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# Behavioral Flexibility Carries Energetic and Informational Costs That Constrain Insect Decision Making Under Environmental Change

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**ABSTRACT**

Behavioral flexibility is often treated as an uncomplicated advantage under environmental change, yet insects must acquire information, process it, revise prior responses, and sometimes tolerate delay or error before a new action becomes profitable. This article develops a proposed behavioral theory in which realized flexibility depends on the balance between the expected benefit of updating and multiple non-equivalent constraints: energetic expenditure, neural and cognitive processing demands, information-acquisition requirements, switching costs, and error or delay. The evidence base does not support a single universal cost of cognition. Metabolic differences accompany cognitive phenotypes in honeybees, faster learning can correlate with lower lifetime resource collection in bumblebees, but experimentally imposed learning demand need not reduce reproduction under tested conditions. Attention, cue conflict, feature selection, and context-dependent valuation further show that informational costs can arise without being reducible to metabolism. The theory therefore treats metabolism, information acquisition, behavioral performance, compensation, and fitness consequence as distinct inference levels. It predicts that flexibility should be most useful when updated information is sufficiently reliable and consequential to outweigh the costs of obtaining and acting on it, with the position of that balance varying among taxa, life stages, tasks, and environments.

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## Introduction

Environmental change does not confront an insect with a generic need to “be flexible.” It changes the reliability, value, and temporal relevance of cues that govern particular actions. Floral rewards, for example, can vary in chemical composition and multidimensional quality, altering what pollinators must perceive, learn, and compare before choosing among resources [1]. A comparative analysis across bee species further found that brain size was associated with urban occurrence, consistent with the possibility that cognitive investment can covary with tolerance of novel environments, but this association does not establish a causal cognitive buffer [2]. The central problem is therefore not whether flexibility is generally advantageous, but when updating behavior yields sufficient return to justify the costs of obtaining, processing, and using new information.

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Environmental predictability provides a necessary conditioning variable because predictability depends on spatial and temporal scale and can itself interact with animal movement [3]. A cue can be reliable over minutes but uninformative across days, or locally stable while regionally heterogeneous. Consequently, any claim that insects should exhibit "more flexibility" under change is incomplete unless the relevant decision scale is specified. Field evidence also shows why flexibility cannot be equated with novelty seeking alone. Wild field crickets altered thermoregulatory behavior when solar insolation was experimentally changed, demonstrating behavioral compensation under an altered physical environment [4]. Such compensation is evidence of behavioral adjustment, not by itself proof of higher fitness or evolved adaptation.

This article proposes that realized behavioral flexibility is bounded by a set of separable costs that arise before, during, and after updating. Energetic costs concern resource expenditure associated with neural activity, sampling, movement, or switching. Cognitive processing costs concern the organization and deployment of neural systems needed to discriminate, remember, compare, or reverse prior associations. Information-acquisition costs arise because cues must be encountered, attended to, and filtered. Error and delay costs arise when additional sampling postpones action or when incomplete, conflicting, or context-sensitive information produces a lower-return choice. These costs are not assumed to share a common currency. Their joint role is proposed as a theoretical integration, while each empirical link is retained at the level at which it was actually measured.

*Theoretical methods*

The article is a behavioral theory constructed by integrating evidence on insect learning, movement, neurobiology, metabolism, attention, reward evaluation, and field performance. Flexibility is operationalized as task-specific behavioral updating rather than as a unitary trait. This choice follows the broader insect-learning literature, which emphasizes that laboratory performance must be connected cautiously to ecological function and fitness-related interpretation [5]. Accordingly, reversal learning, route restructuring, visual search, social acquisition, reward valuation, and thermoregulatory adjustment are treated as distinct behavioral processes unless evidence directly links them.

Ecological context is retained as a moderator rather than assumed to be an evolutionary explanation. In a plant-pollinator network, species specialization covaried with learning performance across six hymenopteran pollinators [6]. Such an association can motivate hypotheses about information demands, but it does not show that specialization caused the evolution of greater learning capacity. Similarly, repeated behavioral order is not taken as sufficient evidence of learning. Spatially explicit null-model work shows that apparently organized traplines can sometimes arise from movement and resource geometry without requiring the inferred learning mechanism [7]. The theoretical rule adopted here is therefore conservative: a behavioral pattern enters the framework as evidence of updating only when alternative structural explanations have been considered.

