Poeciliid Research

Evolutionary models of female mate choice: integrating genetic benefits, sensory bias, learning, and sexual conflict

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Abstract. Female mate choice is a central mechanism of sexual selection and has been explained through multiple evolutionary frameworks that differ in their assumptions about the benefits of choice and the mechanisms driving the coevolution of preferences and male traits. Classical models include Fisherian runaway processes based on genetic correlations, indicator and good genes models emphasizing indirect genetic benefits, and direct benefit models in which females gain material or fertility advantages. More recent theoretical advances have expanded these foundations to incorporate sensory bias, cognitive constraints, learning, and sexual conflict, providing a more comprehensive view of how preferences originate and evolve. Quantitative models have clarified how indirect genetic benefits can rival direct benefits in evolutionary strength and have reshaped interpretations of the lek paradox by demonstrating that sexual selection can maintain or even enhance genetic variation. Sensory exploitation theory highlights the role of perceptual tuning and environmental context in shaping preferences, while social learning and habituation models explain how preferences can remain dynamic and responsive to ecological and social conditions. Additionally, models incorporating coercion and resistance emphasize female choice as part of a broader system of sexual conflict and autonomy. Empirical research on the Trinidadian guppy provides strong integrative support for these theoretical perspectives, demonstrating how genetic, sensory, cognitive, and ecological processes interact to shape mate choice. Together, modern evolutionary models portray female mate choice as a dynamic, multifactorial process that contributes not only to trait diversification but also to the maintenance of genetic variation and adaptive potential.
Key Words: sexual selection, female mate choice, Fisherian runaway, good genes hypothesis, lek paradox, ornament evolution, *Poecilia reticulata.*

Purpose of the study. The aim of this review is to synthesize classical and contemporary evolutionary models of female mate choice and to evaluate how genetic, sensory, cognitive, social, and conflict-mediated processes interact to shape the origin, maintenance, and evolutionary consequences of mating preferences.

Conceptual foundations of evolutionary models of female choice. Female mate choice is a central driver of sexual selection and has been modeled using several major frameworks that differ in the assumed benefits of choosing and in the mechanisms by which preferences and male traits coevolve. Classical models fall into four broad classes: Fisherian runaway models, in which genetic correlations between female preference and male ornament allow self-reinforcing coevolution; "good genes" and indicator models, in which preferences evolve because preferred males transmit alleles that increase offspring viability or overall quality; direct-benefit models, where females obtain material or fertility benefits from preferred males; and sensory bias or sensory exploitation models, where preferences originate from pre-existing properties of the perceptual system that were shaped in nonsexual contexts (Henshaw et al 2022; Lindsay et al 2019; Fry 2022). More recent theory has expanded this landscape to include dynamic learning-based and social models of preference acquisition (DuVal et al 2023; Herdegen-Radwan 2022), as well as models that integrate female choice with sexual conflict and coercion (Snow et al 2019; Snow & Prum 2023). Together, these approaches aim to explain how female preferences arise, persist and interact with genetic variation and ecological constraints.

Direct and indirect benefits: **good genes, sexy sons and the lek paradox**. A central question in the theory of female choice concerns whether preferences are primarily maintained by direct benefits, such as access to resources, reduced harassment or increased fertility, or by indirect genetic benefits, such as producing attractive "sexy sons" or high-quality offspring (Henshaw et al 2022; Lindsay et al 2019; Petrie 2021; Fry 2022). Quantitative theory shows that when male ornaments reliably indicate genetic quality (e.g. resource acquisition ability or overall condition), females that pay search or assessment costs can gain indirect benefits through both good genes and attractive sons, even when ornaments are costly to produce and maintain (Henshaw et al 2022). Importantly, such models now treat the costs of mate search and the costs of preferences separately, revealing that females are more willing to invest in costly search when ornaments track male quality, whereas arbitrary ornaments associated only with attractiveness provide too little benefit to sustain high search effort on their own; instead, they can "piggyback" on search driven by quality-dependent traits (Henshaw et al 2022).

This perspective has reshaped views of the longstanding "lek paradox," the apparent contradiction between the expectation that strong female choice should erode genetic variation in sexually selected traits and empirical evidence that these traits often remain highly variable. Recent infinitesimal models demonstrate that mutual exaggeration of variation in male displays and female preferences is not only possible but common, so that sexual selection via mate choice can increase or only slightly reduce equilibrium variance in ornaments relative to random mating (Xu & Servedio 2025; Petrie 2021). Under many conditions, especially where females compare many males and costs of choice are low, sexual selection can thus maintain the genetic diversity that fuels continued evolution of female choice and male traits rather than depleting it (Xu & Servedio 2025; Petrie 2021).

The relative strength of direct versus indirect selection of preferences has also been reassessed. Arguments that indirect selection are inherently weaker than direct selection rest on restrictive assumptions about evolutionary rates and misunderstanding of how selection is represented mathematically. A careful reexamination shows that, in principle, indirect selection on preferences via genetic benefits can be comparable to or stronger than direct selection, and that the balance between them is an empirical matter rather than a theoretical inevitability (Fry 2022).

