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Insect Movement Emerges as a Sequence of Decisions Linking Sensory Sampling, Internal State, and Dispersal Motivation

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ABSTRACT

Insect movement is often summarized by path length, displacement, emigration, or arrival, yet these endpoints can obscure the distinct decisions that generate a movement episode. A change in trajectory may reflect sensory acquisition, state-dependent valuation, departure, motor control, updating, or target acceptance rather than a single construct called dispersal motivation. This article develops an evidence-constrained behavioral framework in which sensory sampling and internal-state assessment are analytically distinct but reciprocally coupled. Departure is treated as a conditional transition, and movement-mode selection can involve both discrete strategy changes and continuous motor tuning. Chosen locomotor states can, in turn, alter the information available for subsequent decisions. The central contribution is a proposed sequential architecture that will connect these components without claiming that one universal insect decision circuit, threshold, or behavioral sequence has been empirically established. Taxon, life stage, sex, ecological task, environmental reliability, and observational scale are retained as explicit boundaries. The framework is intended to generate transition-specific and scale-indexed predictions that can be tested with experiments and field tracking capable of separating observed movement from inferred motivation. Its value therefore lies in organizing mechanistic evidence and exposing testable discontinuities, not in asserting validated prediction of dispersal outcomes.

Keywords: Insect movement, Sensory sampling, Internal state, Dispersal motivation, Movement-mode selection, Behavioral decision-making

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Introduction

Insect movement is commonly compressed into an endpoint—whether an individual left, how far it travelled, or where it arrived. That compression is analytically risky because dispersal itself can be decomposed into emigration, transfer through the matrix, and immigration, with strong context dependence across stages [1]. A behavioral framework therefore needs to distinguish component decisions before asking what produced the final path.

Stage separation matters because the same predictor need not operate equivalently throughout a movement episode. In *Melitaea cinxia*, intrinsic and extrinsic predictors differed among departure, transfer, and settlement,

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and departure-related predictors explained little realized transfer distance [2]. The defensible inference is cross-stage non-equivalence, not that the effect directions observed in this butterfly are universal.

Information is also not behaviorally meaningful in isolation. Across insect sensory systems, the prominence and use of cues can depend on internal state, ambient context, and taxon [3]. This motivates a separation between sensory sampling—what evidence is acquired—and state assessment—how current physiological or motivational conditions alter the value of that evidence. The distinction is analytical rather than anatomical: the two processes can interact continuously.

Measurement adds another boundary. Laboratory measures of dispersal propensity or locomotion may isolate component mechanisms while failing to reproduce realized field dispersal, which emerges under interacting genetic, physiological, and environmental constraints [4]. Accordingly, this article distinguishes observed path properties, inferred decision states, and ecological outcomes instead of treating one as a direct proxy for another.

Finally, variation among populations should not be collapsed into within-individual decision dynamics. In *Aedes aegypti*, human preference varied geographically and covaried with ecological and genomic features across African populations [5]. Such population-level predispositions may shape the prior distribution of movement-relevant preferences, but they do not by themselves specify the sequence of decisions made during an individual movement episode. The contribution developed here is therefore a proposed behavioral architecture linking sampling, state, departure, movement-mode control, later reassessment, and settlement while keeping these inferential levels separate.

Theoretical methods

This article uses theory-building rather than a new empirical dataset, systematic review, or quantitative synthesis. Evidence is used to constrain individual components of the framework, and no study is treated as validation of the complete sequence. Relationships are retained only at the level directly supported by the underlying task, taxon, life stage, and measurement context; broader links are identified as proposed synthesis.

The first analytical separation is between navigation control and movement motivation. Insect central-complex research supports heading representation and navigation-related computation, but those mechanisms should not be equated with decisions about whether movement should begin, continue, or terminate [6]. The framework therefore treats navigation as a control layer that may implement a chosen movement state without constituting a universal motivational hub.

Second, sampling is treated as action-dependent. During olfactory search, movement changes which intermittent sensory signals are encountered, so information acquisition can be generated partly by the animal's own behavior [7]. Third, sensorimotor transformations are separated from motivational inference. In walking *Drosophila*, odor onset and odor loss can produce different changes in running, turning, and local search [8]; these responses establish cue-linked motor transformations, not a decision to disperse.

