state	Resolve transition-specific control and context dependence	Evidence-supported distinction
Triggered persistence or overshoot	Defensive or avoidance responses	Sustained action following localized sensory triggering	Persistent action may be functional protection or context-dependent overshoot	Cost cannot be inferred from duration alone	Measure both immediate protection and downstream opportunity costs	Evidence-supported distinction
Residual context-inappropriate action	Any decision after alternative sources are excluded	Deviation unexplained by sampling, ambiguity, state, exploration, or sequence control	Candidate behavioral error under the proposed source-resolved scheme	Requires explicit specification of task, information, and state	Test competing source explanations before assigning error	**Proposed synthesis**

The architecture in **Figure 1** makes the corresponding boundary explicit: variability can enter before, during, or after decision formation, whereas ecological consequence lies across a separate scale-transfer boundary.

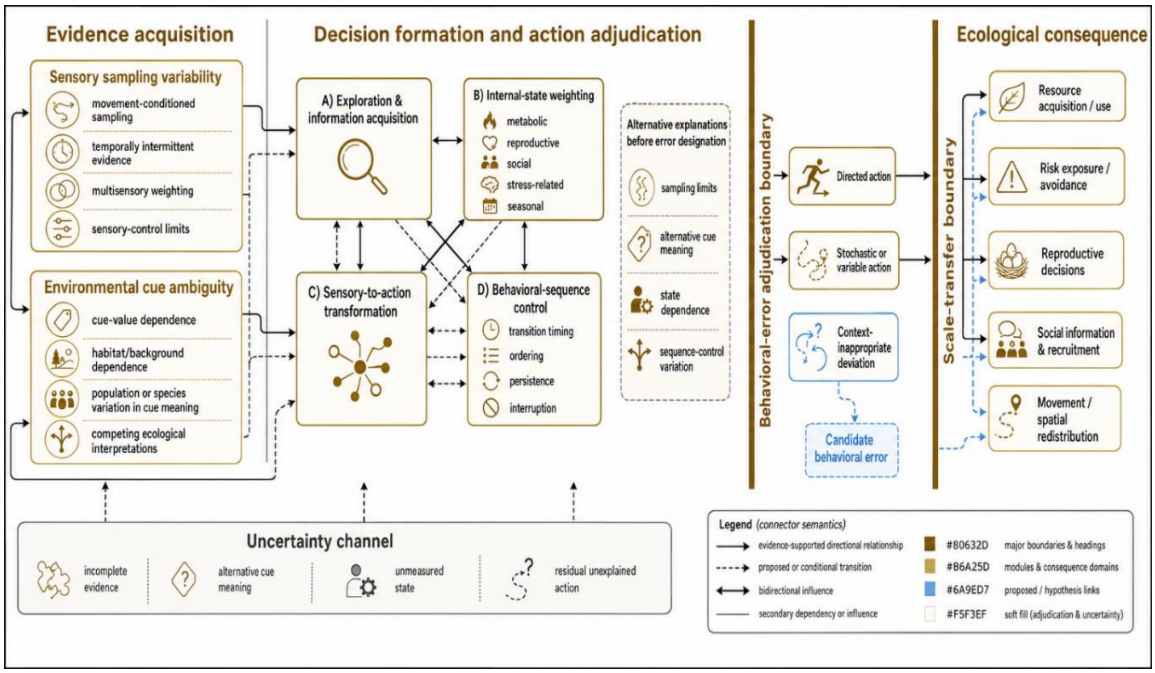


Figure 1. Locating apparent error across sensory evidence, state-dependent choice, and ecological consequence

When noise is adaptive

Noise is adaptive only under a stronger criterion than variability, persistence, or apparent flexibility. The behavior must improve expected performance under a specified distribution of environmental states relative to less variable alternatives, and the advantage must concern an ecologically relevant outcome. Cross-generational pheromonal communication in *Drosophila* illustrates how variable site use can be structured by social information: prior occupancy cues influence oviposition-site choice across generations [29]. This supports information-dependent diversification of choices, but not the general claim that stochasticity itself is adaptive.

Host specialization provides a complementary limit. In a crucifer-specialized moth, host selection depends on a defined molecular detection system for characteristic plant compounds, showing that highly selective behavior can be favored where cue–resource relationships are sufficiently reliable [30]. A noisy policy is therefore not universally preferable. Stable environments, high error costs, or highly diagnostic cues can favor precise exploitation.

The proposed criterion is conditional: decision noise becomes a candidate adaptive feature when variable action increases sampling, reduces repeated commitment to misleading information, or distributes risk across uncertain alternatives, and when those benefits exceed the costs of additional search or mistakes. Demonstrating this requires comparison with less variable strategies under realistic uncertainty. Without that comparison, “adaptive noise” should remain a hypothesis rather than a conclusion.

Ecological consequences of decision variance

Decision variance matters ecologically when repeated individual choices alter resource use, movement, interaction networks, or information flow. Honey-bee waggle-dance recruitment varies with landscape structure and foraging-distance distributions, linking individual foraging decisions to colony-level spatial exploitation [31]. The ecological consequence is therefore not simply the accuracy of one choice but how recruitment redistributes collective effort across space.

Information transfer itself can be behaviorally contingent. Honey-bee dance followers dynamically position their antennae in ways that allow decoding of the waggle dance [32]. Variation in receiver positioning can therefore change access to social information before subsequent foraging decisions are made, providing a route by which individual sensorimotor behavior propagates into collective organization.

