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Repeatable Behavior, Context Dependence, and Fitness Relevance in the Emerging Ecology of Insect Personality

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ABSTRACT

Consistent behavioral differences among individuals are increasingly documented in insects, yet evidence of repeatability is often interpreted more broadly than the underlying designs permit. In particular, short-term behavioral consistency can be conflated with persistence across developmental stages or environments, and associations with physiological performance, task allocation, survival-related outcomes, or reproduction can be interpreted as evidence of generalized fitness advantage. This systematic review evaluates insect-personality research published from 2017 through 2021 with emphasis on three linked questions: whether behavioral differences remain repeatable when contexts change, how environmental and developmental conditions alter behavioral means and variance structures, and when repeatable behavior can legitimately be connected to ecological or fitness-relevant outcomes. Evidence was coded by taxon, life stage, sex, behavioral operationalization, measurement setting, level of biological organization, repeated-measures design, environmental context, and outcome class. The literature demonstrates repeatable behavioral differences in multiple insect systems but also reveals marked stage, trait, sex, environmental, and analytical dependence. Complete metamorphosis can disrupt cross-stage rank consistency; stable local environments can inflate apparent individuality; developmental, social, anthropogenic, nutritional, and physiological conditions can alter means, repeatability, covariance, or their interpretation without changing all components in parallel. Fitness relevance is therefore not a property that follows automatically from repeatability. We propose that insect personality be interpreted through separate evidential stages: demonstrated among-individual consistency, transport across contexts, ecological association, and direct fitness or evolutionary inference.

Keywords: Animal personality, Behavioral repeatability, Context dependence, Behavioral plasticity, Insect ecology, Fitness relevance

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Introduction

Animal personality is commonly defined through consistent among-individual differences in behavior, but in insects the biological meaning of that consistency depends strongly on when, where, and at what organizational level it is measured. Development can reorganize morphology, physiology, sensory systems, resource use, and social roles, while ecological conditions can alter both behavioral expression and the variance components from which repeatability is estimated. Consequently, repeatability within a restricted assay or life stage should not automatically be interpreted as a lifelong behavioral property. Insect-specific and broader ontogenetic syntheses

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instead indicate that developmental continuity is an empirical question, particularly across major life-history transitions [1–3].

This distinction is especially important in holometabolous insects. In *Tenebrio molitor*, behavioral traits could show consistency within a developmental stage while larval measurements failed to predict adult personality after metamorphosis [4]. That result does not establish that complete metamorphosis universally erases personality, but it demonstrates that within-stage repeatability and cross-stage transportability are different evidential claims.

Social insects add a further level-of-analysis problem. Consistent group or colony differences constitute collective personality, but colony-level repeatability need not be reducible to the average personality of constituent workers. Worker composition, interaction structure, colony demography, task organization, and environmental conditions may all contribute to emergent collective phenotypes [5]. Treating individual and collective personality as interchangeable therefore risks assigning mechanisms or ecological consequences to the wrong biological level.

A second inferential expansion occurs when repeatability is translated into fitness relevance. Across animals, individual behavioral differences explain some survival variation, but effect sizes and directions are heterogeneous rather than universally consistent with a single "risky" or "cautious" phenotype [6]. In insects, direct studies likewise resist a simple fast–slow interpretation. Mealworm behavior, immune traits, and reproductive measures show multidimensional covariance rather than a single personality axis determining physiological investment or reproductive success [7]. At broader ecological scales, multidimensional behavioral composition can also predict aspects of space use and survival in interacting arthropod systems, but these group- or community-level relationships should not be recast automatically as individual fitness effects [8].

The central problem is therefore not whether insects exhibit repeatable behavior; numerous systems demonstrate that they do. The more difficult question is what a repeatability estimate allows investigators to infer. This review separates four claims that are often compressed into the same personality terminology: consistent among-individual variation within a defined setting; persistence of rank differences across environmental or developmental contexts; association with ecological performance; and evidence of survival, reproduction, or evolutionary consequences. The synthesis focuses on the boundaries between these claims rather than assuming that movement from one to the next is automatic.

