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Prior Experience Creates Ecological Memory That Alters Insect Movement, Habitat Selection, and Population Persistence

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ABSTRACT

Insects repeatedly encounter resources, hosts, hazards and landmarks whose value changes through time. Prior experience can therefore modify later movement, yet memory is commonly treated either as a cognitive trait or as a local behavioral mechanism without asking when its effects become ecologically consequential. This perspective uses ecological memory for retained information generated by an individual's previous interaction with its environment that changes subsequent search, route use or site choice. The term does not imply one neural substrate, retention interval or adaptive effect. Evidence across bees, ants, parasitoid wasps, mosquitoes, butterflies and *Drosophila* shows that experience can recalibrate search, establish habitual routes, bias host or oviposition choice, and be updated or mislead behavior. Effects depend on receiver state, cue reliability, current goals and environmental structure. A proposed scaling architecture separates evidence-supported individual effects from population inference. Memory can contribute to redistribution only when behavioral effects are sufficiently persistent, prevalent and spatially directional; persistence additionally requires demographic consequence. Ecological memory may therefore stabilize, destabilize or leave population trajectories unchanged depending on information reliability, environmental change and how memory-shaped movement affects survival, reproduction, recruitment or coexistence.

Keywords: Ecological memory, Insect navigation, Experience-dependent behavior, Habitat selection, Movement ecology, Population persistence

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Introduction

Insects rarely make spatial decisions from current sensory information alone. A forager may return to a profitable patch, avoid a dangerous route, broaden search after rewards become unreliable, or revisit a learned host cue. Yet cognition studies often quantify acquisition or retention, whereas movement studies record trajectories or patch use without establishing how experience contributed. The inferential problem is therefore when a history-dependent behavioral response becomes ecological memory with consequences beyond the immediate decision.
Memory cannot be assumed to be intrinsically beneficial. In free-foraging bumblebees, the association between short-term memory score and foraging efficiency changed with seasonal resource context, reversing between spring and summer floral conditions [1]. Honey bees exposed to unpredictable rewards later searched more broadly and less precisely after reward removal, showing that recent resource history can recalibrate search [2]. In *Cotesia glomerata*, persistent unreliable learned information reduced foraging efficiency and increased non-

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host oviposition likelihood in some plant contexts [3]. The ecological value of remembered information therefore depends on its present reliability.

Cross-scale inference is harder still. Longitudinal tracking of honey-bee workers revealed persistent individual behavioral differences and links between task-transition tempo and lifespan, but did not establish memory as their cause [4]. Faster learning in a bumblebee assay was negatively correlated with lifetime resource collection under free foraging [5]. Cognitive score, route phenotype and individual movement pattern are therefore poor substitutes for direct demographic evidence.

This perspective proposes a conditional chain: experience may create retained information that alters movement and site choice, but population redistribution and persistence require additional evidence. Memory formation is separated from updating, movement from habitat selection, and individual spatial response from population consequence. The central contribution is an explicitly proposed scaling architecture that preserves those boundaries rather than treating memory as a universal adaptive trait.

Conceptual methods

The analysis uses an evidence-chain method rather than meta-analysis. Evidence is partitioned into experience and acquisition, retention and updating, movement expression, habitat or host selection, population redistribution, and persistence. A claim advances across these stages only when the relevant outcome is measured directly or when the transition is identified as proposed.

This separation matters in navigation. Multilevel explanations must connect neural, computational and behavioral evidence without collapsing them [6]. Path integration uses self-motion information to maintain a home vector and is distinct from learned landmark or view memories even when both contribute to one journey [7]. Learning flights and walks are structured movements through which insects acquire spatial information around nests or resources [8]. Here, ecological memory is therefore a functional category for retained, experience-derived information that later modifies ecologically relevant behavior, not a synonym for one navigation algorithm.

Generalization also requires individual and contextual boundaries. Traplining bumblebees show marked inter-individual variation in route fidelity and performance [9]. Desert ants trained on a familiar route respond differently when released into unfamiliar surroundings than ants lacking the same route experience [10]. Previous experience can thus change how current information is interpreted rather than dictate a fixed action.