Fourth, the architecture permits dependence among successive decisions. Correlated choices across phases of *Drosophila* olfactory search show that within-episode decisions need not be statistically or behaviorally independent [9]. This supports allowing prior state or action to condition later transitions, while leaving open whether dependence is produced by memory, a shared latent state, or another mechanism. Fifth, movement modes are defined operationally and with explicit scale. Area-restricted search theory shows that intensive and extensive search interpretations depend on encounter history, resource distribution, and the spatial-temporal resolution of measurement [10]. Consequently, path tortuosity alone is not accepted as evidence of a particular motivation.

Sensory sampling

Sensory sampling is the acquisition and transformation of movement-relevant evidence, not a passive reading of environmental variables. Its first complication is multisensory asymmetry. In host-seeking *Aedes aegypti*, CO_2 presented before a visual object enhanced steering and visual-neural responses, whereas the reverse cross-modal influence was not equivalent [11]. The useful principle is that cue order and recent cue history can change the weight of later evidence; the particular mosquito asymmetry should not be generalized to all modalities or taxa.

Sampling can also compress complex mixtures into selective features. In *Aedes aegypti*, human and animal odors produced distinct neural patterns, and particular odor features contributed to enhanced long-range host seeking [12]. The implication for the present architecture is that a sampled "odor" should not be represented as a scalar intensity alone: feature identity can be preserved separately from later judgments about target value or acceptance.

A modality can additionally be reused across behavioral contexts. Ir93a-dependent humidity and temperature sensing contributes to host-proximity behavior and to oviposition-site seeking in mosquitoes, with behavioral relevance depending on state and target [13]. This is evidence against assigning a fixed behavioral meaning to a sensor. It does not establish humidity as a universal settlement cue; rather, it shows why sensor availability, internal state, and current target must remain distinct variables.

Finally, sampling rules need not use fixed absolute thresholds. *Drosophila* larvae can rescale navigational turning decisions to recent stimulus variance, and such adaptation can differ among sensory modalities [14]. Thus, the proposed framework treats sensory evidence as potentially normalized to recent statistics. This creates a boundary condition for field inference: identical physical cue values can have different behavioral meanings after different sensory histories.

State assessment

State assessment represents the internal conditions that gate the meaning or consequence of sampled evidence. It is deliberately not defined as a single "motivation" score. In *Drosophila*, food deprivation changes locomotor search and its dopaminergic control [15], but increased movement in a foraging assay is not equivalent to increased dispersal motivation. Observed activity therefore remains separate from the latent state inferred to influence it.

Internal variables can interact rather than add monotonically. In *Cimex lectularius*, mating status modified how starvation affected host-seeking and feeding responses [16]. The specific interaction is species- and context-bound, yet it provides a strong counterexample to a universal one-dimensional hunger-to-movement axis. Within the proposed architecture, state is therefore represented conceptually as multidimensional, with interactions allowed among components.

State can alter the organization of behavior as well as its amount. In freely hunting *Tenodera sinensis*, starvation changed time allocation to prey-oriented behavior and the stereotypy of behavioral sequences [17]. This supports treating state as capable of modifying transition structure among behavioral options. It does not imply that hunger produces the same sequence changes in other insects or in dispersal contexts.

Mechanistic work further supports distinct but combinatorial state channels. In *Drosophila*, metabolic and reproductive states altered choice through distinguishable neural logic and combined effects [18]. The relevant inference is not that the complete insect "state vector" is known, but that multiple internal variables can jointly gate choice without collapsing into one scalar quantity.

State can also persist beyond the cue that initiated it. In female *Aedes aegypti*, a brief fictive CO_2 event induced a host-seeking state that altered responses to later cues after the initiating signal had ended [19]. The reported persistence is system-specific, but the broader implication is important: temporally separated sensory samples may be linked through a continuing internal state. In the framework, this persistence provides one mechanism by which earlier encounters can alter later departure or movement decisions without requiring the environmental cue to remain continuously present.

Departure decision

Departure is defined here as a conditional transition from remaining within the current local behavioral domain to initiating movement that expands or redirects search. It is not inferred from activity alone. Recent experience can modify departure-like exploration: honey bees exposed to different forms of resource unpredictability subsequently altered exploratory search behavior [20]. Because the study concerns foraging exploration rather than habitat emigration, it supports experience-dependent modification of exploration, not a measured dispersal probability.