Sampling is also treated as dynamic rather than as a single preliminary step. Bumblebee route development contains repeated exploration–exploitation cycles, with exploration persisting even after efficient routes begin to emerge [8]. The theory therefore distinguishes information search, exploitation of a current policy, and switching between them. It does not infer energetic expenditure from movement pattern alone. Instead, energetic, informational, and opportunity costs are assigned only when the supporting evidence measures or justifies the corresponding level.

*Energetic costs of sampling and switching*

Direct evidence that cognition is energetically embedded comes from honeybees in which slow and fast cognitive phenotypes differed in brain and whole-animal metabolic characteristics [9]. This result supports coupling between cognitive phenotype and energy metabolism, but it does not establish that greater flexibility necessarily consumes more energy, nor that the measured metabolic profile causes the behavioral phenotype. For theory, the important implication is narrower: the energetic state of cognition cannot be presumed independent of decision phenotype.

The translation from energetic demand to fitness-related cost is even less direct. In post-diapause bumblebee queens, experimentally imposed learning demands had no detectable effect on reproductive success under the tested conditions, whereas nutritional treatment affected reproduction [10]. This null result is crucial because it blocks a simple chain from learning demand to energetic expenditure to reproductive loss. A cost can be buffered, compensated, too small for the measured endpoint, or expressed in another trait or time window.

Conversely, a longitudinal study linking laboratory learning to free foraging found that faster-learning worker bumblebees collected fewer resources over their lifetimes and had fewer foraging days [11]. The relationship was correlational, so it cannot identify the mechanism. It nevertheless shows that favorable performance on a learning assay need not map monotonically onto lifetime field performance. The proposed theory therefore distinguishes a metabolic cost from an opportunity or life-history cost: both may constrain realized flexibility, but evidence for one cannot substitute for evidence for the other.

Switching itself is likewise context dependent. Work on bumblebee flower constancy indicates that spatial arrangement changes the balance between cognitive costs of switching among flower types and travel costs associated with remaining constant [12]. A switch that is costly in a mixed patch may be useful when resource geometry changes. The theoretical quantity of interest is therefore not a fixed "switching tax," but the change in expected return produced by updating relative to persisting with the current behavior. No universal numerical exchange rate among neural energy, travel, time, and missed resources is assumed.

*Neural and cognitive processing costs*

Neural investment should not be reduced to total brain size. Comparative neuroanatomy across Heliconiini butterflies shows mosaic evolution within learning- and memory-related circuitry, indicating that different components can diverge semi-independently [13]. This matters because a theory of processing cost must allow capacity, specialization, and expenditure to be distributed across neural components rather than represented by a single enlarged "cognition module."

Neural phenotype is also partly conditional on developmental and environmental history. Comparisons among Heliconius butterflies reared in the wild and insectary showed that different axes of neural divergence vary in their sensitivity to environment, with some differences persisting and others becoming context dependent [14]. These patterns do not by themselves demonstrate the energetic price of neural plasticity, but they establish that the neural substrate entering a decision can be developmentally contingent. Processing cost should therefore be treated as state dependent rather than fixed for a species.

At the behavioral level, honeybee slow and fast cognitive phenotypes differ across multiple learning and life-history traits [15]. Such covariation supports a multidimensional view of cognitive strategy, but it does not justify a universal slow–fast continuum across insects. More importantly, morphology and performance can decouple. Bumblebee queens, gynes, and workers can differ in brain morphology without corresponding one-to-one differences in learning performance across adult states [16]. Neural tissue investment, task performance, and realized behavioral flexibility must therefore occupy separate levels of inference.

These distinctions are compressed in the stage-specific comparison below because prose alone obscures where evidence changes level—from metabolic support, through neural allocation, to task performance and life-stage expression.

**Table 1.** Where neural and cognitive processing constraints enter the path from neural state to behavioral updating

| Insect context with observed basis | Interpretation for flexi within its limit | Discriminating check |
|---|---|---|
| **Energetic support of cognition** | | |
| ***Evidence-supported distinction*** | | |
| **Honeybee workers** | Processing is metabolically embedded | Manipulate energetic state while measuring updating and metabolism jointly |
| **Brain and whole-animal metabolic phenotype varies with cognitive phenotype** | Association does not identify causal energetic burden | |
| **Component-specific neural investment** | | |
| ***Evidence-supported distinction*** | | |
| **Heliconiini butterflies** | Processing capacity may be distributed across neural components | Relate component-level neural variation to multiple tasks |
| **Learning- and memory-related circuitry evolves mosaically** | Neuroanatomy does not equal behavioral performance | |
| **Environment-sensitive neural state** | | |
| ***Evidence-supported distinction*** | | |
| **Heliconius butterflies** | Processing substrate can depend on developmental environment | Cross-rearing and longitudinal designs |