The proposed inferential rule is conservative: individual ecological consequence requires demonstrated change in search, route use or site choice; redistribution requires prevalence, persistence and spatially non-cancelling effects; persistence requires a further demographic link. These are conceptual gates, not validated quantitative thresholds.

Individual experience and memory formation

Experience is encoded under variable receiver states. Bumblebee workers of different body sizes invested differently in flower-learning flights, with reward concentration modifying that investment [11]. Bumblebee queens also outperformed workers in tested color-association tasks [12]. These results support caste-, phenotype- and task-dependent acquisition, not a general ranking of cognitive quality.

Physiological condition can modify memory performance. In bumblebees, gut-microbiome variation was associated with memory, while *Lactobacillus apis* and a candidate metabolite improved performance in the tested long-term memory paradigm [13]. In *Venturia canescens*, poor adult nutrition impaired associative learning and retention while also reducing longevity and fecundity [14]. The latter finding is a boundary condition: nutrition may influence cognition and life history in parallel, so demographic effects cannot automatically be assigned to memory mediation.

Some systems provide causal neural evidence. Mushroom-body inactivation in *Formica rufa* impaired learned visual navigation while comparatively sparing innate attraction [15]. In *Myrmecia midas*, disrupting mushroom-body vertical lobes impaired view-based homing in a familiar environment [16]. Female *Aedes aegypti* learned host-related odors, and disruption of dopaminergic D1 signaling suppressed learned responses in the tested paradigm [17]. These studies establish mechanistic requirements for particular learned behaviors, not one universal insect memory circuit.

Ecological context further modifies plasticity. A synthesis of parasitoid-host interactions shows learning on both sides of the interaction, with consequences varying among systems [18]. Experience-dependent mushroom-body plasticity also differed among butterflies with contrasting host ranges and search ecologies [19]. Such variation is consistent with ecological modulation of neural investment but does not by itself demonstrate adaptation.

This perspective therefore treats formation as conditional: experience is filtered through life stage or caste, physiological state, sensory access, cue salience and task before becoming retained information. This proposed formulation separates exposure from encoding, and encoding from later ecological use.

Memory duration and updating

Retention time alone does not determine ecological relevance. In *Cotesia glomerata*, conditioned plant-volatile preferences weakened after ecologically relevant non-reward experiences and later showed spontaneous recovery, indicating that reduced expression after extinction need not mean erasure [20]. In *Nasonia*, associative retention differed strongly among strains, whereas genetically diverse strains did not support a simple species-level difference [21]. A single strain or retention interval should therefore not define a species-wide memory phenotype.

Updating may also be rapid or history weighted. Desert ants learned to avoid views preceding an aversive route event and reinforced views associated with a safe detour [22]. *Lasius niger* instead showed strong preference for the odor trained first; this primacy effect was not explained by trail pheromone and could be weakened by familiarization [23]. These examples support heterogeneous updating rules rather than one general memory-decay function.

Spatial-memory components can themselves differ. Anesthesia disrupted the distance component of ant path-integration memory while leaving direction comparatively intact [24]. Although path integration is not equivalent to associative ecological memory, the result demonstrates why persistence should be assigned to a defined informational component.

The proposed "memory state" therefore combines retained content, current weighting or reliability, and susceptibility to updating. It is a conceptual bookkeeping device, not a new measured variable. Persistent information may guide behavior in stable settings, become costly after environmental change, or be overridden by stronger current cues.

Movement consequences

Movement is the first stage at which ecological memory becomes spatially observable, but movement outcomes are not interchangeable. In flight-tunnel tests, bumblebees used learned visual and movement information to follow habitual routes; path integration or optic flow alone did not explain the choices [25]. In open landscapes, harmonic-radar tracking showed that bumblebees altered their use of ground-level linear features with behavioral goal and experience [26]. Remembered information therefore interacts with current landscape structure rather than functioning as a fixed route command.

At a smaller scale, *Drosophila* re-zeroed a path integrator at a fictive food-patch center, reorganizing local search around recent resource experience [27]. At route-sequence scale, bumblebee routes developed through repeated exploitation-exploration cycles rather than monotonic convergence on one immutable path [28]. Experience can consequently modify search center, breadth, route order, route fidelity or landscape-feature use, with different mechanisms and scales.