Materials and Methods

Search strategy, eligibility, behavioral-trait coding, and quality assessment

The evidence base was reconstructed with an eligibility cutoff of 31 December 2021. Searches were designed for Web of Science Core Collection, Scopus, PubMed/MEDLINE, Zoological Record where accessible, and backward/forward citation chaining. Core search logic combined insect or major-order/taxon terms with personality, behavioral-type, behavioral-syndrome, consistent-individual-difference, repeatability, and among-individual-variation terms, together with contextual terms addressing environment, plasticity, survival, reproduction, life history, metabolism, physiology, field conditions, urbanization, pollutants, temperature, nutrition, metamorphosis, and ontogeny. DOI, title, author, journal, year, and bibliographic metadata were independently checked against publisher- or Crossref-facing records.

The reconstruction did not preserve a complete export-level audit trail from the original database interfaces. Consequently, source-specific retrieval totals, duplicate-removal totals, title/abstract exclusion totals, full-text retrieval totals, exclusion-reason arithmetic, and a numerically verified final included-study total could not be recovered. These quantities were therefore not estimated from the citation set, reverse-engineered from the final bibliography, or represented as zero. This limitation prevents quantitative statements about prevalence of particular taxa, behavioral categories, study settings, or exclusion frequencies. The synthesis that follows is consequently restricted to evidence patterns supported by the approved eligible literature rather than numerical claims about the frequency of those patterns.

For substantive coding, direct evidence of personality required repeated behavioral measurement capable of estimating consistent among-individual differences [9]. Studies based on a single observation were not discarded when they addressed relevant environmental or performance responses, but they were coded as behavioral or contextual evidence rather than as direct demonstrations of personality, because one observation combines among-individual variation with reversible within-individual variation and measurement noise [10].

Repeatability estimates were interpreted as model-dependent variance decompositions rather than intrinsic constants of a behavioral trait. Where reported, the review distinguished among-individual variance, residual or

within-individual variance, model adjustment, response distribution, and uncertainty around repeatability estimates [11]. Within-context repeatability was also kept separate from cross-context correlation: a trait can be repeatable in two environments without individuals retaining the same rank ordering across environments, and conversely cross-context covariance can have a biological interpretation that is not reducible to a pair of repeatabilities [12].

Contextual changes in repeatability were interpreted alongside behavioral means and variance components where these were available. Because repeatability is a ratio, a higher or lower value can arise through changes in between-individual variance, within-individual variance, or both; it does not by itself identify an increase or decrease in absolute behavioral individuality [13]. Statistical quality assessment therefore considered model specification and random-effect structure rather than treating the use of a linear or generalized mixed model as sufficient evidence of valid variance inference. Simulation work indicates that mixed models may tolerate some distributional departures while remaining vulnerable to omitted or inappropriate structure [14].

Behavioral labels were also coded conservatively. Novel-object and related assays can produce repeatable responses, but heterogeneous protocols, stimuli, arenas, latency definitions, activity measures, and interpretations prevent automatic equivalence among constructs labelled boldness, exploration, or neophobia [15]. Comparative work further shows that similarly named behavioral assays can occupy different covariance structures among taxa [16]. Accordingly, the synthesis preserved the operationally measured behavior rather than assuming that an identical trait label represented an identical latent construct across insect orders.

Results and Discussion

Direct repeated-measures evidence demonstrates that personality-like variation occurs across taxonomically and biologically distinct insect systems. Adult paper-wasp queens exhibit repeatable differences across multiple behavioral dimensions, carabid beetles show temporally consistent activity, exploration, threat-response, and phototaxis-related traits, and a floriphilic katydid displays consistent variation at both individual and population levels [17–19]. These studies establish breadth of occurrence, but they do not justify an estimate of how common personality is across insect orders because the evidence base is neither taxonomically representative nor standardized in assay design.

Experience can also contribute to the construction of individuality. In crickets, manipulated agonistic experience during development produced persistent inter-individual differences in subsequent approach–avoidance behavior [20]. The result demonstrates causal influence of a particular developmental social history in that experimental system; it does not establish agonistic experience as a universal origin of insect personality.