Sensory bias, **perceptual tuning and cognitive constraints**. Sensory bias models propose that female preferences arise because male traits exploit pre-existing properties of the female perceptual and cognitive systems, rather than because the traits initially conveyed information about genetic or material benefits. Such biases can originate in foraging, predator avoidance or social interactions, and male signals that tap into these biases may enjoy an initial mating advantage even in the absence of any correlation with male quality (Henshaw et al 2022; Lindsay et al 2019). Empirical work increasingly shows that receiver psychology—sensory tuning, perceptual salience and cognitive processing—critically shapes which ornaments evolve and how preferences respond to environmental context (Lindsay et al 2019; Corral-López et al 2017).

The Trinidadian guppy (*Poecilia reticulata*) provides a key example linking sensory bias and coevolution of preferences and ornaments. Female guppies typically prefer males with larger and more saturated orange spots, and this preference varies across populations in parallel with male coloration (Sandkam et al 2015; Valvo et al 2019;

Kawamoto et al 2021). Molecular and physiological studies show that guppies possess an expanded set of long-wavelength-sensitive opsins, and that expression of long-wavelength-sensitive (LWS) opsins is elevated in low-predation populations where sexual selection is strong and female preference for orange is pronounced (Sandkam et al 2015). Females from such populations invest disproportionately in color vision tuned to detect orange–red light, indicating that visual sensitivity has coevolved with mating preferences and male signals in a way predicted by sensory exploitation theory (Sandkam et al 2015).

Perceptual and cognitive limitations also constrain female choice. Experimental selection lines in guppies demonstrate that females with larger brains and higher cognitive performance express stronger preferences for males bearing the color traits associated with attractiveness, whereas small-brained females show weak or no preference despite having similar visual sensitivity (Corral-López et al 2017). This indicates that the assessment and integration of multiple sexual traits depend on cognitive capacity and that variation in brain size can generate individual differences in choosiness and in the ability to track subtle indicators of male quality (Corral-López et al 2017).

Environmental degradation of sensory channels further modifies realized female choice. Elevated water turbidity experimentally reduces guppy females' ability to discriminate orange coloration and erodes preferences for more ornamented males, particularly at intermediate levels where signal reliability becomes unpredictable (Venkatesan et al 2024). Such sensory noise can weaken sexual selection on color patterns and potentially shift the balance among different cues or mating tactics (Venkatesan et al 2024; Lindsay et al 2019).

Social and learning-based models of female choice. Classical models often assume genetically fixed preferences, but there is growing recognition that social learning, habituation and context-dependent evaluation can generate complex and dynamic mate choice patterns. The "Inferred Attractiveness" model formalizes a general mechanism whereby females acquire preferences by observing the choices of other females and then inferring which male feature best distinguishes chosen from unchosen males (DuVal et al 2023). Because this process depends on context and variation in the local male pool, it can generate repeated switches in dominant preferences, maintain trait polymorphism and yield either adaptive, quality-tracking preferences or nonadaptive biases depending on how social information aligns with viability selection (DuVal et al 2023).

In the guppy, both associative learning and simple forms of non-associative learning have been shown to alter female preferences in ways consistent with such models. Conditioning females to associate orange or black food rewards with feeding can shift subsequent sexual preferences toward males bearing the rewarded color, and these learned preferences translate into differential male reproductive success, providing a route for learned biases to become genetically coupled to fitness benefits (Herdegen-Radwan 2022). Short-term habituation to familiar male color patterns reduces responsiveness to those patterns while preserving or enhancing interest in novel ones, fulfilling key criteria for habituation and explaining female preferences for rare or unfamiliar male color morphs that maintain polymorphism via negative frequency-dependent selection (Valvo et al 2019; Daniel et al 2019). Population-level field studies confirm that in natural guppy populations females consistently direct more attention to males with rare or unfamiliar color patterns, independent of their orange area, supporting the idea that a preference for novelty is widespread and evolutionarily important (Valvo et al 2019).

These learning-based mechanisms challenge purely genetic models of female choice and suggest that evolutionary dynamics of preferences and ornaments reflect an interplay between inherited biases, developmental and social experience, and environmental context (DuVal et al 2023; Valvo et al 2019; Herdegen-Radwan 2022; Daniel et al 2019).

Conflict, **coercion and the evolution of female autonomy**. Female choice rarely operates in isolation from male strategies that attempt to circumvent or constrain it. Models that incorporate sexual conflict over mating highlight that mate choice should be understood as part of a broader system involving male display, female preference, male coercion and female resistance (Snow et al 2019; Snow & Prum 2023; Lindsay et al 2019). Recent quantitative models show that female resistance traits can evolve not only to mitigate direct costs of coercion but also to preserve access to indirect genetic benefits when coercive males limit the expression of preferences for attractive males (Snow et al 2019). In such scenarios, resistance enhances the efficacy of female choice, allowing females to maintain or re-establish mate choice for preferred males even when coercion is common (Snow et al 2019).