External conditions can also be filtered through intrinsic phenotype. In bumblebee workers, anti-predator behavior varied with body size and ecological context [21]. This supports individual-specific weighting of risk-related information while cautioning against a fixed "large" or "small" disperser phenotype. Energetic, biomechanical, and ecological mechanisms may all contribute to the observed trait-by-context pattern.

Departure inference must additionally separate persistent individual differences from transient state and task. Continuous tracking of honey bees revealed substantial among-individual movement variation and differences in task-transition timing within the colony [22]. Those patterns demonstrate stable movement heterogeneity within a social and spatially constrained setting, not field dispersal syndromes. The proposed departure construct therefore has three non-interchangeable inputs: recent experience, current internal state/context, and relatively persistent individual propensity. None is sufficient by itself to identify ecological emigration.

Because these inputs can generate similar outward movement while carrying different inferential meanings, a mechanism–boundary matrix is more informative than a single departure score.

Table 1. Distinguishing departure-like states from ecological emigration in the proposed decision architecture

Departure-decision state or mechanism	Experience-conditioned exploration	Phenotype × risk weighting	Persistent individual movement propensity	State-driven activation without emigration	Multi-input departure condition
Evidence · Interpretation for departure	Change in later exploratory search Prior environmental history can modify readiness to expand search	Trait-dependent anti-predator movement response Intrinsic phenotype can alter weighting of external risk in a departure-relevant decision	Repeatable movement differences and variable task-transition timing Stable individual propensity should be separated from short-term state	Increased activity or search effort Higher activity is insufficient evidence for departure motivation	Convergence or conflict among history, state, phenotype, local cues, and task Departure is treated as a conditional transition rather than a scalar threshold
Limits and uncertainty	Exploration is not equivalent to habitat emigration	Body-size direction need not transfer across species, tasks, or landscapes	Within-hive movement is not field dispersal; age and social task may contribute	Motor activation, local search, and emigration can produce similar path expansion	Input weights and interactions are not established as universal
Research or test	Manipulate recent resource reliability while measuring both local search expansion and actual boundary crossing	Cross trait classes with controlled risk cues and quantify whether effects occur before, during, or after departure	Re-identify individuals across laboratory and field contexts to test persistence across movement domains	Pair locomotor metrics with explicit boundary-crossing or habitat-leaving criteria	Test factorial perturbations and model transition probability without prespecifying one universal score
Biological setting · Framework standing	Honey-bee foraging after predictable versus unpredictable resource histories Evidence-supported premise; departure linkage proposed	Bumblebee workers differing in body size under ecological risk Evidence-supported premise; generalized weighting rule proposed	Individually tracked honey bees within a colony Evidence-supported heterogeneity; cross-context interpretation proposed	Foraging/search systems in which hunger or arousal increases locomotion Proposed inferential boundary	Cross-taxon synthesis Proposed synthesis

Movement mode selection

Once movement has been initiated or redirected, the relevant question is not simply whether the insect moves faster or farther, but how locomotor control is configured for the current informational problem. In odor-guided insects, the temporal statistics of odor change with distance from a source and are associated with different locomotor strategies; near a target, additional modalities can contribute to assessment [23]. Mode selection is therefore treated as conditional on cue structure and range-to-target context, not as a compulsory sequence of universally named search modes.

Nor must mode change be categorical. In two ant species, endogenous lateral oscillations were modulated by visual cues, changing the balance between exploratory and directed components of navigation [24]. This provides an empirical example in which a motor pattern is continuously tuned. Accordingly, the framework allows both discrete strategy transitions and continuous parameter changes; which description is appropriate must be established from the organism and measurement scale rather than imposed from path geometry.

The chosen locomotor state can also change subsequent information processing. In monarch butterflies, flight and steering altered heading-neuron tuning and cue hierarchy under a tethered, migration-related navigation paradigm [25]. This shows that locomotor state can modify sensory-neural representations used for navigation. It does not show that compass coding determines dispersal motivation, and migration-specific physiology should not be generalized to routine local movement.