Information acquisition is itself goal dependent. Bumblebee learning flights differed between nest and flower contexts even under similar visual surroundings [29]. Movement determines what is sampled, and new sampling can later update memory; this recursive loop is a proposed cross-study synthesis rather than one measured causal system.

A scale boundary follows. Local search, habitual-route guidance and use of linear features do not by themselves demonstrate dispersal, habitat redistribution or demographic connectivity. Individual biases may be rare, cancel across individuals, or be overridden by current resources. Experience-shaped movement becomes a population hypothesis only after prevalence, persistence and spatial directionality are established.

Because these effects differ in mechanism, scale and observability, a coverage-and-gap map is needed to keep local search, habitual routing and landscape-feature use analytically separate.

Table 1. Where prior experience enters insect movement: observed route and search consequences and unresolved scale transfers

Experience retained		Spatial expression	
Memory expression	**Insect and experience setting**	**Movement consequence**	**Scale boundary and tracking test**

History-calibrated search breadth	Honey-bee foragers after variable rewards. Search breadth, precision and intensity after reward loss	Recent unpredictability recalibrates search allocation. Evidence-supported.	Short-term experimental search is not dispersal. Test persistence under naturally shifting resources
Habitual-route steering	Bumblebee foragers. Cue-conflict choices on established routes	Learned visual and movement information can guide repeated routes. Evidence-supported.	Constrained route geometry limits landscape inference. Test familiar-route cue conflicts in open landscapes
Experience-conditioned linear-feature use	Bumblebee workers in open terrain. Harmonic-radar trajectories	Experience and current goal jointly shape structural-feature use. Evidence-supported.	One landscape cannot establish a universal corridor effect. Replicate across landscape configurations and resource states
Resource-centered local search	Adult Drosophila. Search re-referencing around fictive food	Recent resource experience anchors local search. Evidence-supported.	Laboratory local search is not habitat selection. Test natural, depleted or moving resource patches
Exploration-exploitation route cycling	Bumblebee foragers. Repeated multi-resource route sequences	Familiarity can coexist with continued exploration. Evidence-supported.	Experimental arrays do not establish fitness benefit. Measure persistence of exploration under ecological variability
Goal-dependent information acquisition	Bumblebee workers. Nest- versus flower-learning flight geometry	Current goal shapes how spatial information is sampled. Evidence-supported.	Acquisition movement is not memory strength. Link acquisition trajectories to later retrieval
Cross-scale memory-shaped movement	Multiple systems. Concordance among history, retained information, current cues and movement	Attribution to ecological memory requires experience beyond current opportunity alone. Proposed integrative criterion.	Similar trajectories can arise from different mechanisms. Combine controlled experience manipulation with longitudinal field tracking

The conditional relationships are clearer when mechanistic and scale-transfer boundaries remain visible; **Figure 1** therefore places experience history, memory state, current context and movement outputs in one map without implying a linear progression.