Within eusocial systems, worker-level personality can be associated with specialized task performance. In *Aphaenogaster senilis*, a relatively small subset of workers repeatedly performed tool use, and specific exploratory or prey-attraction tendencies were associated with participation [21]. The appropriate inference is therefore a worker-level association between behavioral phenotype and task performance, not demonstration that personality causes division of labor or increases colony fitness.

Field evidence further shows why positive repeatability should not be treated as an all-or-none property. In wild *Calopteryx splendens*, courtship and boldness-related traits remained repeatable across altered territory conditions, whereas most aggression measures did not show comparable consistency [22]. Null or weak repeatability for particular behavioral domains is thus biologically informative rather than merely an analytical inconvenience.

Population contrasts likewise require caution. In *Carabus convexus*, repeatable behaviors coexisted with urban–rural and sex-associated differences in behavioral expression [23]. Such contrasts may be compatible with developmental plasticity, persistent environmental effects, population history, or genetic differentiation. Without designs that separate these alternatives, they should not be described as adaptive urban personality divergence.

Repeatability across contexts

Repeated behavior can arise from persistent individuals, persistent environments, or both. A field translocation experiment in *Gryllus campestris* demonstrated that stable local environmental differences can inflate apparent individual repeatability when insects repeatedly occupy the same sites or burrows [24]. Relocation separated individual effects from site-associated consistency, establishing “pseudo-repeatability” as a concrete interpretive risk. The finding does not imply that field personality is usually artifactual; instead, it shows that site fidelity and

environmental persistence must be considered whenever individual and environment remain statistically confounded.

Developmental conditions can change the structure of individuality without producing an equivalent shift in average behavior. In a butterfly, early developmental environment altered adult among-individual variation and repeatability, whereas effects on the population mean did not necessarily change in parallel [25]. This distinction is important because environmental effects on behavioral means, among-individual variance, within-individual variance, and rank stability represent different biological responses.

Repeatability is also not interchangeable with heritability or evolutionary potential. Experimental social cues in *Teleogryllus oceanicus* changed additive genetic variation and covariation in personality traits across environments [26]. Behaviors may therefore remain phenotypically repeatable while their quantitative-genetic architecture changes. Evolutionary predictions require genetic data obtained in the relevant environment rather than inference from repeatability alone.

At the collective level, context dependence remains equally important. *Temnothorax rugatulus* colonies differed consistently in collective tempo and synchrony, yet crowding and queen presence contributed to the expression of those dynamics [27]. Colony-level consistency and contextual modulation are thus compatible rather than mutually exclusive, and neither establishes that worker-level personalities caused the collective phenotype.

These distinct sources of behavioral consistency are easier to compare when repeatability is treated as a state requiring interpretation rather than as a binary trait. The resulting state-and-response ledger is summarized below.

Table 1. When behavioral consistency represents an individual property, a transported phenotype, or a context-bound state

Repeated behavior			Transportability
Locus of repeatability	**Construct and design**	**Pattern transported across context**	**What synthesis may carry forward**
Persistent individual effect within a stable setting. Individual insect	Repeated focal behavior	Stable among-individual differences across observations	Stable environments may remain confounded with individuals. Supports within-context personality only
Site-associated consistency. Wild insects with repeated use of locations	Repeated field behavior	Apparent consistency decreases or changes after environmental relocation	Habitat choice itself may be phenotype-linked. Requires a test separating individual and environmental persistence
Developmentally restructured repeatability. Individual across developmental environments	Adult repeated behavior after early-life treatment	Repeatability or among-individual variance changes without a parallel mean shift	Selection, mortality, or treatment-specific effects may also alter variance. Mean plasticity and individuality must be analysed separately
Context-dependent genetic architecture. Individual and quantitative-genetic level	Repeated behavior plus genetic variance/covariance	Phenotypic consistency persists while genetic variance structure changes	Estimates are environment- and population-specific. Repeatability cannot substitute for heritability
Context-sensitive collective consistency. Colony	Tempo, synchrony, or other repeated collective traits	Colonies remain distinguishable while social conditions modify expression	Worker composition and interaction processes remain potential mediators. Colony-level repeatability must remain separate from worker-level personality

Note: The final column is a proposed synthesis of the evidence patterns developed in this review; it is not a validated classification system.