| | | |
|---|---|---|
| **Neural divergence differs between wild and insectary contexts** | Morphological plasticity is not proof of adaptive benefit | |
| **Multidimensional cognitive phenotype** | | |
| ***Evidence-supported distinction*** | | |
| **Honeybee workers**<br>**Learning and life-history traits covary within slow/fast phenotypes** | A single performance score may conceal trade-offs<br>One species does not establish a general syndrome | Test repeated tasks with shared individuals |
| **Morphology–performance decoupling** | | |
| ***Evidence-supported distinction*** | | |
| **Bumblebee adult roles and life stages**<br>**Brain morphology varies without proportional learning differences** | Neural investment and expressed flexibility are distinct<br>Role, stage, and task can alter the mapping | Measure morphology, energy use, and updating in the same individuals |
| **Processing-cost state** | | |
| ***Proposed synthesis*** | | |
| **Cross-taxon theoretical level**<br>**Joint neural state, energetic state, and task demand** | Realized flexibility depends on their interaction rather than any one proxy<br>No integrated causal test yet | Factorial manipulation across state and task demand |

*Information acquisition costs*

Flexibility requires information to be encountered before it can be used. Bumblebee visual-search experiments show that learning changes inspection behavior: attention is redistributed toward rewarding flowers and away from unrewarding alternatives [17]. This provides direct evidence of selective information allocation, not of its calorimetric price. The cost is informational and temporal in the first instance: inspecting one option occupies sampling capacity that cannot simultaneously be devoted elsewhere.

The informational value of sampling also depends on what is actually observed and whether sequential cues agree. In social-learning experiments, the time bumblebees spent facing different flowers correlated with later learning outcomes, while separate experiments showed that conflicting information available at different phases of flower interaction altered learning [18, 19]. Together, these findings support the same narrow claim: the structure and timing of sampled information matter. They do not justify treating visual orientation as a complete measure of encoded information, nor do they imply that all cue conflict degrades performance equally.

Filtering can reduce these demands. When bumblebees learned complex visual stimuli, consistent components could dominate discrimination and generalization, allowing relatively simple learning processes to account for apparently complex performance [20]. The implication is not that insect cognition is simple in general. Rather, selective use of reliable features can reduce the effective dimensionality of a decision. The proposed theory therefore distinguishes three informational burdens: finding relevant cues, allocating attention among them, and resolving inconsistency among sampled cues.

*Error and delay costs*

Information can improve a decision only if its value exceeds the loss created while waiting for it. Bumblebees show limited tolerance for delayed rewards, demonstrating that postponement itself constrains choice under experimental conditions [21]. This does not establish a field fitness penalty, but it provides a behavioral basis for treating delay as a distinct component of decision cost. An insect that samples indefinitely can avoid some errors while losing opportunities that disappear during sampling.

Error is equally context dependent. Bumblebee choice experiments show that asymmetrically dominated alternatives can alter preference in a reward-dimension-specific manner, while wild bumblebees use both absolute and relative evaluation when choosing among floral rewards [22, 23]. These results support a critical distinction: deviation from an experimenter's context-independent optimum should not automatically be labelled irrational or maladaptive. Relative valuation may sometimes exploit useful ecological structure, whereas in other contexts the same sensitivity could shift choice away from the highest-return option.

The proposed theory therefore separates three loss states. Delay cost accumulates while action is postponed. Conflict cost arises when temporally or spatially inconsistent cues increase uncertainty or resampling. Context

error occurs when valuation changes with the available comparison set in a way that lowers realized return. These states can co-occur, but they should not be collapsed into one score because they have different observables and different falsifiers.

Because similar choice outcomes can arise from different combinations of waiting, conflict, and context sensitivity, the prediction-and-test ledger below keeps their empirical signatures and falsification requirements analytically separate.

