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Learning, Plasticity, and Socially Acquired Information Can Produce Behavioral Adaptation in Insects Without Immediate Genetic Change

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ABSTRACT

Behavioral change in insects is often described either as short-lived flexibility or as an outcome of evolutionary adaptation, yet this binary obscures an intermediate class of phenomena in which learning, developmental plasticity, and socially acquired information alter behavior on ecologically relevant timescales without demonstrating contemporaneous genetic change. This perspective argues that behavioral adaptation should be treated as an evidence-bounded description of context-sensitive adjustment rather than as shorthand for evolutionary adaptation. Evidence from bees, flies, mosquitoes, moths, butterflies, crickets, and ants shows that insects can acquire new actions, retain reward information, carry effects of earlier environments across life stages, use conspecific-derived cues, and sometimes transmit behavioral variants among individuals. However, persistence is conditional, social information does not always imply copying, apparent traditions can be method-sensitive, and laboratory cognition does not map uniformly onto ecological or reproductive performance. The article therefore separates five inferential questions: what changed in behavior, what information generated the change, how long the change persisted or was updated, whether it spread among individuals, and whether any genetic or population-level evolutionary change was actually demonstrated. The central synthesis is a proposed multilevel distinction between rapid behavioral adjustment and genetic adaptation that allows both processes to coexist without conflation. This framing clarifies where insect behavioral evidence is strong, where mechanisms remain taxon- or task-specific, and which experiments are needed to connect plastic responses to ecological consequences and longer-term evolutionary feedbacks.

Keywords: Behavioral plasticity, Insect cognition, Social learning, Developmental carryover, Behavioral transmission, Evolutionary inference

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Introduction

Insects can alter behavior faster than populations can plausibly complete a detectable evolutionary response, yet rapid behavioral change is often interpreted through vocabulary developed for genetic adaptation. The problem is not semantic alone. When an insect modifies a foraging tactic, mating decision, route, oviposition preference, or communication signal after experience, at least four distinct explanations remain possible: individual learning, developmental plasticity, socially acquired information, or genetically structured behavioral variation. These processes can also overlap. Bumblebees, for example, acquired a two-step puzzle solution after observing trained

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demonstrators even though naïve individuals did not independently innovate the complete sequence under the tested conditions [1]. Such results establish behavioral acquisition, not an allele-frequency shift, and therefore make the inferential boundary in the title experimentally meaningful.

Whether a learned response is advantageous cannot be inferred from acquisition alone. In free-foraging bumblebees, the association between memory performance and foraging efficiency changed with seasonal ecological conditions, showing that the realized value of cognition depends on the environment in which it is deployed [2]. Developmental and population background can further complicate interpretation. In *Pararge aegeria*, larval environment, adult experience, and ecotype jointly contributed to oviposition behavior [3]. A persistent behavioral difference is therefore not automatically evidence of genetic control, while an experience effect does not demonstrate that inherited variation is irrelevant.

Social experience adds another level. Honey-bee workers deprived of normal early opportunities to follow experienced dancers showed larger errors when they later danced, although different components of the dance system recovered differently [4]. Social exposure can thus calibrate adult behavioral performance without requiring that the entire behavior be socially created. Conversely, apparently strong claims of tradition can prove method-sensitive. Laboratory *Drosophila* experiments reported conformist transmission of mate-choice preferences across sequential cohorts [5], but later work has questioned how robustly this phenomenon generalizes. The central argument developed here is therefore deliberately narrower than a claim for widespread insect culture: insects can achieve behaviorally consequential adjustment through non-genetic routes, but the source, persistence, transmission, ecological value, and evolutionary meaning of that adjustment require separate evidence.

Individual learning

Individual learning is the most direct route by which an insect can modify behavior within its own lifetime. Its importance is not that insects merely form associations, but that learning can generate behavioral states that differ from the response expected from prior experience or naïve performance. Bumblebees observing a demonstrated ball-manipulation solution subsequently improved on the observed behavior rather than reproducing it mechanically [6]. This supports flexible modification within an artificial task, while stopping short of showing that the improved action increased fitness or would arise under field conditions.