Odor-guided movement offers a broader spatial case. Insects navigating windborne pheromone or resource-linked plumes use temporally structured encounters and wind information, and successful navigation depends on how intermittent signals are converted into movement [33]. Small differences in sampling or turning can thus alter source-finding trajectories without implying that each deviation is either error or adaptation.

Modeling of turbulent odor navigation further shows that complementary temporal features can improve navigation across diverse plume statistics [34]. This establishes a mechanism by which decision rules matched to signal structure can influence movement performance, but ecological extrapolation still requires field-relevant distributions of turbulence, resources, competitors, and risk.

Learning adds temporal carry-over. *Aedes aegypti* can learn host-associated cues and alter subsequent host-oriented behavior [35]. Choice variance at one encounter can therefore change later decisions through experience, potentially creating path dependence in host use. The ecological magnitude of such carry-over will depend on encounter frequency, memory persistence, host availability, and costs of incorrect generalization.

The proposed framework therefore distinguishes propagation from origin. Sensory noise, ambiguity, exploration, state variation, and behavioral error can all alter ecological outcomes, but the pathway is conditional. Individual variance becomes ecologically important only when it changes exposure, acquisition, survival-related behavior, reproduction, dispersal, or social information sufficiently and consistently to affect higher-level patterns.

Results and Discussion

The central implication is methodological as much as theoretical: variance should be decomposed before it is interpreted. A choice distribution is the endpoint of several processes that can produce similar statistical signatures. Temporal odor sampling can generate variable turns [6]; internal metabolic state can change food choice [20]; inhibitory control can structure locomotor variability [24]. Treating these outcomes as one residual noise term would erase biologically meaningful differences.

This source-first approach also changes how laboratory assays should be read. Controlled experiments are valuable precisely because they can isolate particular stages, such as multisensory weighting [10], visual counterevidence [9], or decision transformation [26]. Their strength is mechanistic resolution, not automatic ecological generality. Field or semi-natural studies provide complementary evidence that cue distributions, host heterogeneity, artificial light, and landscape structure alter the conditions under which those mechanisms operate [3]. Neither scale should substitute for the other.

A practical consequence is that studies should report the variance structure they seek to explain rather than only mean choice or average performance. Within-individual dispersion, switching probability, latency, bout structure, and among-individual persistence answer different questions. High-dimensional individuality in genetically matched flies shows that stable behavioral differences can coexist with apparently uniform rearing conditions [19]. Ambiguous-choice assays in stressed bumblebees further show that altered choice probabilities can reflect changed reward expectation rather than degraded sensory discrimination [22]. Seasonal shifts in honey-bee risk sensitivity demonstrate that the same nominal decision can be recalibrated as ecological conditions change [23].

Consequently, a variance component should be interpreted only after specifying the relevant timescale, repeated-measures structure, cue statistics, and state variables. The framework also predicts that identical summary statistics can conceal different biological processes: two groups may show equal choice entropy even if one reflects persistent specialists and the other rapid within-individual switching. Future tests should therefore combine distributional summaries with trajectory-level or repeated-individual analyses and, where feasible, manipulations that selectively alter sensory reliability, state, or action-control constraints.

The framework has important taxonomic limits. Much of the mechanistic evidence comes from *Drosophila*, with bees and mosquitoes providing major but non-equivalent extensions. Species differences in olfactory processing [16] and population differences in mosquito host preference [15] demonstrate why a control rule should not be generalized across insects merely because the behavioral label is similar. Life stage and sex also remain unevenly represented, particularly where host seeking, oviposition, aggression, and reproductive state create sex- or stage-specific decision problems.

A second limit concerns adaptation. Structured stochasticity, persistent individuality, and context-sensitive switching are all compatible with functional roles, but none alone proves that variance was favored by selection. The proposed adaptive criterion therefore requires comparative performance under relevant environmental uncertainty. Similarly, ecological consequence should not be inferred from behavioral effect size alone;

propagation depends on encounter structure, temporal persistence, spatial scale, and whether individual differences accumulate or cancel.

Several predictions follow from the synthesis. Manipulating sensory reliability while holding state constant should shift variance attributable to sensory sampling but not stable individual policies. Manipulating nutritional or social state under identical cues should redistribute choices without requiring increased sensory noise. Repeated-measures designs should separate within-individual stochasticity from persistent among-individual differences. Field validation should test whether laboratory-defined variance components predict source finding, resource use, risk exposure, or recruitment under natural cue statistics. These are proposed tests of the framework, not claims of existing validation.

The conceptual gain is that "error" becomes an adjudicated interpretation rather than a leftover category. This preserves mechanistic alternatives, makes uncertainty explicit, and creates a tractable route from neurobehavioral observations to ecological hypotheses without collapsing across levels of organization.

Conclusion

Insect decision variance is generated by more than imperfect sensing. It can arise from ambiguous environments, active exploration, shifting internal state, flexible sequence control, persistent individuality, and context-inappropriate action. These sources can produce similar outward variability while implying different mechanisms and ecological consequences. The proposed source-resolved framework therefore places behavioral error after, rather than before, alternative explanations have been evaluated. It also separates the existence of noise from claims that noise is adaptive and separates individual behavioral effects from higher-level ecological consequence. Progress will depend on experiments and field studies that manipulate uncertainty, state, and control architecture independently, quantify within- and among-individual variance, and test when those components propagate across ecological scales

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