An extension of this framework introduces the concept of "remodeling" male coercion, where females evolve novel preferences for male traits that indirectly reduce male coercive capacity, thus increasing female sexual autonomy without necessarily triggering arms-race escalation (Snow & Prum 2023). Preferences for autonomy-enhancing male traits can act as a public good because all females benefit from reduced coercion, and such traits can spread despite costs to males, leading to oscillatory dynamics and complex coevolutionary trajectories (Snow & Prum 2023). These models emphasize that female choice is not only about selecting particular males but also about shaping the overall mating environment in which choice is expressed.

The Trinidadian guppy as an integrative model of female choice. *Poecilia reticulata* has become a cornerstone empirical system for testing evolutionary models of female choice because its populations vary in predation regime, ecological conditions and social environment, while exhibiting high polymorphism in male color patterns and well-characterized female preferences (Sandkam et al 2015; Venkatesan et al 2024; Valvo et al 2019). Female guppies typically prefer males with greater orange area, but this baseline preference is modulated by novelty, male behavior, brain size and environmental conditions (Petrescu & Mag 2006; Petrescu-Mag 2007; Corral-López et al 2017; Valvo et al 2019; Daniel et al 2019; Herdegen-Radwan 2022; Petrescu-Mag 2023; Venkatesan et al 2024).

Female choice in guppies yields both direct and indirect benefits. Preferences for orange males are associated with offspring bearing enhanced expression of sexually attractive coloration and, in some contexts, with markers of genetic quality such as multilocus heterozygosity and immune-related genotype, suggesting good-genes and sexy-sons' components (Venkatesan et al 2024; Kawamoto et al 2021; Sato et al 2021; Lindsay et al 2019). At the same time, females pay attention to cues of male fertility: when given a choice between males matched for size and color but differing in recent mating history, virgin females preferentially associate with males that have not recently mated and thus are less likely to be sperm-depleted, a pattern consistent with the phenotype-linked fertility hypothesis and direct fertility benefits of choice (Scarponi et al 2015).

Guinea preferences also respond rapidly to social and learning processes. Associative learning experiments show that ecological experiences, such as the color of food items, can be translated into sexual preferences and alter male reproductive success across generations (Herdegen-Radwan 2022). Habituation and preference for rare or unfamiliar patterns generate negative frequency-dependent sexual selection, maintaining extraordinary genetic variation in male color patterns even under strong directional and viability selection (Valvo et al 2019; Daniel et al 2019). These behavioral mechanisms align with theoretical models in which dynamic, socially mediated preferences stabilize polymorphisms and fuel ongoing coevolution of traits and preferences (Henshaw et al 2022; DuVal et al 2023; Xu & Servedio 2025; Petrie 2021).

Finally, guppies illustrate how sensory systems evolve in concert with female choice. Differences in LWS opsin expression among populations track both light environment and predation regime, and populations with stronger female preferences for orange invest more in red–orange sensitivity, directly supporting sensory exploitation models in which variation in visual tuning drives divergence in mate preference and ornaments (Sandkam et al 2015; Venkatesan et al 2024; Lindsay et al 2019).

Taken together, evolutionary models of female choice in animals now encompass a spectrum from classic genetic correlation and indicator frameworks to sensory, cognitive and conflict-based perspectives. Work on *Poecilia reticulata* has been pivotal in demonstrating that female choice is shaped by coevolving sensory systems, learning and social information, and that these processes can maintain genetic variation while producing both adaptive and nonadaptive preferences in complex ecological landscapes (Sandkam et al 2015; Henshaw et al 2022; DuVal et al 2023; Venkatesan et al 2024; Valvo et al 2019; Xu & Servedio 2025; Lindsay et al 2019; Herdegen-Radwan 2022; Corral-López et al 2017; Daniel et al 2019).

Conclusions. Modern evolutionary theory demonstrates that female mate choice emerges from the interaction of multiple mechanisms rather than a single dominant process. Classical genetic models, including Fisherian runaway and indicator frameworks, remain essential for explaining how preferences and male traits coevolve and how indirect genetic benefits can sustain costly choice. However, recent advances show that sensory biases, perceptual tuning, and cognitive capacity play equally important roles by determining which signals females can detect, evaluate, and preferentially select. Learning and social experience further introduce flexibility into mating preferences, allowing rapid behavioral shifts that can stabilize polymorphisms and maintain genetic diversity. At the same time, sexual conflict and coercion models highlight that mate choice evolves within a broader ecological and behavioral system in which female autonomy and resistance can shape the direction and strength of sexual selection. Empirical evidence, particularly from integrative model systems, confirms that these mechanisms operate simultaneously and interactively, linking genetic inheritance, neural processing, environmental conditions, and social context. Collectively, these findings redefine female mate choice as a dynamic and adaptive evolutionary process that not only drives ornament evolution but also contributes to maintaining genetic variation, promoting population divergence, and shaping the structure of mating systems across ecological landscapes.

Conflict of interest. The authors declare that there is no conflict of interest.

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