The informational content of reinforcement also matters. *Bactrocera dorsalis* learned sugar quality, and post-ingestive information contributed to longer retention than could be explained by immediate sensory properties alone [7]. This distinction is useful because acquisition and persistence are separate dimensions: an insect may detect a profitable cue rapidly yet retain it only briefly, or it may integrate consequences that are available only after consumption. The resulting memory can influence later choice without implying that the preference is irreversible.

Experience can also modify decisions directly tied to reproduction. Female *Drosophila melanogaster* changed subsequent oviposition preference after actual egg-laying experience, with effects persisting for multiple days [8]. Such persistence shows that behavioral history can become a state variable carried into later decisions. It does not by itself establish that the modified preference improves offspring performance, nor that the effect is transmitted to descendants. Similarly, bumblebees trained with delayed reinforcement later waited longer for reward in a stimulus-specific manner [9]. Reinforcement history can therefore shape temporal persistence, but the effect should not be generalized into a stable personality trait without evidence outside the learned stimulus context.

A further complication is methodological. Cognitive assays test only animals that enter, remain in, or complete the task. Comparative work on wild non-eusocial bees found that participation differed among ecological types even where clear learning-performance differences were not recovered [10]. Apparent cognitive contrasts may consequently reflect who engages with the assay rather than only what participating insects can learn. For this perspective, individual learning is therefore treated as demonstrated when experience changes subsequent behavior under a defined test, whereas ecological adaptiveness remains a separate question requiring performance or fitness evidence in the relevant environment.

Developmental behavioral plasticity

Behavioral change need not begin in the adult stage. Conditions encountered during development can alter later decisions, but the persistence of these effects depends on when information is acquired and on the environment encountered afterward. In *Aedes aegypti*, larval exposure to predation risk altered pupal antipredator responses

under resource limitation, whereas the same carryover was not equivalent under food-rich conditions [11]. Developmental history can therefore survive a major life-stage transition while remaining contingent on current state.

Sensitivity to information may itself be developmentally gated. In *Ephestia kuehniella*, exposure of male larvae to cues from adult rivals altered later sperm-investment patterns when exposure occurred late in larval development, whereas earlier exposure did not produce an equivalent response [12]. This does not establish that the resulting reproductive allocation is adaptive; it establishes that the timing of social information can determine whether developmental plasticity is expressed in adulthood.

The interaction between plasticity and persistent population differences is especially important for the article's genetic boundary. In a common-garden experiment with *P. aegeria*, adult oviposition experience shifted behavior while ecotype-associated differences also remained [13]. Neither observation alone identifies the genetic basis of the ecotype effect. A behavioral phenotype may therefore contain components attributable to immediate experience, developmental history, and more persistent population-level variation at the same time.

Nor is a social environment necessarily genetically neutral. In male *D. melanogaster*, the genotype of prior social partners altered later aggression, with effects depending on the combination of focal and partner genotypes [14]. These indirect genetic effects make a simple learned-versus-genetic dichotomy untenable. A response induced by social history can still contain a genetic component because the social environment itself is partly constructed by genetically variable conspecifics. Developmental behavioral plasticity is consequently best interpreted as a time-structured response process whose causes may span environmental, social, and genetic levels.

Socially acquired information

Social information can enter behavior through mechanisms ranging from ordinary associative reinforcement to observation of another individual's actions. Honey-bee contact provides a particularly clear mechanistic example: antennal interaction with a nestmate functioned as appetitive reinforcement and supported associative learning under controlled conditions [15]. This finding shows that a social stimulus can recruit reinforcement processes, but it does not imply that all social learning in insects depends on the same pathway.

Crickets provide a more specific neural case. Experimental manipulation supported a role for octopamine neurons in reward signaling during a social-learning paradigm consistent with second-order conditioning [16]. The evidence supports involvement of octopaminergic reward mechanisms in that system; it does not establish a general insect “mirror-neuron” mechanism or a universal specialized circuit for social cognition. The broader implication is that socially acquired behavior may often be assembled from learning processes already used in nonsocial contexts.