**Table 2.** Distinguishing delay, cue conflict, and context error as separable constraints on behavioral updating

| Cost state with evidential standing | Observable evidence pattern linked with decisive research test | Decision consequence within its limit |
|---|---|---|
| **Delay accumulation** | Choice becomes constrained as reward is postponed | Waiting can reduce the practical value of additional information |
| **Evidence-supported phenomenon; cost interpretation proposed** | Vary information gain and opportunity decay independently | Laboratory delay tolerance is not equivalent to field fitness loss |
| **Cue-conflict cost** | Sequentially inconsistent cues alter learning | Updating may require resampling or weighting one cue over another |
| **Evidence-supported phenomenon; integrative cost role proposed** | Manipulate reliability and temporal order factorially | Interference depends on timing and cue structure |
| **Context-dependent valuation** | Preference changes with comparison context or reward dimension | Choice can shift without a change in focal option value |
| **Evidence-supported phenomenon** | Compare context sensitivity against realized ecological return | Relative evaluation may be useful rather than erroneous |
| **Compounded delay–conflict state** | Unreliable information requires further sampling before action | Delay and uncertainty may reinforce one another |
| **Proposed synthesis** | Measure sampling duration, accuracy, and payoff in the same design | No direct integrated test in the cited evidence |
| **Context error** | Context sensitivity lowers realized return in a specified environment | Flexible valuation becomes a cost only relative to an explicit payoff criterion |
| **Proposed classification** | Predefine ecological payoff function and test field transfer | "Bias" is not synonymous with maladaptation |

*Benefits of flexibility*

Costs constrain flexibility only because changing behavior can also generate benefits. In wild field crickets, behavioral thermoregulation compensated for experimentally altered solar insolation, showing that adjustment can preserve access to suitable thermal conditions when the physical environment changes [4]. Flexibility may also enlarge the set of attainable actions: bumblebees exposed to demonstrators acquired a two-step behavior that naïve individuals rarely or never innovated in the assay [24]. These findings establish compensation and socially enabled acquisition in particular systems, not universal fitness advantages.

Benefits also depend on resource structure. Associations between pollinator specialization and learning performance [6], together with repeated exploration–exploitation during route formation [8], indicate that ecological topology can change the value of acquiring and revising information. The proposed theory therefore defines benefit as the increment in expected return obtained by updating relative to retaining the current behavior, with "return" left endpoint-specific rather than assumed to mean fitness.

Benefit cannot be identified from behavioral change alone. A new action may restore access to a resource without offsetting the time or energy spent learning it, whereas social information can lower individual search requirements while introducing dependence on demonstrators. The social-learning result [24] therefore supports expansion of accessible behavior, not a measured reduction in total decision cost. Likewise, thermoregulatory compensation [4] identifies maintained behavioral access to suitable conditions, but not the energetic balance or reproductive consequence of that compensation. In the proposed theory, benefit must consequently be defined against an explicit alternative policy and endpoint.

*Optimal flexibility under environmental predictability*

Environmental predictability should affect both the value of new information and the cost of acting on it. Predictability is scale dependent [3]; therefore, the relevant comparison is not stable versus variable habitat in

general, but whether cues remain informative over the spatial and temporal horizon of a particular decision. Spatial flower arrangement can alter the balance between switching and travel costs [12], illustrating how the same behavioral rule can change value when resource geometry changes.

Nor should greater neural investment be assumed to produce greater general flexibility. Heliconiini species with expanded mushroom-body investment did not show superior reversal performance in the tested comparison [25], and comparison of solitary red mason bees with eusocial honeybees found that apparent flexibility differed with task, species, and sex [26]. The proposed optimum is consequently conditional: flexibility is favored only insofar as expected improvement from updating exceeds the energetic, informational, temporal, and opportunity costs relevant to that organism, task, and environment. No universal intermediate optimum, threshold, or quantitative response curve is claimed.

This formulation also prevents unpredictability from being treated as a single environmental category. If conditions change faster than information remains useful, repeated updating may become unprofitable even when an insect is capable of learning. Conversely, stable environments can still reward updating when local resource states change at a decision-relevant scale. Spatially dependent switching trade-offs [12] illustrate why temporal predictability and resource geometry must be considered jointly. Comparative differences among bee tasks and groups [26] further caution that the same environmental schedule may impose different effective decision problems on different organisms.

The taxonomy below separates environmental states that can lead to superficially similar behavior but require different predictions and tests.