Environmental modulation

Environmental modulation is most informative when behavioral means, repeatability, and covariance are analysed separately. In larval *Coenagrion puella*, pesticide exposure altered behavioral components in ways that depended on urbanization background, but mean behavior, repeatability, and covariance did not all move in the same direction [28]. The result argues against describing environmental exposure simply as increasing or decreasing "personality." The affected statistical component must be specified.

Multivariate environmental effects can also vary geographically. In *Ischnura elegans*, warming and pollution altered integrated behavioral, physiological, and life-history relationships in ways that differed among latitudinal populations [29]. These patterns demonstrate environmental and geographic contingency, but they do not establish that all measured behaviors constituted personality traits or that the observed population differences represented adaptive evolution.

Nutritional stress provides an especially useful terminology boundary. Experimental nutritional limitation reduced exploratory behavior and flight performance in a butterfly [30]. This is clear evidence of behavioral and performance plasticity, but the available repeated-personality evidence does not justify translating a mean reduction in exploration into a change in personality or repeatability. State-dependent behavioral change and altered among-individual consistency are analytically different outcomes.

Physiological associations are similarly conditional. In *Carabus hortensis*, exploration and metabolic traits showed repeatability, but relationships between metabolic rate and exploration depended on sex, body mass, measurement temperature, and metabolic measure; male resting metabolic rate was not itself repeatable [31]. A simple high-metabolism/high-activity personality axis would therefore erase biologically important null and moderator effects.

The level at which covariance is estimated can change the interpretation still further. In *Drosophila melanogaster*, locomotor activity and resting metabolic rate were repeatable, yet their among-individual relationship was sex-specific and was not mirrored by an equivalent within-individual association [32]. Between-individual covariance consequently cannot be treated as evidence that an acute change in metabolism causes a corresponding behavioral change within an individual.

The environmental evidence therefore supports a component-wise interpretation in which mean plasticity, repeatability, covariance, physiological association, and geographic or sex moderation remain separate unless a design explicitly connects them.

Table 2. Environmental changes that can resemble personality change but imply different biological processes

Environmental change	System and exposure	Mean/covariance signature	Personality interpretation	Within-individual discrimination
Exposure-dependent mean shift	Pollutant- or resource-exposed insects	Change in average behavioral expression	Behavioral plasticity. Evidence-supported distinction.	Does not establish altered among-individual consistency. Repeatedly assay the same individuals and partition variance
Repeatability change without equivalent mean change	Developmental or environmental treatment	Changed ratio of among- to within-individual variance	Restructured individuality. Evidence-supported distinction.	Direction depends on which variance component changed. Report means and both variance components
Covariance restructuring	Multivariate behavioral or physiological traits	Changed association among traits	Context-dependent integration. Evidence-supported distinction.	Covariance is not causal mechanism. Estimate level-specific covariance under each environment
Geographic moderation	Populations differing in environmental history	Treatment response differs among source populations	Population-specific environmental response. Evidence-supported distinction.	Plasticity, population history, and genetic differentiation remain alternatives. Common-garden or reciprocal designs are needed for stronger evolutionary inference
Sex-specific physiology–behavior association	Adult beetles or flies	Relationship differs between males and females	Sex-bounded phenotypic integration. Evidence-supported distinction.	Sampling, mass, temperature, or reproductive state can modify estimates. Analyse sexes and physiological states explicitly
Between-individual association without within-individual coupling	Repeated behavioral and metabolic data	Covariance appears among individuals but not within individuals	Different statistical levels need not share a mechanism. Evidence-supported distinction.	Unmeasured stable individual factors can generate among-individual covariance. Fit multilevel models that partition both covariance levels
"Personality changed" as a single environmental label	Cross-study synthesis	Any of the preceding outcomes is collapsed into one term	Proposed failure category. Proposed synthesis.	Masks which statistical or biological component actually changed. Replace with component-specific terminology

Because this review is reconstructed from an evidence set for which the original export-level screening arithmetic is not recoverable, the selection process is represented transparently rather than by invented numerical counts.