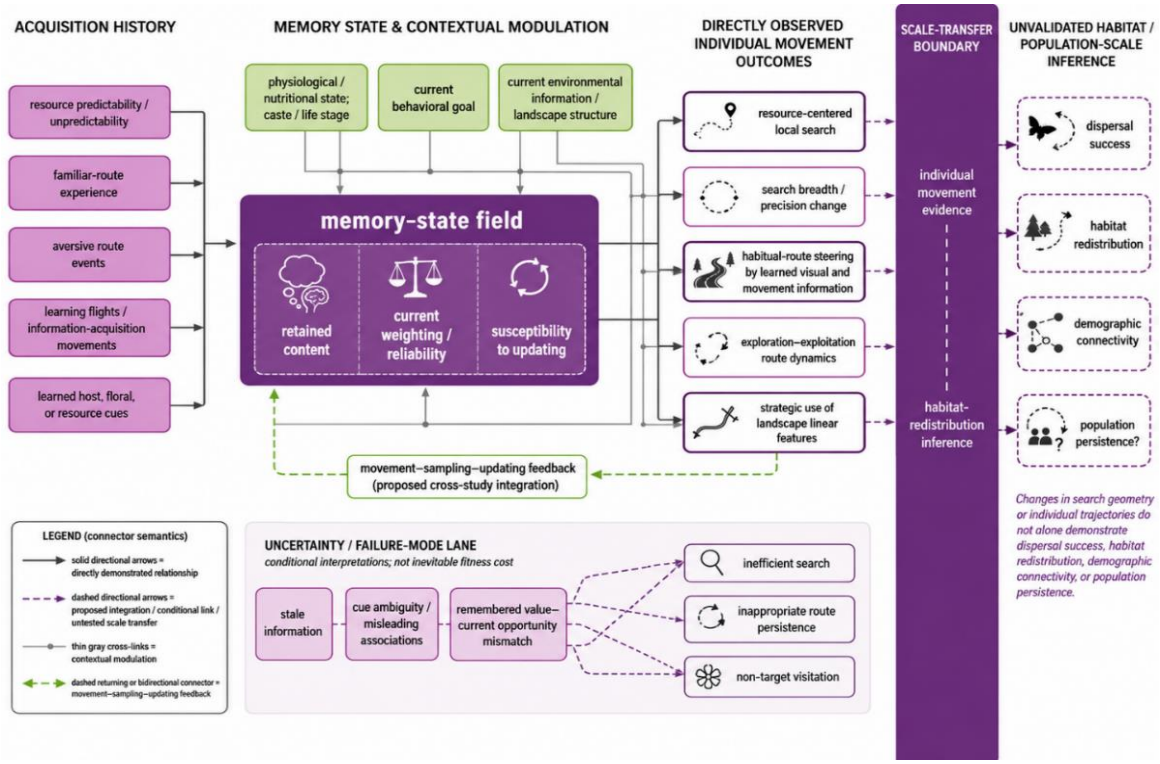


Figure 1. State-dependent conversion of prior experience into search geometry and habitual route use

Habitat-selection consequences

Experience-dependent movement becomes habitat selection only when it changes use of alternative places, hosts or reproductive sites rather than merely the geometry of travel. In *Pararge aegeria*, prior oviposition experience altered subsequent search and site-selection behavior, with plasticity differing among ecological backgrounds [30]. The result supports history-dependent reproductive-site choice in that butterfly system, but it does not establish that learning caused niche expansion or that the observed plasticity was adaptively beneficial.

Current opportunity structure can also dominate choice. In discontinuous landscapes used by bumblebees, patch size and distance strongly influenced patch selection [31]. Repeated use of a patch therefore cannot be interpreted as memory without distinguishing prior experience from accessibility, resource amount and spatial configuration. Host preference presents the same problem at another ecological interface: mosquito host choice reflects interacting genetic, physiological, sensory, availability and experience-related determinants rather than memory alone [32].

A second distinction is between selection memory and movement memory. An insect may use remembered route information while retaining an unchanged valuation of the destination, or may change destination preference without relying on the same route. Conflating these processes risks assigning habitat choice to a navigation mechanism. The relevant ecological unit is therefore the alternative selected after experience, not simply whether the path to that alternative becomes more efficient or stereotyped. This distinction is especially important when resources are patchy, ephemeral or renewed on timescales shorter than memory persistence.

This analysis motivates a proposed attribution rule. A habitat-selection effect should be described as memory shaped only when an experience contrast predicts later selection after relevant current-environment alternatives are considered. Otherwise, spatial fidelity remains compatible with innate preference, energetic state, cue accessibility or simple resource geometry. Ecological memory is therefore one possible determinant of habitat selection rather than its default explanation.

Scaling memory to population redistribution

Population redistribution requires more than detectable memory in individuals. Repeated aversive experience can alter hesitation and route behavior in navigating ants [33], but an individual detour establishes neither a population-level shift nor net redistribution. Individuals may differ in learning history, memory persistence and route preference, and opposing responses may cancel when aggregated.

The direction of scaling is also not necessarily beneficial. In *Cotesia glomerata*, learning reduced foraging efficiency in some environments containing non-host-infested plants because previous information could promote additional non-host visitation under ambiguous cue conditions [34]. Thus, memory-shaped movement can concentrate individuals toward useful locations, maintain inefficient fidelity, or redirect them toward misleading cues.

