LoveBug: An ABM on Sexual Selection

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Abstract

The evolution of mate choice is not governed by genetic factors alone; empirical evidence demonstrates that perceptual constraints, social learning, and cultural transmission are crucial drivers. To unify these mechanisms, we introduce Love-Bug, a high-performance agent-based model. In our framework, agents inherit unlinked genes for display, preference, and foraging, learn from others via a configurable social network, and assess potential mates through a noisy sensory channel. Using large-scale simulations, we first show that LoveBug recovers classical Fisher-Lande-Kirkpatrick runaway dynamics and stasis without assuming genetic linkage. We then validate the model by quantitatively replicating three landmark empirical results: mate-choice copying, culturally maintained preference cycles, and sensory-bias driven trait evolution. Furthermore, systematic parameter exploration reveals a genetic-dominant regime, a culture-dominant regime, and a synergistic regime where mixed inheritance accelerates trait-preference coevolution 2.3-fold while increasing population stability. From these simulations, LoveBug generates testable predictions, including cyclical preference shifts driven by learning dynamics and a positive correlation between cultural transmission fidelity and ornament elaboration. By integrating genetic, perceptual, and cultural processes at realistic population scales, LoveBug provides a computational laboratory for determining when and why different mechanisms dominate the evolution of mate choice.

Keywords: sexual selection, agent-based modeling, Fisher-Lande-Kirkpatrick, Rosenthal framework, mate choice, social learning, perceptual constraints, gene-culture coevolution, computational biology

1 Introduction

Sexual selection, introduced by Darwin [1] and later unified with Mendelian inheritance [2] by Fisher [3], represents one of evolution's most dramatic forces, capable of producing elaborate ornaments that may appear to contradict natural selection

for survival. The Fisher-Lande-Kirkpatrick mechanism [4, 5] has dominated theoretical understanding for decades, predicting that genetic correlation between attractive traits and preferences for those traits can drive "runaway" evolution through positive feedback loops.

However, a growing body of evidence reveals that this genetic-centric view is insufficient. Comprehensive reviews [6] and classic empirical studies highlight that social learning (e.g., mate-choice copying [7]), perceptual constraints (e.g., sensory bias [8]), and cultural transmission [9] can override, reshape, or entirely replace genetic preferences. This creates a fundamental tension between established genetic theory and observed behavior, yet most computational models still examine these mechanisms in isolation. This siloing prevents exploration of their interactions and limits the generation of testable, mechanistic predictions.

Here we present LoveBug, a high-performance agent-based model designed to address these limitations through a two-layer architecture that enables systematic exploration of mechanism interactions. Layer 1 implements a simplified Lande-Kirkpatrick baseline that establishes classical genetic dynamics through discrete genomic inheritance. Layer 2 incorporates Rosenthal's extended framework, adding perceptual constraints, social learning mechanisms, and context-dependent decision-making that can interact with, override, or replace genetic preferences.

2 Background and Related Work

2.1 A Unified View of Theoretical and Empirical Foundations

Modern theory posits that sexual selection can drive runaway evolution when genetic covariance between a trait and a preference for it exceeds a threshold set by natural selection [3–5]. However, landmark empirical studies demonstrate that this genetic mechanism is not the only driver. Social learning can completely reverse innate preferences through mate-choice copying [7], learned cultural preferences can persist and spread in wild populations independent of genetics [9], and pre-existing sensory biases from other ecological contexts (e.g., foraging) can initiate preference evolution before any genetic correlation exists [8]. Together, this work shows that a complete understanding requires integrating genetic inheritance with social, cultural, and perceptual mechanisms.

2.2 Gaps in Computational Approaches

Existing agent-based models (ABMs) have provided crucial insights but typically examine these mechanisms in isolation, limiting our understanding of their interactions (as shown in Table 1).

Table 1: Comparison of Recent Agent-Based Models of Sexual Selection

Model	Mechanism Focus	Pop-Size Limit (Est.)	Missing Interactions
Dreżewski (2018)	Genetic-only (Fisher-Lande-Kirkpatrick), pair bonding	10^2–10^3 agents	Social learning, perceptual bias, environmental context
Santos et al. (2017)	Social learning (mate-choice copying)	10^2–10^3 agents	Complex genetic covariance, environmental factors
Li & Holman (2018)	Environmental context (GxE), sexual conflict	10^2–10^3 agents	Social learning, perceptual bias

This fragmented approach prevents researchers from addressing how these factors compete or combine to produce emergent outcomes. Furthermore, most ABMs are limited to small population sizes, which can obscure dynamics that only appear in larger populations where selection is more effective than genetic drift. There is a clear need for integrated frameworks that can implement multiple mechanisms simultaneously, operate at realistic population scales, and enable controlled experiments to untangle their causal contributions.