Links with survival and reproduction

Evidence that personality is repeatable does not establish that it improves survival or reproduction. In male *Pararge aegeria*, personality-related traits were associated with territorial contest outcomes, while contest experience subsequently altered aspects of behavioral expression and repeatability [33]. The reciprocal relationship is important: behavior may influence performance, but performance-generating experiences can also modify later behavior. Contest success is therefore a fitness-relevant performance proxy rather than direct evidence of realized reproductive fitness.

A comparable scale problem occurs in social insects. In *Myrmica rubra*, exploration was positively associated with colony productivity across habitats, whereas other behavior–productivity relationships depended on habitat and colony characteristics [34]. Because productivity is a colony-level outcome, these associations cannot be translated directly into individual worker fitness. More broadly, survival analyses across animals indicate heterogeneous and generally modest associations between behavioral individuality and survival [6]. The insect evidence therefore supports fitness relevance in selected systems, but not a universal direction or magnitude of advantage.

The distinction among performance, productivity, survival, and reproduction is summarized below because these outcomes occupy different inferential levels.

Table 3. Fitness-relevant outcomes differ in scale, directness, and vulnerability to reverse influence

Behavior-linked outcome			Fitness validation
Outcome pathway and scale	**Evidence available**	**Inferential level reached**	**Reverse influence and stronger test**
Personality–contest association. Adult individual	Repeated behavior linked with contest outcome	Behavior may contribute to competitive performance	Contest experience can modify subsequent behavior. Reproductive follow-up after repeated contests
Personality–productivity association. Worker/colony	Behavioral phenotype linked with colony productivity	Behavioral variation may correlate with collective performance	Colony demography, habitat, and resources can mediate association. Multilevel worker-to-colony outcome analysis
Behavior–survival association. Individual	Survival-related observational or experimental evidence	Repeatable behavior can be fitness-relevant	Direction varies among traits and settings. Insect-specific longitudinal survival tests
Direct reproductive consequence. Individual	Survival or reproduction measured directly	Strongest route to organismal fitness inference	Requires appropriate life-stage, sex, and environmental scope. Lifetime or repeated reproductive measurement

Note: The distinction among outcome levels is a proposed synthesis intended to prevent performance proxies from being treated as equivalent to realized fitness.

Publication and methodological bias

The principal methodological risk is classification inflation. Studies labelled “personality” may not contain the repeated observations needed to estimate consistent among-individual differences [9]. Assay terminology adds another source of heterogeneity because nominally similar novelty or exploration tests can differ substantially in stimulus, arena, behavioral metric, and inferred construct [15].

Reporting repeatability without its underlying variance structure creates a further interpretive bias. A change in repeatability can result from altered among-individual variance, altered within-individual variance, or both [13]. Field studies introduce an additional problem when repeated environments remain confounded with repeated individuals, as demonstrated experimentally by translocation work in crickets [24]. Conversely, experimental studies showing changes in mean exploration under environmental stress should not be counted automatically as evidence that personality itself changed when repeatability was not established [30].

These problems are not independent. Assay choice, repeated-measures design, environment, life stage, sex, analytical level, and outcome definition jointly determine how far an inference can travel. **Figure 1** therefore represents publication and methodological bias as a sequence of cross-scale boundaries rather than as a single study-quality score.