These observations create a recursive structure: cue statistics and internal context can influence movement control, while the resulting locomotor state changes the future sensory samples and, in some systems, their neural

weighting. **Figure 1** distinguishes evidence-supported mode mechanisms from the proposed feedback links that connect mode choice back to sampling and forward to later reassessment.

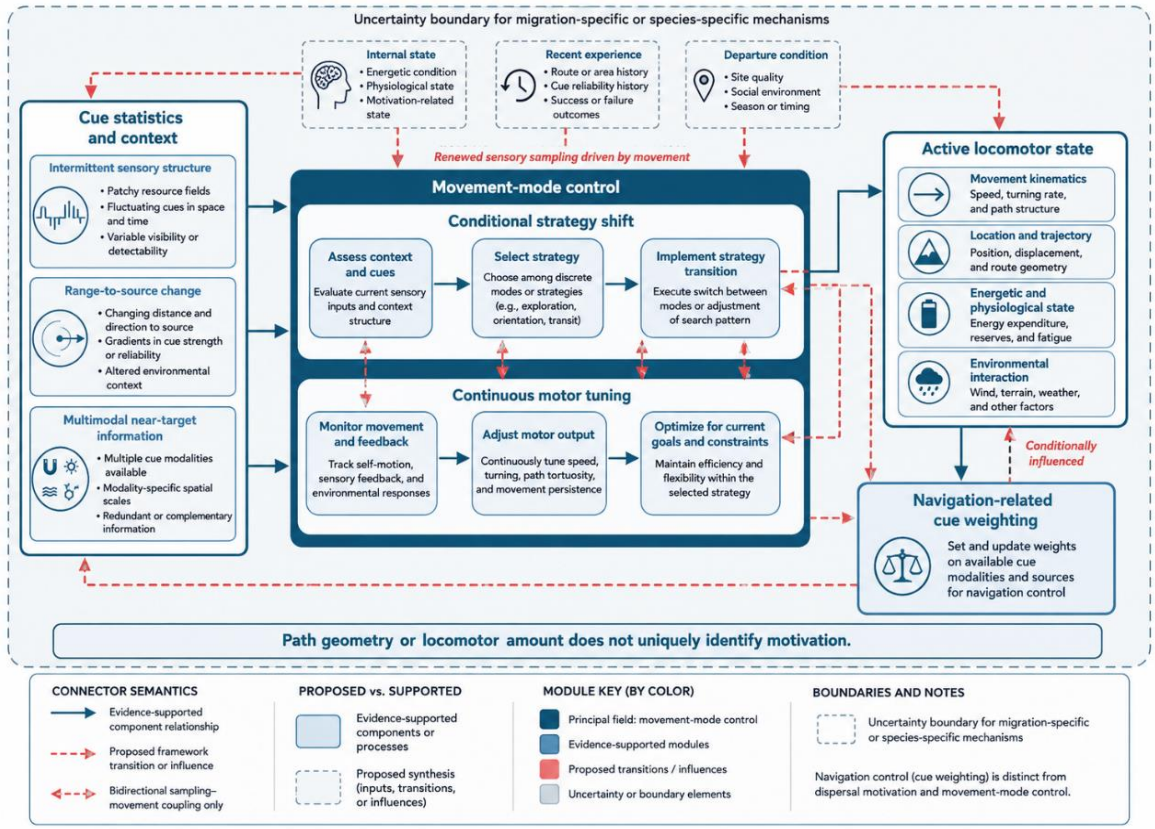


Figure 1. Movement mode control as a recursive field between cue statistics, motor tuning, and renewed sampling

Reassessment during transit

Movement does not end inference. During transit, information can support, weaken, or overturn the current interpretation. In *Drosophila* self-motion control, stationary visual patterns provided counterevidence against self-rotation and suppressed inappropriate stabilizing responses [26]. This is an existence proof that ongoing control can use negative evidence; it is not evidence that the same circuit governs ecological route reassessment.

Reassessment also has a temporal-resolution problem. A rapid motor correction, a local return to a previously sampled patch, and abandonment of a learned route may all look like "updating," yet they operate over different intervals and may depend on different information stores. The proposed architecture therefore uses reassessment as a functional category, not a claim that one memory system or neural circuit spans these scales. A test should identify what prior expectation is being revised, what new evidence caused revision, and which movement variable changes afterward.