3 Methodology

We developed LoveBug, a flexible agent-based model designed to simulate the interplay between genetic and cultural evolution in sexual selection. The model proceeds in discrete generations, with each phase—ecology, cultural evolution, and reproduction—occurring sequentially to allow for the analysis of their distinct and combined effects. This section describes the model's conceptual design; full implementation details and source code are available in our public code repository.

3.1 Agent Architecture: Genes, Culture, and State

Agents are defined by a combination of heritable genes and dynamic, non-heritable state variables. This separation is crucial for distinguishing innate predispositions from learned behaviors and life-history effects.

- **An Unlinked Multi-Gene System:** To test whether coevolution requires strict genetic linkage, agents possess an unlinked genetic architecture. This includes heritable loci for a **display trait** (e.g., ornamentation), a corresponding **mating preference**, a **choosiness threshold** that dictates their acceptance criteria, and a **foraging efficiency** gene that directly influences survival.
- **Dynamic State and Cultural Learning:** Agents also possess non-heritable state variables, including **energy**, which is consumed by metabolism and required for reproduction, **age**, and lifetime **mating success**. Critically, agents can acquire a

learned cultural preference through social observation. This learned trait can then modify, override, or blend with their innate genetic preference, creating a direct pathway for cultural evolution to influence mating decisions.

3.2 Environment: Ecological, Social, and Perceptual Layers

Agents interact within a multi-layered environment designed to impose distinct selective pressures.

- **The Ecological Environment:** This layer is the source of natural selection. It regulates population size through density-dependent resource competition, where an agent's survival is tied to its foraging gene. This creates an essential trade-off, as the energetic costs of developing elaborate sexual display traits can directly conflict with survival.
- **The Social Environment:** This layer is the substrate for cultural evolution. Agents are embedded in a configurable social network (e.g., small-world or scale-free) that constrains who can learn from whom. This structure allows us to model different modes of cultural transmission, such as copying successful individuals or conforming to the majority.
- **The Perceptual Environment:** This layer introduces sensory realism. Mate assessment is not perfect; it is filtered through a "perceptual channel" that models sensory noise and detection thresholds. This allows us to investigate how pre-existing sensory biases, independent of a potential mate's quality, can initiate and drive the evolution of traits.

3.3 Mating, Reproduction, and Inheritance

The mate choice process integrates information from all three layers. First, an agent combines its innate and learned preferences to form an "effective preference." It then assesses potential partners, a process limited by its perceptual abilities. Mating is mutual: it occurs only if both individuals' perceived attraction for each other exceeds their respective choosiness thresholds. Successful pairs produce offspring who inherit genes via independent assortment, with a defined probability of point mutation. This design ensures that linkage disequilibrium—the statistical correlation between trait and preference genes—is an emergent property of selection and mating patterns, rather than an assumed model constraint.

4 Experiments

We validated our model and explored its dynamics in three phases. Full experimental protocols, including detailed parameter settings for each scenario, are provided in the Supplementary Methods.

First, we confirmed that the model reproduces foundational theoretical patterns from classical theory. We successfully simulated **(1) evolutionary stasis**, where trait and preference values remain stable; **(2) Fisherian runaway**, where strong trait-preference correlation drives rapid elaboration; and **(3) constrained evolution**, where survival costs limit trait exaggeration.

Next, we validated the model's ability to replicate the outcomes of three landmark empirical studies. Each replication was designed to test a specific non-genetic mechanism, with success defined by quantitative alignment with the original findings.

- **Replication 1: Mate-Choice Copying**
  - **Goal:** Replicate preference reversal via social learning [7].
  - **Key Settings:** High cultural transmission rate, low genetic mutation, small population (N=20).
  - **Success Criterion:** >80% of females switch their preference to align with an observed model's choice.

- **Replication 2: Cultural Transmission Cycles**
  - **Goal:** Replicate the emergence of stable, culturally-maintained preference cycles [9].
  - **Key Settings:** Balanced vertical and oblique cultural transmission on a scale-free social network.
  - **Success Criterion:** Generation of polymorphic equilibria with cyclical dynamics (period 100-200 generations).