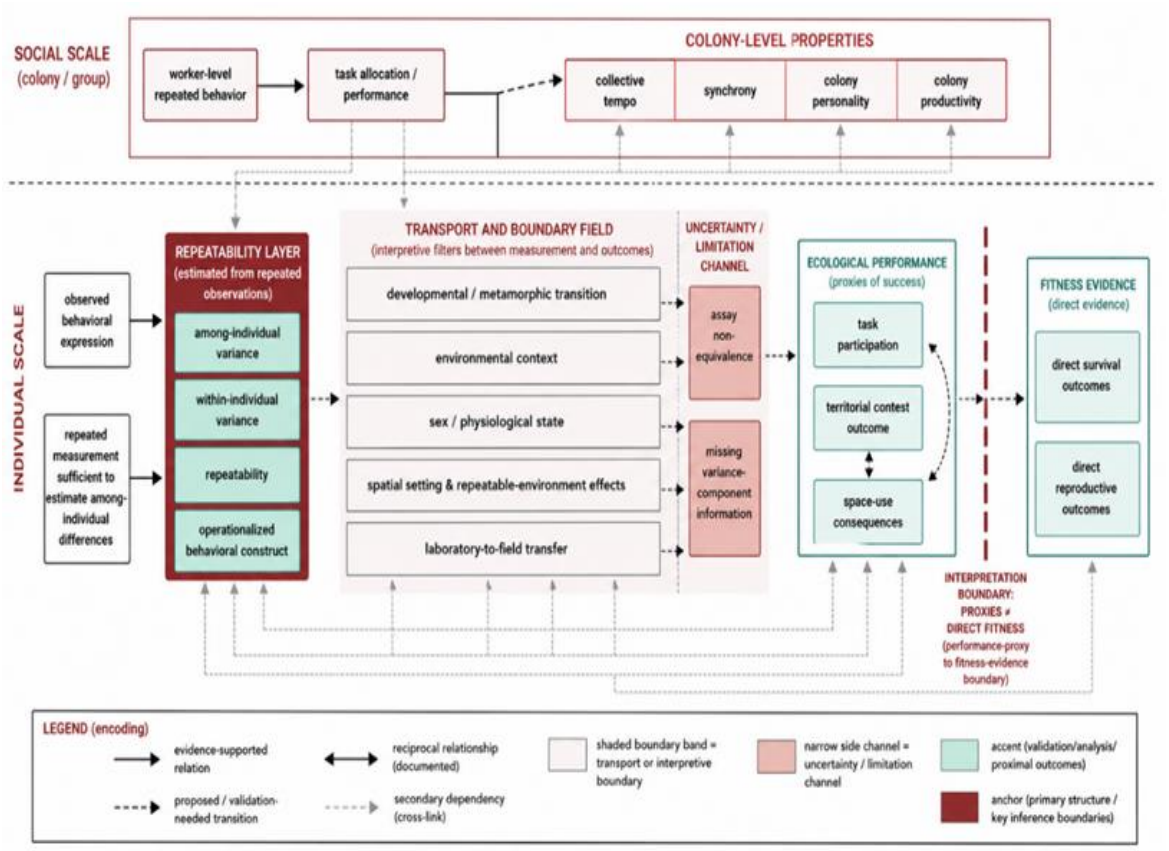


Figure 1. Inference boundaries that separate repeated insect behavior from ecological and fitness claims

Cross-scale architecture showing where insect-personality inference can fail or require additional validation. Evidence begins with observed behavior and repeated measurement, proceeds through estimation of among-individual consistency, then encounters context-transport, developmental, environmental, sex, and level-of-analysis boundaries before ecological or fitness consequences can be inferred. Solid arrows denote transitions directly supported as legitimate evidential steps when measured; dashed arrows denote the review's proposed inferential links requiring additional validation; bidirectional connectors denote relationships in which experience or ecological performance may also alter subsequent behavior. A parallel uncertainty channel contains assay non-equivalence, pseudo-repeatability, missing variance components, laboratory-to-field transfer, and proxy-outcome ambiguity. The architecture is a proposed synthesis rather than an empirically validated causal model.

The evidence supports a staged interpretation of insect personality rather than a single continuum from behavioral repeatability to evolutionary importance. Developmental discontinuity across metamorphosis illustrates why short-term consistency cannot establish lifelong transportability [1]. Field evidence similarly shows that some behavioral domains remain repeatable across altered conditions while others do not [22]. Context dependence should therefore be treated as biological information, not automatically dismissed as measurement noise.