Information flow can also be reciprocal. Male *D. melanogaster* altered aggression when watched, and observers subsequently changed their own behavior after eavesdropping, whereas comparable effects were not equivalently expressed in females [17]. Social information is therefore not always a one-way transfer from demonstrator to observer: the presence of an audience can modify the behavior that becomes available to be observed. Sex and behavioral context must remain explicit boundaries.

Equally important, conspecific-derived information is not automatically social learning. Female *D. melanogaster* altered oviposition decisions in response to information deposited by other flies, demonstrating strong use of social cues without proving imitation or copying of another individual's decision [18]. The distinction becomes especially important in mate-choice research. An independent replication found the reported female mate-copying effect to be much less robust than earlier results had suggested [19]. Yet chemical-cue experiments later showed that copying-like mate choice can emerge when information contributed by both males and females is available [20]. These findings are not necessarily mutually exclusive: different paradigms may provide different sensory information. The evidence therefore favors a graded interpretation in which “social information use” is broad, whereas social learning, copying, and stable tradition require progressively more specific demonstrations.

Persistence and updating of learned responses

Persistence is not simply the absence of forgetting. Learned information can be retained, overwritten, reweighted, or stored alongside a new response, and those alternatives have different implications for behavioral adaptation. Field experiments with *Cataglyphis velox* made this distinction visible. Ants fitted with visual impairments rapidly learned altered routes, yet when normal vision was restored they could recover the earlier route memory rather

than behaving as if it had been erased [21]. Updating can therefore coexist with retention of a previous representation.

Sequential social information introduces a related problem. When *D. melanogaster* females received conflicting demonstrations, the resulting mate-choice pattern was described as a primacy trend rather than as a definitive rule [22]. That weaker outcome matters because a perspective on behavioral adaptation should not convert suggestive order effects into a general law of memory. Persistence may depend on information type, reinforcement history, developmental stage, and the relation between old and new cues.

Across the approved evidence, several non-equivalent response states emerge. Honey-bee dance calibration shows that some socially influenced components can improve with experience while another component remains persistently altered [4]. *B. dorsalis* demonstrates reward-dependent retention [7], *Drosophila* oviposition shows multi-day experience effects [8], and bumblebees trained with delayed reward show stimulus-specific persistence [9]. These observations motivate a proposed distinction among retention, component-specific updating, coexistence of old and new memories, and context-gated expression. The categories are not claimed as a validated taxonomy; they are an inference tool for deciding what kind of persistence has actually been demonstrated.

Because the same surface observation—"the insect behaved differently later"—can arise from several memory states, **Table 1** separates the evidential signatures needed to distinguish retained, updated, parallel, and context-dependent responses without assigning unsupported scores.

Table 1. Persistence is not one state: an inference register for retained, updated, parallel, and context-gated insect responses

Response mode	Taxonomic setting	Behavioral evidence	Adaptive meaning within its boundary	Updating test and state
Retained and recalibrated memory				
Retained learned preference	Adult fruit flies and tephritid flies	Later choice remains shifted after prior rewarding or oviposition experience	Earlier experience remains behaviorally available after the learning episode Persistence duration and ecological value may differ from laboratory choice persistence	Extend retention tests into changing environments and ecologically relevant decisions Evidence-supported pattern
Component-specific recalibration	Honey-bee dance communication	Some performance errors decrease with experience while another socially calibrated component remains altered	Updating can be partial rather than all-or-none Communication-specific ontogeny; cannot be generalized to all learned traits	Separate behavioral components when measuring recovery or persistence Evidence-supported pattern
Parallel and stimulus-specific memory				
Parallel old/new route memory	Desert-ant navigation	A route learned under altered vision is used, while an earlier route reappears after normal vision returns	New learning need not erase an older representation Artificial sensory impairment; navigation may recruit multiple cue systems	Test whether parallel retention occurs under naturally changing landmarks Evidence-supported pattern
Stimulus-specific persistence	Bumblebee delayed-reward learning	Increased waiting appears for trained or related stimuli rather than as a global behavioral shift	Reinforcement timing changes a learned expectation, not necessarily general temperament Laboratory reward schedule and stimulus identity	Compare transfer across stimuli and motivational states Evidence-supported pattern
Context and information-order gating				
Context-gated developmental carryover	Mosquito development	Earlier experience affects later behavior only under particular current resource conditions	Persistence may be latent and expressed only when state or environment permits Cross-stage effect shown in one developmental and ecological configuration	Manipulate current state independently of developmental history Evidence-supported pattern