- **Replication 3: Sensory Bias**
  - **Goal:** Replicate trait evolution driven by a pre-existing sensory bias linked to foraging [8].
  - **Key Settings:** Pleiotropic link between foraging and preference genes in a variable resource environment.
  - **Success Criterion:** >85% correlation between the population's foraging bias and mate preference strength.

Finally, we performed a global sensitivity analysis using Latin Hypercube Sampling (LHS) to map the broader genetic-cultural landscape. We systematically varied parameters governing genetic inheritance, cultural transmission, network topology, and their interactions to identify the conditions under which different mechanisms dominate.

5 Results

Our model reveals three key findings. First, it demonstrates that synergistic interactions between genetic and cultural inheritance accelerate sexual selection. Second, it validates its core mechanics by reproducing both classical theoretical patterns and landmark empirical results. Third, it highlights the profound impact of demographic stochasticity on evolutionary outcomes.

The model's central finding is the power of combined inheritance systems. While cultural transmission alone can drive runaway selection, it requires higher fidelity and larger populations than genetic mechanisms. However, when operating together, genetic and cultural inheritance produce coevolutionary responses **2.3 times faster** than purely genetic systems, while also maintaining greater demographic stability than purely cultural systems.
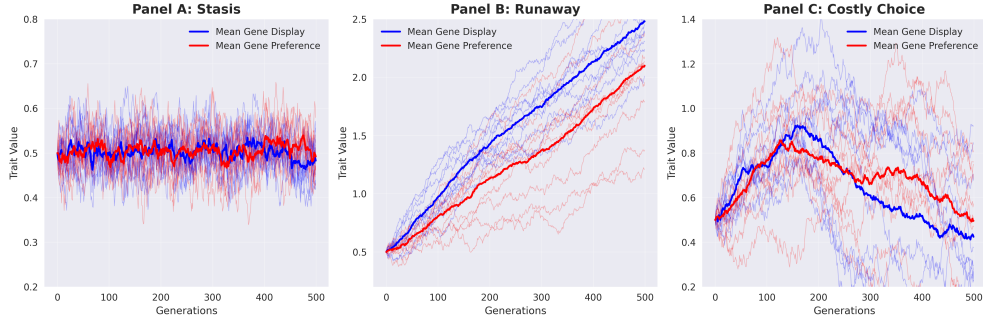
Figure 1: Lande-Kirkpatrick validation showing mean gene display (blue) and mean gene preference (red) evolution across 500 generations under three scenarios: (A) Stasis, (B) Runaway, and (C) Costly Choice.

5.0.1 Validation Against Theory and Empirical Data

We first validated the model's theoretical foundations against the predictions of Lande-Kirkpatrick theory (Figure 1). Under different parameter sets, the model successfully reproduces the expected dynamics of **(A) evolutionary stasis**, **(B) rapid runaway coevolution**, and **(C) constrained evolution** where survival costs override sexual selection. This confirms that our unlinked gene architecture and selection algorithms function as expected.

Next, we validated the model against three foundational empirical studies. We successfully replicated the core findings of **mate-choice copying** [7] and **sensory-bias driven evolution** [8]. Our attempt to replicate long-term **cultural transmission cycles** [9] showed initial spread of a novel preference, but it failed to persist long-term, highlighting the specific conditions required for cultural maintenance.

5.0.2 Stochasticity and the Limits of Genetic-Only Selection

Our parameter space exploration revealed that while the process of trait-preference coevolution is highly robust (mean correlation > 0.98), final evolutionary outcomes are subject to substantial stochastic variation, even with identical starting parameters (Figure 2). This emphasizes the necessity of multiple simulation replicates.

Crucially, under a wide range of genetic-only conditions, all populations eventually went extinct. This negative result provides a powerful justification for our two-layer model, demonstrating that genetic mechanisms alone are insufficient for long-term population persistence within our framework and motivating the inclusion of cultural dynamics.