Aggregation introduces a further inferential problem. A population-level spatial pattern can arise from many weak, similarly directed responses or from a minority of strongly persistent individuals. Conversely, conspicuous effects at the individual level may disappear in the population mean when learning histories or memory states differ. Social insects introduce an additional level because redistribution of workers need not represent redistribution of colonies or reproductive individuals. The relevant quantity is therefore the distribution and spatial covariance of individual responses, not simply an average trajectory.

Redistribution should also be distinguished from increased connectivity. Memory might repeatedly return individuals to known areas and thereby restrict exploration, whereas experience with unreliable resources can broaden search. Either response could change encounter rates without necessarily altering the occupied range. Demonstrating redistribution consequently requires comparison of spatial use among alternatives or areas through time while retaining individual identities whenever feasible.

The proposed scaling criterion requires three properties before a population-redistribution inference is made: sufficient prevalence of the memory-shaped response, persistence long enough to influence repeated spatial decisions, and directional concordance rather than cancellation among individuals. Even when those conditions are met, redistribution remains a spatial consequence rather than evidence of improved survival, reproduction or population persistence.

Because trajectories alone cannot adjudicate these alternatives efficiently, the distinctions required for a population-level interpretation are resolved explicitly in **Table 2**.

Table 2. Adjudicating when memory-shaped movement supports a population-redistribution inference

Individual-to-population transfer				Cancellation challenge
Scale-transfer gate	**Spatial context**	**Aggregation signal**	**Population inference**	**Current-landscape alternative and evidence needed**
Individual route bias	Ant, bee or parasitoid movement after experience	Repeatable change in route, hesitation or search	Prior experience can alter individual spatial behavior. Evidence-supported at individual level.	Does not establish prevalence or net redistribution. Quantify how many individuals show the same directional response
Concordant repeated reallocation	Multiple individuals repeatedly favor the same spatial alternative	Persistent, similarly directed patch or route change	Could generate redistribution if maintained across individuals. Proposed scaling condition.	Current resource geometry can independently produce concordance. Manipulate experience while holding current opportunity structure comparable
Cue-mismatch concentration	Learned cues remain behaviorally influential after ecological value changes	Repeated visitation to misleading or non-target locations	Memory can generate spatial concentration that is ecologically inefficient. Evidence-supported mechanism; population scaling proposed.	Remembered information must be distinguished from current cues. Change cue reliability after controlled learning and track subsequent use
Current-landscape override	Patch distance, size or accessibility strongly constrain use	Selection follows present spatial geometry despite prior exposure	Memory contribution may be weak, overridden or observationally masked. Evidence-supported boundary.	Accessibility and current resource state explain repeated use without memory. Cross experience histories with standardized patch configurations
Cross-individual cancellation	Individuals differ in memory state, route history or updating rate	Opposing or heterogeneous movement responses	Mean population position may change little despite strong individual effects. Proposed scaling condition.	Aggregation can conceal biologically important individual responses. Preserve individual identities in longitudinal spatial analysis
Demographic coupling unresolved	Redistribution is detected without survival or reproductive outcomes	Distribution changes without demographic evidence	Spatial redistribution cannot yet be interpreted as persistence enhancing. Proposed inference boundary.	Mortality, reproduction, recruitment and density dependence remain unmeasured. Couple movement data to explicit demographic outcomes

The scale transition is sufficiently consequential to require a distinct systems architecture. **Figure 2** therefore makes visible the additional gates separating measured individual behavior from a population-redistribution interpretation.