**Table 3.** Decision states linking environmental predictability to the expected return from behavioral updating

| Information condition with observed basis | Main boundary | Discriminating test |
|---|---|---|
| **Stable and informative** | | |
| ***Proposed state*** | | |
| **Current cues remain reliable across decisions**<br>**Repeated updating may add little return** | Persistence can be efficient rather than inflexible | Compare updating with policy retention under stable contingencies |
| **Variable but learnable** | | |
| ***Proposed state*** | | |
| **Cue–outcome relations change yet retain short-term reliability**<br>**Updating can improve return if sampling costs are recoverable** | Relevant temporal scale must be specified | Manipulate change rate and cue reliability independently |
| **Variable and conflicting** | | |
| ***Proposed state*** | | |
| **Multiple cues disagree or change asynchronously**<br>**Additional sampling may help or compound delay** | Conflict structure, not variability alone, matters | Cross cue reliability with sampling opportunity |
| **Rapidly unpredictable** | | |
| ***Proposed state*** | | |
| **New information has low persistence**<br>**Frequent updating may yield little durable advantage** | Bet-hedging or fixed rules are alternative explanations | Compare flexible updating with fixed or diversified strategies |
| **Taxon/task contingent** | | |
| ***Evidence-bounded proposed classification*** | | |
| **Same environment, different sensory or cognitive demands**<br>**Apparent optimum may shift among species, sexes, stages, or tasks** | No unitary flexibility ranking | Use matched multi-task, multi-taxon designs |

These states require a cross-scale representation because predictability resides in the environment, information is sampled at the individual level, and consequences emerge only after behavior is expressed.

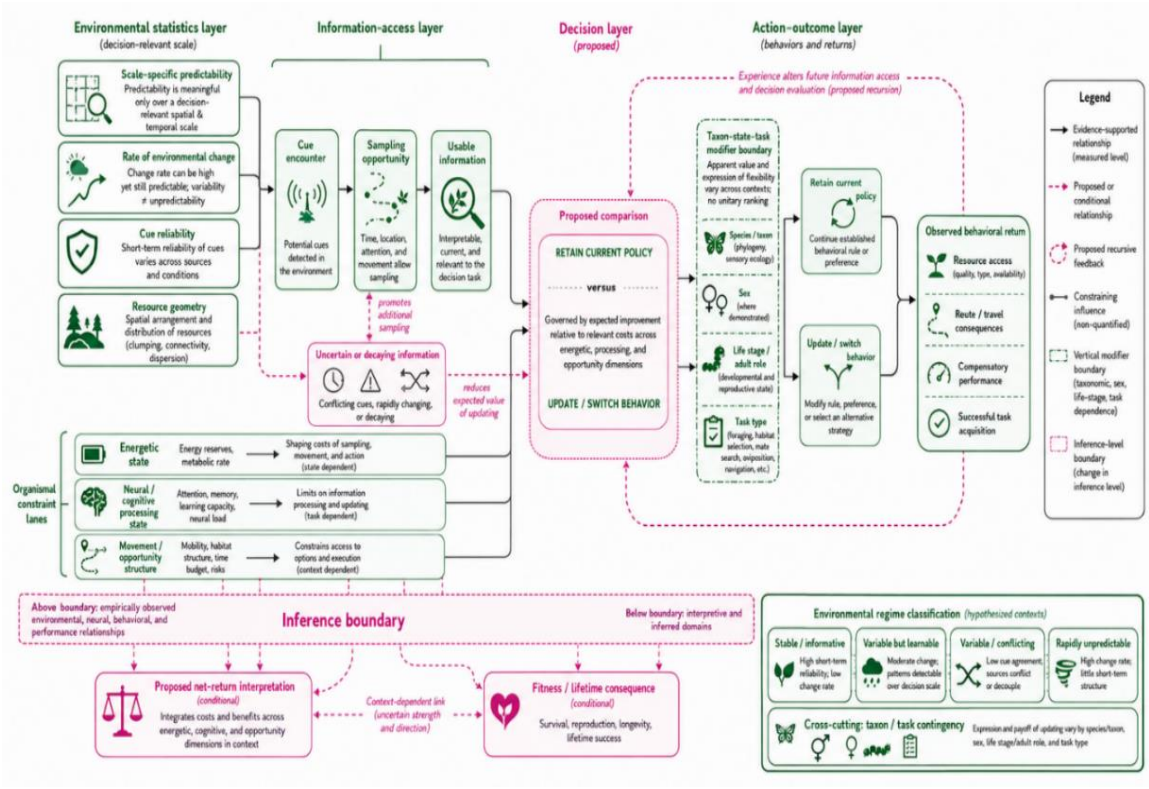



**Figure 1**. Predictability sets the decision scale on which updating can repay its costs

*Testable predictions*

The theory generates four falsifiable predictions. First, energetic state should modify the return from repeated updating, but the direction need not be uniformly negative because metabolic phenotype, reproductive outcome, and lifetime field performance are distinct endpoints [9]. Null reproductive effects under imposed learning demand [10] and negative lifetime correlations with fast learning [11] predict context-dependent rather than universal costs.