Stored information is similarly conditional. Multi-camera field monitoring of *Cotesia glomerata* showed that learned information could carry costs when cue reliability was low [27]. In *Bombus terrestris audax*, the association between memory performance and wild foraging performance changed across ecological seasons, including reversal under contrasting resource conditions [28]. Thus, the framework proposes that transit reassessment should update both current sensory interpretation and the weight assigned to memory, with reliability rather than memory presence alone determining whether stored information remains useful.

The distinction matters because the same observed course correction can arise from counterevidence, stale memory, or changing environmental value. A cross-scale grid is therefore needed to distinguish these reassessment routes without converting them into a single confidence score.

Table 2. Cross-scale evidence grid for distinguishing routes of reassessment during transit

Evidential standing	Evidence · Interpretive consequence	Limits and uncertainty · Research or test	Operational scale · Biological setting
Counterevidence suppression			
Evidence-supported premise; ecological extension proposed	Evidence against predicted rotation suppresses stabilizing response Current movement interpretation can lose support	Controlled visual task, not ecological dispersal Introduce conflicting motion evidence during ongoing movement	Moment-to-moment motor control Adult Drosophila; self-motion task
Reliability-dependent memory revision			
Evidence-supported premise; weighting rule proposed	Learned information can reduce performance when reliability falls Stored information should not receive fixed weight	One parasitoid field system Alter cue reliability after learning and track rerouting	Foraging bout to route use Parasitoid Cotesia
Ecology-dependent memory value			
Evidence-supported contextual boundary	Memory–performance association changes with resource context Information value can change direction among environments	One bee taxon and memory assay Compare identical memory measures under contrasting resource states	Seasonal ecological context Bumblebee foraging
Cross-scale reassessment state			
Proposed synthesis	Conflict among current cues, stored information, and transit control Continue, resample, or redirect remain distinct outcomes	Transition rules are not validated universally Match cue conflict to action changes at the relevant temporal scale	Multiple movement intervals Proposed cross-taxon synthesis

Settlement decision

Settlement is treated as target acceptance rather than mere arrival. In female *Drosophila*, parasitoid-threat assessment reduced oviposition commitment through a task-specific sensory and signaling system [29]. This provides an acceptance/rejection analogue, not evidence that oviposition choice is equivalent to habitat settlement. Near a target, the cues used for assessment can also differ with state and target: mosquito hygrothermal sensing contributes to host-proximity and oviposition-site seeking [13], while odor-guided locomotion can recruit additional modalities as insects approach a source [23]. Detection therefore need not imply acceptance.

A target may consequently be detected, reached, and still rejected after local information is sampled. The proposed framework keeps terminal guidance and terminal commitment separate because the sensory conditions that make a target locatable need not be identical to those that make it acceptable.

When arrival, target evidence, and internal state disagree, a discordance-triage representation is needed to keep acceptance, renewed sampling, and rejection analytically separate.