Information-order weighting	Fruit-fly mate-choice experiments	Earlier and later social demonstrations produce non-identical influence	Updating may depend on sequence rather than simple replacement Current evidence supports a trend, not a universal primacy rule	Replicate with preregistered order manipulations and sensory controls Evidence-supported but uncertain
Proposed persistence classification				
Proposed persistence-state classification	Cross-taxon synthesis	Distinguishes retention, recalibration, parallel memory, stimulus specificity, and context gating	Prevents "persistent learning" from being treated as a single mechanism Categories have not been validated as a universal insect taxonomy	Test whether the distinctions predict behavior across taxa and tasks **Proposed synthesis**

Transmission across individuals

A behavioral change becomes a transmission problem only when information acquired by one individual affects the probability that another individual expresses a corresponding variant. Open-diffusion experiments in bumblebee colonies satisfy this criterion more directly than isolated observer tests: demonstrated puzzle-box solutions biased which alternative solution spread through groups, and variants could persist over the experimental period [23]. Independent innovation was not eliminated, however, so diffusion should not be described as perfect copying or as evidence that the group-level pattern could not arise partly through individual exploration.

Transmission also requires stricter evidence than acquisition. The *Drosophila* mate-choice study that reported socially maintained traditions [5] is important precisely because it attempted repeated transfer across cohorts, but the later failure to obtain an unambiguous mate-copying effect [19] limits how confidently the phenomenon can be generalized. A useful inference rule is therefore that acquisition by an observer, persistence within an observer, and repeated transmission across individuals are three separate evidential achievements. Demonstrating one does not automatically establish the next.

The direction of information flow can further vary with system architecture. In honey bees, young workers learn aspects of dance calibration by following experienced dancers [4], whereas in fruit-fly aggression the presence of an audience changes the performer as well as the later behavior of observers [17]. Transmission may consequently be asymmetric, reciprocal, or embedded within feedback between information producers and users. The proposed perspective treats these structures as behavioral processes operating on ecological timescales. Only when transmission is linked to differential survival or reproduction, heritable variation, and temporal change in genetic composition would it support a stronger claim about evolutionary adaptation.

Distinguishing behavioral adaptation from genetic adaptation

Behavioral adaptation and genetic adaptation answer different questions. The first concerns whether behavior changes in a way that alters performance under a particular context; the second requires evidence that heritable variation and evolutionary change are involved. Direct genetic manipulation illustrates the difference. In *Drosophila melanogaster*, variation in the gene *degrees of kevin bacon* (*dokb*) causally altered a social-network behavioral metric in the tested system [24]. That result identifies a genetic contribution to one social phenotype. It does not imply that social behavior is genetically fixed, nor that experience-dependent changes in the same broad behavioral domain are genetically caused.

The converse error is to treat evidence for learning as evidence against genetic influence. Prior social-partner genotype can modify later aggression [14], meaning that an apparently environmental social history may contain an indirect genetic effect. Likewise, persistent ecotype differences in *Pararge aegeria* coexist with experience-dependent oviposition changes [3], and common-garden evidence shows that short-term learning need not erase those differences [13]. Stable behavioral variation, developmental plasticity, individual learning, and genetic effects are therefore potentially overlapping explanatory layers rather than mutually exclusive categories.