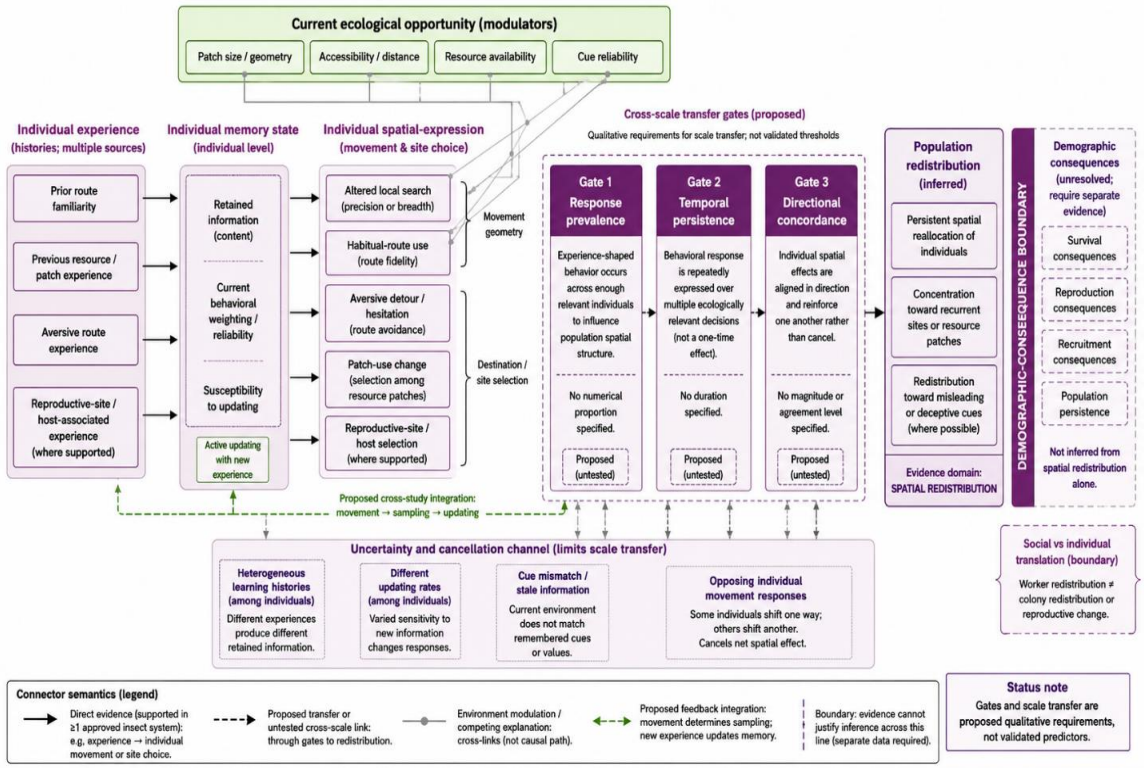


Figure 2. The scale-transfer gates separating remembered routes from population redistribution

Conditions linking memory to persistence

Population persistence is the most demanding inference because spatial redistribution can have positive, negative or negligible demographic consequences. A population model of aphid–parasitoid dynamics showed that learning-induced switching costs could maintain host-phenotype diversity under some parameter regimes, whereas abiotic stress could destabilize the system [35]. This demonstrates theoretical plausibility for behavior-dependent population feedback, not empirical confirmation that ecological memory generally increases persistence.

The evidence assembled here instead supports a proposed set of persistence gates. First, the ecological value of memory must remain aligned with current conditions; seasonal reversal of the memory–performance relationship in bumblebees shows that this alignment can change [1]. Second, retained information must not become persistently misleading, because stale parasitoid memories can reduce foraging efficiency [3]. Third, cognitive performance itself cannot be treated as a proxy for demographic benefit, as faster bumblebee learning was negatively associated with lifetime resource collection [5]. Physiological state may additionally influence cognition and life-history traits in parallel, complicating mediation claims [14]. Cue ambiguity can further convert learning into inefficient patch use [34]. Finally, population feedback is expected to depend on ecological context and stress regime rather than operating as a fixed stabilizing mechanism [35].

These gates are deliberately qualitative. The evidence does not justify thresholds for how many individuals must respond, how long a memory must remain behaviorally influential, or what magnitude of demographic change would constitute a persistence effect. Such quantities could vary with generation time, colony organization, resource renewal, environmental temporal structure and the demographic role of the moving life stage.

Accordingly, this article proposes that persistence effects require a demonstrated demographic pathway linking memory-shaped spatial behavior to survival, reproduction, recruitment or coexistence. No universal sign is predicted. Memory may improve matching to recurring opportunities, preserve obsolete preferences, generate switching costs, or have little net effect when individual responses cancel.

Results and Discussion

The evidence supports a conditional sequence rather than a single insect-wide mechanism. The value associated with measured memory changes with ecological context [1]. Persistent inaccurate information can impose field-realized foraging costs [3]. At population scale, the strongest evidence in this set is theoretical and conditional

rather than an empirical demonstration of persistence [35]. Ecological memory is therefore most useful as a cross-level concept when it preserves the distinction between retained experience and the consequence attributed to it.