Environmental effects also act on different statistical components. Pesticide exposure, developmental history, and physiological state can modify means, among-individual variance, covariance, or their moderators without producing equivalent changes in repeatability [28]. At the outcome end of the inferential chain, colony productivity illustrates why ecological relevance must remain tied to the biological scale on which it was measured [34]. Evidence connecting behavioral individuality to survival further suggests heterogeneous rather than universally directional consequences [6].

We therefore propose an inference-boundary architecture in which four questions are answered separately: Is behavior repeatable within the defined measurement setting? Does individual rank or variance structure persist across relevant contexts? Is behavior associated with an ecological performance outcome? Is there direct evidence linking those differences to survival or reproduction? Failure at one boundary does not invalidate preceding evidence; it restricts the strength and scope of the next inference.

The principal failure modes generated by collapsing these questions are summarized below.

Table 4. Conditions under which insect-personality inference fails or requires qualification

Inference failure	Warning → distortion	Qualification or repair
Temporal and environmental attribution		
Short-term consistency treated as lifelong stability. Metamorphic or developmental transition	Within-stage repeatability without cross-stage prediction. Overstates behavioral persistence	Stage-specific restructuring. Test transport directly across stages
Repeatable environment treated as repeatable individual. Field site fidelity	Individual and site remain confounded. Inflates apparent individuality	Stable habitat or burrow effects. Cross individuals and environments where feasible
Mean plasticity labelled personality change. Environmental exposure	Population mean changes without variance evidence. Confuses state response with altered individuality	Exposure- and trait-specific. Report mean and variance components separately
Construct and scale attribution		
Assay label treated as construct equivalence. Cross-taxon comparison	Different protocols share one trait label. Creates false behavioral homology	Species and assay architecture. Preserve operational definitions
Worker and colony levels collapsed. Social insects	Worker trait linked directly to colony outcome. Misassigns mechanism and consequence	Emergent collective dynamics. Analyse individual and colony levels separately
Performance proxy treated as realized fitness. Contest or productivity studies	Ecological performance measured without survival/reproduction. Overstates evolutionary relevance	Outcome- and life-stage-specific. Measure direct survival or reproductive consequences

Note: These failure modes constitute the review's proposed interpretive synthesis; they are not a formal certainty-grading system.

Research standards for insect personality

Future studies should treat repeated measurement and explicit variance decomposition as minimum requirements for direct personality inference [9]. Where designs span environments, investigators should distinguish within-context repeatability from cross-context correlation and report means and variance components whenever estimable [12]. Field studies in systems with strong site fidelity should additionally separate persistent individuals from persistent environments through relocation, crossed-site designs, repeated environmental sampling, or comparable approaches [24].

Claims extending across developmental stages should test transportability directly rather than infer it from within-stage consistency [4]. Sex and life stage should likewise be modeled explicitly when physiological or ecological associations differ among demographic classes.

Social-insect studies require particularly careful separation of levels. Worker personality may be associated with repeated task participation [21], but worker behavior, task allocation, collective phenotype, and colony performance should be measured as distinct variables. Task-syndrome theory offers a useful hypothesis-generating framework for linking consistent individual differences with task organization, but these links remain conditional predictions rather than a universally established mechanism [35].

A practical minimum standard is therefore not simply "measure repeatability." Strong insect-personality studies should identify the behavioral construct operationally, repeat observations at the appropriate biological level, partition relevant variance, test transport across the contexts implicated by the claim, retain null and contradictory responses, and match ecological or fitness conclusions to the outcome actually measured.

Conclusion

Insect personality research has moved beyond demonstrating that individuals can behave consistently. The more consequential challenge is determining when that consistency survives developmental, environmental, physiological, spatial, and social changes and when it bears directly on ecological performance or fitness. Existing evidence shows substantial heterogeneity across traits, stages, sexes, environments, and organizational levels. Repeatability is therefore best treated as the beginning of an inference chain rather than its endpoint. A rigorous ecology of insect personality should distinguish behavioral consistency, contextual transportability, ecological consequence, and direct fitness evidence, while treating failures of transport or null associations as informative biological results. This evidence-bounded approach can make insect personality a more precise tool for studying behavioral individuality without converting repeatable behavior into unsupported claims of adaptation, mechanism, or universal fitness advantage.

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