This perspective consequently proposes an inference boundary based on what has actually been measured. A demonstrated change following experience supports behavioral plasticity; acquisition from conspecific-derived information supports social information use when alternative cue mechanisms are addressed; persistence supports temporal stability of the response; and population diffusion supports transmission. None alone demonstrates genetic evolution. Conversely, a genetic effect on behavior does not show that a particular short-term behavioral

adjustment resulted from selection. The critical distinction is temporal and evidential: rapid adjustment can occur without requiring immediate genetic change as its proximate explanation, while genetic architecture may still shape the capacity, sensitivity, or social environment within which adjustment occurs.

A second safeguard concerns terminology. "Behavioral adaptation" is used here only for a context-responsive behavioral adjustment with plausible or measured performance relevance, not as a synonym for adaptation by natural selection. Where performance has not been evaluated, "behavioral change," "plastic response," or "learned response" is preferable. Absence of measured genetic change is not evidence that genetic change is impossible; it marks an untested evolutionary level. This vocabulary keeps claims aligned with the scale of observation.

Figure 1 is needed here because the central problem is not a linear sequence but reconciliation of evidence operating at different biological levels, with several routes capable of producing superficially similar behavioral change.

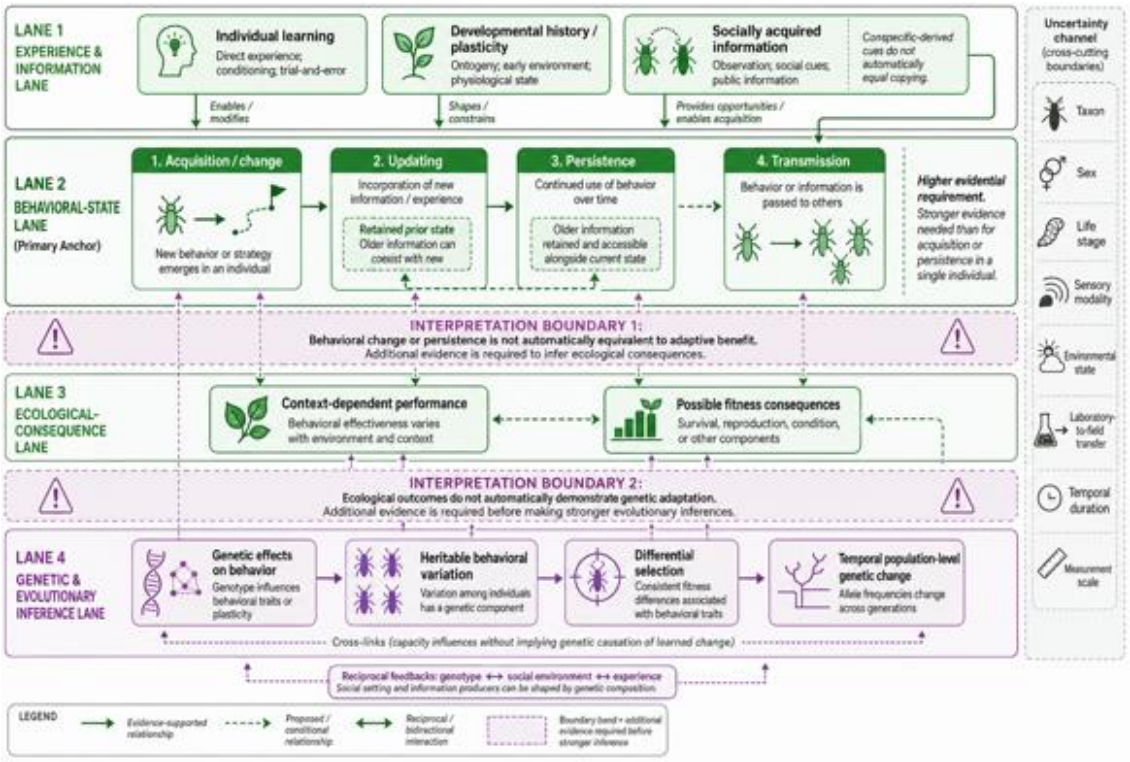


Figure 1. Evidence boundaries that separate rapid insect behavioral adjustment from claims of genetic adaptation

Ecological consequences

A learned behavior is not ecologically adaptive merely because it is acquired quickly or performed accurately. In free-foraging bumblebees, faster laboratory learning was negatively correlated with lifetime resource collection [25]. The result is compatible with a cognitive trade-off, but because learning ability itself was not experimentally manipulated in the field it does not establish that faster learning caused lower resource collection.