Second, lower information reliability should increase selective sampling or resampling only while additional information remains useful; attention reallocation [17], cue conflict [19], and feature filtering [20] provide separable mechanisms to test this prediction. Third, the benefit of updating should vary jointly with predictability, environmental compensation, and switching structure [3, 4, 12]. Fourth, cross-task rankings should be unstable when flexibility is not a unitary trait, particularly across life stages, species, or sexes [16, 25, 26]. These predictions require factorial experiments and field-relevant outcomes rather than a single flexibility score.

Predictions should therefore be tested by crossing environmental statistics with organismal state rather than by correlating a single cognitive score with environmental variability. Designs should manipulate cue reliability, rate of change, sampling opportunity, and resource consequences independently while measuring both retention and updating. Repeated tests on the same individuals would distinguish stable task-general covariance from assay-specific performance, while field transfer would reveal whether laboratory gains survive movement, competition, and opportunity costs. A prediction is falsified if its specified interaction is absent under the conditions for which it is proposed; failure should not be reclassified post hoc as hidden flexibility.

**Results and Discussion**

The evidence supports the components of the theory more strongly than their integration. Reward structure, predictability, and switching ecology each affect decisions [1, 3, 12], but no approved study validates the proposed net-return rule as a unified mechanism. Its value is therefore organizational: it prevents energetic expenditure, information processing, behavioral performance, compensation, and fitness consequence from being treated as interchangeable evidence.

Nulls and dissociations are especially informative. Learning demand can show no detectable reproductive cost [10], brain morphology can vary without proportional learning differences [16], and expanded neural investment

need not improve reversal performance [25]. These findings rule out a simple monotonic model in which more cognition necessarily yields either more cost or more benefit.

Generality is limited by a strong Hymenoptera emphasis, substantial laboratory evidence, and heterogeneous assays. Ecological-validity arguments [5], multi-species pollinator comparisons [6], and task-, species-, and sex-dependent flexibility [26] together indicate that validation should cross taxa, tasks, and environmental scales. Alternative explanations must also be tested explicitly because ordered behavior can emerge without the inferred learning mechanism [7]. Field manipulations such as experimental alteration of thermal conditions [4] provide a stronger template for connecting updating to environmental consequence without assuming adaptation.

The framework also has explicit boundaries. It does not equate plasticity with adaptation, assume that all information processing is metabolically expensive in the same way, or infer population consequences from individual choice. Neural morphology, metabolic phenotype, learning rate, route organization, and reproductive output remain distinct observables. The present evidence is also uneven across orders and life stages, so the theory should be treated as a portable hypothesis structure rather than a taxonomically universal model. Its strongest future test would jointly manipulate environmental predictability and information reliability while measuring energetic state, sampling behavior, switching, realized resource return, and a biologically relevant downstream endpoint in the same system.

Such tests should also include null or mechanistically simpler alternatives. Apparent route regularity, for example, should not be attributed to updating until resource geometry and movement constraints are excluded [7]. Similarly, an apparent advantage of rapid learning should be evaluated against lifetime performance rather than assay speed alone [11]. This keeps validation focused on decision consequences rather than preferred cognitive interpretations.

## Conclusion

Behavioral flexibility is best treated not as a cost-free capacity but as a conditional decision process. Insects can gain from changing behavior, yet useful updating requires information to be encountered, selected, processed, and acted upon before opportunities disappear. The proposed theory therefore separates energetic, neural, informational, switching, delay, error, and opportunity constraints and asks whether the expected benefit of updating exceeds the subset relevant to a particular decision. The balance should vary with predictability, taxon, life stage, sex, task, and ecological context. Its empirical value will depend on future tests that measure these components jointly while preserving the boundary between behavioral adjustment, physiological mechanism, and fitness consequence.

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