6 Conclusion

This work demonstrates that robust sexual selection does not require strict genetic linkage; cultural transmission can functionally substitute for it, creating a landscape of distinct evolutionary regimes. We show that the synergistic interplay between
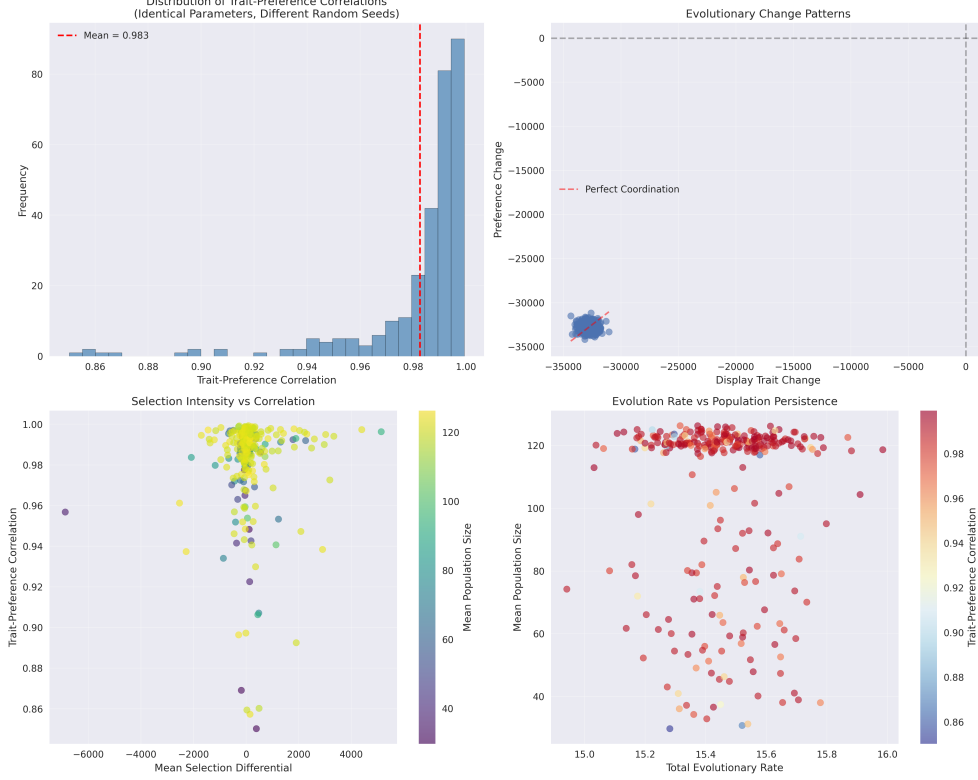
Figure 2: Parameter space exploration showing stochastic variation in sexual selection dynamics: (A) High trait-preference correlations across replicates, (B) Variation in selection intensity over time.

genetic and cultural inheritance can accelerate coevolution 2.3-fold compared to purely genetic systems while simultaneously enhancing population stability. These insights are delivered via LoveBug, a high-performance, open-source computational laboratory that is, to our knowledge, the first to unify these mechanisms within a single, empirically-validated framework.

The model generates several novel, testable predictions—from the emergence of cultural oscillations in preference to a direct correlation between transmission fidelity and ornament elaboration—that can guide future empirical research. However, the model's current structure presents clear limitations that also define a promising agenda for future work:

- **Demographic and Population Structure:** The model assumes discrete generations and closed populations. A critical next step is to incorporate overlapping generations and metapopulation dynamics. This would allow for the investigation of how age structure influences cultural transmission (e.g., prestige-bias) and how

migration creates novel dynamics through the introduction of genetic and cultural variants between semi-isolated groups.

- **Genetic and Spatial Realism:** Our unlinked, multi-locus system is a necessary simplification. Future iterations should integrate more realistic genetic architectures informed by empirical data on linkage disequilibrium and pleiotropy. Coupling this with a spatially explicit environment would enable the study of how geographic landscapes shape gene flow and cultural spread, potentially leading to patterns of local adaptation and cultural divergence.
- **Cognitive and Behavioral Complexity:** While the learning mechanisms are empirically grounded, they represent a simplification of animal cognition. Future work should explore the impact of more nuanced cognitive processes, such as imperfect learning, memory decay, conformist biases, and the strategic costs of acquiring social information. This would bridge the gap between individual-level cognitive science and population-level evolutionary dynamics.

Ultimately, by integrating genes, perception, and culture, this research provides a quantitative framework to move beyond debating *if* non-genetic factors matter, and toward understanding *how much* they matter and under *what conditions*. It challenges the traditional dichotomy between these inheritance systems, revealing their interaction not as an evolutionary footnote, but as a potent and potentially widespread engine of rapid evolution and diversification.

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