Context can also change the apparent value of memory. Seasonal field work showed that relationships between memory and foraging efficiency differed with ecological conditions [2]. Thus, a cognitive trait that is useful under one resource distribution may yield little advantage, or a different association, under another. The ecological consequence belongs to the interaction between phenotype and environment rather than to the cognitive score alone.

Null evidence is equally informative. In post-diapause bumblebee queens, a learning treatment did not produce a detectable reproductive penalty under the tested laboratory conditions, whereas nutritional restriction affected reproductive outcomes [26]. Learning therefore cannot be assigned a universal cost. Similarly, experience-dependent oviposition changes in butterflies can alter habitat use [3], while oviposition experience in fruit flies can alter subsequent substrate choice [8]. Such behavioral shifts should not be converted into fitness claims unless offspring performance, survival, reproductive output, or another relevant consequence is measured.

The coverage-and-gap structure in **Table 2** separates what has been observed ecologically from the additional evidence needed before a behavioral response can be called advantageous, costly, or evolutionarily consequential.

Table 2. When learned insect behavior reaches ecology—and where the evidence still stops

Cognitive value and performance evidence			
Behavior to ecology comparison dimension	**Context-dependent cognitive value**	**Negative cognition–performance association**	**No detectable reproductive learning cost**
Behavioral context and observation	Bumblebee memory during natural foraging Memory–performance relationships vary with seasonal ecology	Bumblebee learning and lifetime resource collection Faster laboratory learners collect fewer lifetime resources in the observed field sample	Bumblebee queen colony founding Learning treatment does not reduce measured reproductive success under tested conditions
Ecological claim enabled	Ecological conditions modify the realized value of cognition	Laboratory learning metrics can covary negatively with natural performance	A measurable learning cost is not inevitable
Missing bridge	One species and seasonal resource regimes; fitness is not equivalent to foraging efficiency	Correlation does not identify a causal cognitive cost	Laboratory environments may reduce ecological costs; nutrition changes outcomes
Next test and state	Repeat across resource landscapes while tracking survival and reproduction Evidence-supported pattern	Manipulate learning demands or information complexity under free-foraging conditions Evidence-supported pattern	Cross learning demand with naturalistic energetic and environmental variation Evidence-supported null pattern
Experience-altered resource or site use			
Behavior to ecology comparison dimension	**Experience-altered resource or site use**		
Behavioral context and observation	Butterfly and fruit-fly oviposition Prior developmental or adult experience shifts later oviposition choice		
Ecological claim enabled	Learning and plasticity can redirect where reproductive behavior occurs		
Missing bridge	Choice change does not itself establish offspring or maternal fitness benefit		
Next test and state	Couple learned choice to offspring performance and maternal lifetime output Evidence-supported behavioral consequence		
Behavior-to-fitness and fitness-to-evolution transfer			
Behavior to ecology comparison dimension	**Behavior-to-fitness transition**	**Fitness-to-evolution transition**	
Behavioral context and observation	Cross-taxon synthesis Behavioral change plus an ecologically relevant performance measure	Cross-taxon synthesis Differential fitness linked to heritable behavioral variation across generations	
Ecological claim enabled	Performance consequences should be evaluated separately from acquisition	Required before ecological benefit becomes evidence for evolutionary adaptation	
Missing bridge	Fitness may depend on season, state, sex, life stage, and environment	Not demonstrated by the learning studies considered here	
Next test and state	Measure behavior, ecological performance, and reproductive consequences longitudinally **Proposed synthesis**	Combine selection estimates, heritability or genomic evidence, and temporal population sampling **Proposed synthesis**	

Evolutionary feedbacks

Plasticity can influence the conditions under which future selection occurs without itself constituting genetic adaptation. A model and empirical reanalysis of bee–flower interactions suggest that social organization can alter opportunities for acquiring complex foraging tasks, while also showing that sociality is not necessary for such learning [27]. This provides a useful evolutionary scaffold, not evidence that social learning has already driven a specific genetic transition.