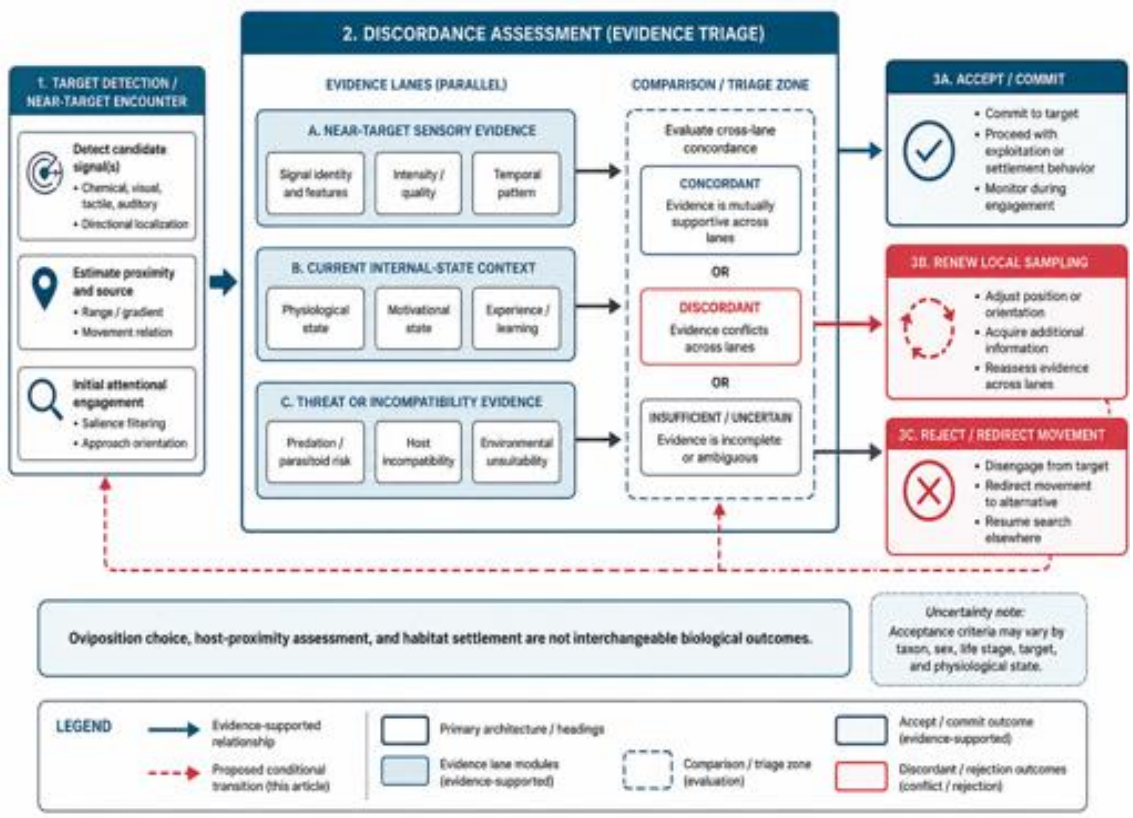


Figure 2. Discordance at the target boundary separates detection from acceptance

Sequential movement architecture

The proposed architecture does not require one anatomical decision center. In cockroaches, mushroom-body output activity preceded and predicted whether food odor would be followed by feeding-related behavior [30], showing that choice-related neural activity can precede overt action without establishing a universal controller. Computational modeling likewise demonstrates one plausible way multimodal signals could be transformed into steering-compatible coordinates [31], but in-vivo generality is not established.

Transit control also carries uncertainty. Path integration can accumulate directional and distance error, with complementary cues and recalibration correcting estimates in task-specific ways [32]. The framework therefore represents uncertainty as something that can change during movement rather than as a fixed property established at departure.

Two additional constraints follow. First, transitions may overlap: sampling can continue during locomotion, and settlement-like assessment can begin before translational movement has fully stopped. Second, a latent decision variable is used only as a modeling convenience for unobserved commitment; neural activity that predicts action does not establish that the same variable is encoded in a single structure. These constraints make the architecture sequential in inferential organization rather than necessarily serial in neural time.

The resulting sequential movement architecture is proposed: sensory samples are evaluated through current state; departure changes the available sampling field; movement mode alters subsequent information acquisition; transit evidence can revise current interpretation; and settlement requires target acceptance rather than target encounter. Stage-specific predictors in dispersal can differ [2]. Sensory information is context-dependent [3]. Dispersal itself is usefully partitioned into component stages [1]. These premises support separability, but they do not validate the exact ordering or connector topology proposed here.

Because several distinct inferential errors can produce the same trajectory-level description, a conditionality and failure-mode matrix is needed to show where the sequential interpretation can break down.

Table 3. Conditionality and failure modes in interpreting the proposed sequential movement architecture

Failure mode	Limits and uncertainty · Observable or evidential signature	Interpretive consequence · Biological or inferential context	Research or test · Evidential standing