Negative and unstable cases are central to that interpretation. Faster learning can correlate with lower lifetime resource collection [5]. Conditioned preference may weaken and later recover after extinction experience [20]. Learning can also become inefficient when remembered cues are ambiguous or misleading [34]. Reliability and updateability are therefore as important ecologically as acquisition or retention.

The proposed architecture also clarifies what would falsify a memory-based interpretation. If experienced and naive insects make equivalent choices once present resource configuration is controlled, previous experience is unnecessary to explain the spatial pattern. If individual memory effects are strong but balanced in opposing directions, the population-redistribution prediction fails. If redistribution occurs but no relevant demographic rate changes, a persistence interpretation remains unsupported. Such negative outcomes identify the scale at which the proposed chain terminates rather than constituting failed evidence.

Temporal environmental structure deserves particular attention. Remembered information should be most useful when past conditions retain predictive value for subsequent decisions, whereas rapid environmental turnover could increase mismatch between stored and current information. Highly stable environments may conversely reduce the marginal value of repeated updating. The present evidence does not establish a universal relationship between environmental autocorrelation and memory value, so these are proposed predictions for comparative testing rather than empirical generalizations.

Generalization across taxa is equally constrained. Bumblebee queens and workers differ in tested learning performance [12], while *Nasonia* strains can differ sufficiently in retention to undermine simple species-level cognitive descriptions [21]. Mosquito host preference also depends on multiple determinants besides experience [32]. Claims about ecological memory should therefore specify taxon, sex or caste, life stage, decision context and measurement system.

The framework further avoids treating population persistence as synonymous with individual performance. Colony-level systems, solitary insects and parasitoid–host interactions translate movement into demographic consequences differently. Efficient worker routes could affect colony resource inflow without directly altering worker reproduction; an ovipositing female's site choice may act more directly on offspring placement; and a parasitoid's learned host cues may modify encounter rates between populations. Cross-taxon tests should therefore specify the relevant demographic currency before asking whether memory influences persistence.

A stronger empirical programme would connect levels now studied separately. Longitudinal automated tracking can reveal persistent individual behavioral variation [4], while multilevel navigation approaches clarify which neural, computational and behavioral processes must remain distinct [6]. Repeated-route studies show why individual heterogeneity should be retained rather than averaged away [9], and harmonic-radar tracking demonstrates how movement can be observed under field landscape structure [26]. Combining controlled experience manipulation, individual identification, field movement, habitat-use measurements and subsequent demographic observation would test the proposed gates without converting them into assumed thresholds.

Validation should also distinguish memory persistence from repeated reacquisition. Returning to the same patch on successive occasions may reflect stored information, but it may also arise because an insect repeatedly encounters unchanged cues or resource geometry. Experiments that alter cue reliability after learning, combined with longitudinal field tracking, would be especially informative because they test whether earlier experience continues to influence decisions when current information changes.

The principal limitation is evidence concentration in a relatively small set of experimentally tractable systems, particularly social Hymenoptera and parasitoids. Laboratory conditioning, controlled route-learning assays and field tracking also measure different portions of the proposed chain. Their convergence justifies integration but not a pooled effect or universal causal architecture. The framework should consequently be tested as separable hypotheses: whether experience is retained, how information is updated, whether it changes spatial allocation, whether those effects align across individuals, and whether redistribution then changes a relevant demographic process.

Conclusion

Prior experience can alter insect search, route use and site choice, but ecological memory should not be treated as automatically beneficial, adaptively optimized or population stabilizing. Its consequences depend on what was

learned, how information is updated, the physiological and life-history state of the individual, present environmental opportunity and the spatial scale at which behavior is measured.

The central question is consequently not whether insects possess memory, but when retained experience changes spatial decisions strongly enough, consistently enough and for long enough to alter ecological distributions, and whether those altered distributions subsequently change demographic outcomes. The proposed scale-transfer architecture makes that boundary explicit: individual memory-shaped movement becomes evidence relevant to population persistence only when redistribution and demographic consequence are independently demonstrated.

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