Population persistence strengthens the possibility of feedback but not the inference of evolution. Laboratory fruit-fly traditions were reported under defined transmission conditions [5], and alternative puzzle solutions diffused through bumblebee groups [23]. Such persistence can change repeated exposure to resources, competitors, mates, or social partners. The proposed synthesis is that these behaviorally modified environments could alter later selection when consequences are differential and heritable; the selected studies do not themselves demonstrate that full sequence.

Genetic evidence likewise belongs inside, not outside, this feedback problem. Direct manipulation shows that genetic variation can affect social-network behavior [24], while indirect genetic effects show that conspecific genotype can alter later behavior through the social environment [14]. Evolutionary feedback should therefore be tested as reciprocal coupling among behavioral plasticity, socially generated environments, ecological consequences, and heritable variation, with each transition measured rather than presumed.

The feedback hypothesis is testable only when studies span more than one inferential level. Repeated behavioral transmission should be measured alongside the environmental consequences it creates, while genetic sampling must establish whether heritable variants change through time. Failure to detect one transition would be informative: persistent social transmission without differential fitness would support behavioral stabilization but not selection, whereas fitness differences without heritable behavioral variation would not establish genetic adaptation. Temporal replication matters because short-lived ecological episodes may not generate persistent evolutionary responses.

Research priorities

Progress requires designs that distinguish biological uncertainty from assay artifacts. Comparative cognitive work should report participation and exclusion patterns because ecological types can differ in willingness to engage with tasks [10]. Social-learning claims also require independent replication and sensory controls: ambiguous mate-copying replication [19] alongside chemically mediated copying-like effects [20] shows why apparently conflicting results cannot be adjudicated without identifying the information actually available to observers.

Laboratory competence should be connected explicitly to natural performance. Seasonal variation in the value of memory [2], negative associations between learning speed and resource collection [25], and an experimentally undetected reproductive learning cost [26] collectively argue against treating cognitive performance as a universal proxy for fitness. Future studies should follow individuals across ecological states and, where feasible, connect behavior to survival and reproductive output.

Mechanistic work should also distinguish social reinforcement from more specific social-learning processes. Honey-bee contact can serve as appetitive reinforcement [15], cricket experiments implicate octopamine reward signaling [16], and fruit-fly oviposition demonstrates strong use of conspecific cues without requiring copying [18]. These mechanisms should be tested comparatively rather than merged into a single social-cognition pathway.

Finally, longitudinal experiments should combine developmental history, social transmission, ecological performance, and genetic information. Experience and ecotype effects can coexist [3], social-partner genotype can generate indirect genetic effects [14], behavioral variants can diffuse through groups [23], and individual genes can alter social-network phenotypes [24]. Preregistered replications should preserve null and trend-level results, including weak information-order effects [22]. Such designs could test the proposed transitions without assuming that persistence, transmission, ecological benefit, and evolutionary change are interchangeable.

Conclusion

Learning, developmental plasticity, and socially acquired information give insects multiple routes to behavioral change on timescales shorter than those required to demonstrate genetic evolution. The resulting responses can persist, be updated, coexist with earlier memories, or spread among individuals, yet none of these outcomes alone establishes improved fitness or evolutionary adaptation. The central contribution of this perspective is therefore an evidence boundary: behavioral acquisition, persistence, transmission, ecological consequence, genetic

contribution, and population-level evolutionary change should be treated as distinct inferential achievements. This separation does not oppose plasticity to evolution. It allows genetic and non-genetic influences to coexist while preventing evidence at one level from being promoted automatically to another. Testing the proposed connections will require longitudinal, ecologically grounded and genetically informed experiments across a wider range of insect taxa, life stages, sexes, sensory systems, and environments.

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