Sampling–state conflation	State dimensions may interact Same cue produces different actions across states	Cue strength is mistaken for fixed preference Cue response under changing physiological context	Manipulate cue and state independently Proposed synthesis
Departure–transfer conflation	Stage predictors can differ Leaving predicts transfer weakly or differently	Emigration propensity is mistaken for movement distance Ecological dispersal	Estimate transitions separately Evidence-bounded synthesis
Mode–motivation conflation	Scale and task alter interpretation Similar path geometry occurs under different control states	Speed or tortuosity is overread as motivation Search and navigation	Pair trajectories with cue/state perturbations Proposed inferential boundary
Transit-update failure	Correction mechanisms vary among systems Movement persists despite counterevidence or growing uncertainty	Outdated interpretation continues to govern movement Navigation with conflict or accumulated error	Introduce conflicting cues during transit Proposed test
Arrival–acceptance conflation	Acceptance criteria are task-specific Target is reached but commitment changes after local assessment	Encounter is mistaken for settlement Near-target behavior	Measure arrival and commitment separately Proposed synthesis

Scale-dependent predictions

Scale changes both what can be observed and which mechanism is plausible. Global butterfly migration evidence is geographically and evidentially uneven, so lack of strong records cannot be treated as biological absence and migration labels cannot be assumed equally supported [33]. At the other extreme, monarch migration includes specialized orientation systems and seasonal biology that should not be projected unchanged onto local movement [34].

This scale indexing produces three proposed prediction classes. Within a bout, sensory perturbations should be most informative when aligned to immediate steering or turning responses. At habitat-transfer scales, departure, route control, and arrival should be estimated as separate transitions rather than summarized by displacement. At migratory scales, specialized orientation and seasonal-state variables may become indispensable, so parameters learned from local search should be expected to transfer only after explicit validation. Apparent contradiction across studies may therefore reflect different observational windows rather than genuinely opposing behavioral rules.

The framework consequently predicts discontinuities rather than one scale-free parameter set. A variable associated with departure need not predict transfer [2]. Area-restricted search interpretations depend on observational scale and encounter structure [10]. Persistent individual movement differences can coexist with changing task-transition timing [22]. Predictions should therefore name the observable unit—within-bout turning, local search, boundary crossing, transfer, or migration—and the time window over which a latent decision is inferred.

Results and Discussion

The evidence supports separable component mechanisms, not the complete architecture as an empirically validated sequence. Sensory information can change meaning with internal and external context [3], while odor-guided locomotion can vary with cue statistics and target range [23]. Parallel control, overlapping decisions, or taxon-specific shortcuts may therefore fit some systems better than a strict serial chain.

Generality is further limited by concentration of mechanistic evidence in model insects. Geographic variation in *Aedes* host preference shows population-level heterogeneity [5], and mosquito sensory channels can be reused across state-dependent targets [13]. Neither result supplies universal constants for other orders, sexes, or life stages.

Methodological precision must also be distinguished from ecological validity. Laboratory dispersal measures may diverge from realized field movement [4], and learned information can become costly under altered reliability in a parasitoid field system [27]. Validation should therefore pair controlled perturbations with field-relevant transitions rather than rely on path metrics alone.

A useful validation program should include negative cases. If manipulating internal state changes activity but not boundary crossing, that result would argue against treating the state as a departure determinant in that context. If cue conflict changes steering without changing subsequent acceptance, movement-mode control and settlement should remain separable. Conversely, if one perturbation repeatedly shifts several transitions, the architecture can accommodate a shared upstream influence without collapsing those transitions into one decision.

Comparative work is especially important because homologous sensory or navigation machinery can be embedded in different ecological tasks. Tests should replicate the same transition-level perturbation across sexes, life stages, and species only where the relevant behaviors are sufficiently comparable. The objective is not to discover one canonical insect sequence, but to determine which links are conserved, which are contingent, and where a parallel or nonsequential description is superior.

The strongest tests would target falsifiable transitions: whether counterevidence changes an ongoing movement interpretation [26], whether navigation uncertainty is corrected during transit [32], and whether predictors differ across departure, transfer, and settlement [2]. Failure of these transition-specific predictions would require revision of the proposed architecture rather than reinterpretation as hidden “motivation.”

Conclusion

Insect movement is more defensibly interpreted as a set of linked, context-sensitive decisions than as a single behavioral output. The proposed architecture separates sampling, state assessment, departure, movement-mode control, reassessment, and acceptance while allowing feedback and uncertainty between them. Its principal boundary is equally important: component evidence does not establish a universal sequence. Progress therefore depends on measuring transitions directly, specifying scale and taxon, and testing when the proposed links fail.

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