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SEXUAL SELECTION IN ANIMALS: PIGMENT-BASED SIGNALING AND ECO-EVOLUTIONARY TRADE-OFFS

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Abstract: Sexual selection is a fundamental evolutionary process shaping phenotypic diversity, reproductive strategies, and ecological interactions across vertebrates. This review synthesizes contemporary perspectives on the definition, mechanisms, and evolutionary consequences of sexual selection, with particular emphasis on pigment-based signaling systems. We examine how carotenoid- and pteridine-derived coloration functions as condition-dependent sexual signals, linking ornament expression to physiological processes such as oxidative balance, metabolism, and immune function. Empirical evidence demonstrates that red carotenoid-based traits often reliably indicate individual quality, reproductive performance, and fertilization success, although their honesty is mediated by complex trade-offs and biochemical constraints. In parallel, pteridine pigments and mixed pigment systems reveal alternative or complementary signaling pathways, often shaped by ecological conditions and sensory biases. The review further explores the concept of sensory traps and sensory drive, highlighting how pre-existing perceptual biases influence the evolution of sexual signals. A central focus is placed on the coevolution of mate choice and predation pressure, where sexually selected traits are simultaneously shaped by attractiveness and survival costs, generating dynamic eco-evolutionary feedbacks. At broader scales, sexual selection contributes to phenotypic diversification but plays a nuanced role in speciation. Overall, this synthesis underscores the importance of integrating physiology, ecology, and evolutionary theory to understand the multifaceted roles of sexual selection in vertebrate evolution.

Keywords: sexual selection, vertebrates, carotenoids, pteridines, sexual signaling, mate choice, sensory bias, sensory traps, predation, eco-evolutionary dynamics, ornamentation, physiological condition.

INTRODUCTION

Sexual selection represents a central mechanism of evolutionary change, operating through differential reproductive success driven by variation in access to mates and fertilizations. While historically conceptualized as a subset of natural selection, modern evolutionary biology recognizes sexual selection as a distinct but interacting process, responsible for the evolution of elaborate traits such as ornaments, weapons, and complex courtship behaviors. In vertebrates, these traits often exhibit strong condition dependence and are tightly linked to physiological, ecological, and genetic factors.

Among the most intensively studied sexually selected traits are pigment-based color signals, particularly those derived from carotenoids and pteridines. These pigments not only generate visually striking phenotypes but also reflect underlying biological processes, including metabolic efficiency, oxidative stress management, and immune competence. Consequently, coloration provides a powerful framework for investigating the honesty, costs, and constraints of sexual signaling.

At the same time, sexual selection does not operate in isolation. Ecological context, especially predation pressure and environmental variability, plays a critical role in shaping both signal expression and mate choice. The interplay between attractiveness and survival generates trade-offs that influence evolutionary trajectories, often mediated through mechanisms such as sensory bias, sensory drive, and sensory traps.

The aim of this review is to provide an integrative synthesis of sexual selection in vertebrates by linking theoretical frameworks with empirical evidence on pigment-based signaling, physiological mechanisms, and eco-evolutionary interactions, with particular emphasis on the coevolution of mate choice and environmental constraints such as predation.

SEXUAL SELECTION IN VERTEBRATES: DEFINITION, ORIGINS, AND EVOLUTIONARY CONSEQUENCES

Sexual selection is a form of selection that arises because individuals differ in their success at securing mating and fertilizations, rather than simply surviving. It typically acts through competition for access to gametes and mate choice (Mag-Mureșan & Bud, 2004; Petrescu-Mag, 2008), and is now viewed as conceptually distinct—though intertwined—from natural selection, as already emphasized by Darwin and defended in recent theoretical work (Campbell, 2017; Petrie, 2021; Shuker & Kvarnemo, 2021; Tuschhoff & Wiens, 2023). A modern definition stresses that sexual selection operates whenever variation in reproductive success is caused by differences in access to gametes, via traits such as ornaments, weapons, courtship

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displays or sperm traits (Shuker & Kvarnemo, 2021; Candolin, 2019; Tuschhoff & Wiens, 2023).

Sexual selection is both based on and promotes sexual dimorphism (Houde 1997; Bitalas et al 2015; Garcia & Giraldo-Gongora 2023; Serihollo *et al.*, 2024; Luna-Vivaldo & Hernandez-Lopez 2026). Historically, Darwin introduced sexual selection to explain extravagant traits like the peacock's train that seemed maladaptive for survival but beneficial for attracting mates, arguing for a distinct process based on mate choice and intrasexual competition across arthropods and vertebrates (Campbell, 2017; Pyatnitskiy, 2024). Contemporary syntheses confirm that similar principles apply broadly in chordates and other animals: male–male competition, female choice, male choice and mutual choice all occur, with especially diverse sexual traits in arthropods and chordates (Janicke *et al.*, 2025; Candolin, 2019).

Sexual selection acts in both sexes wherever reproductive success increases with mating success. Meta-analytic work across many animal taxa shows that females, as well as males, commonly gain fitness from multiple mating, supporting widespread sexual selection on females and helping explain the evolution of polyandry and "reversed" sex roles in some vertebrates (Fromonteil *et al.*, 2023; Hare & Simmons, 2018). Comparative analyses also find that net selection is generally stronger on males, consistent with intense sexual selection shaping male phenotypes and exposing male-expressed genotypes to harsh selective scrutiny (Winkler *et al.*, 2021; Candolin, 2019).

Consequences for vertebrate evolution are manifold. At the individual and population level, sexually selected traits can impose costs through sexual conflict and harm, but experimental evolution and meta-analyses indicate that, on average, sexual selection tends to improve population fitness, especially under stressful conditions, by favoring high-quality genotypes and purging deleterious mutations (Candolin, 2019; Giery & Layman, 2019; Cally *et al.*, 2019; Rowe & Rundle, 2021). The alignment or misalignment of sexual and natural selection is crucial: when they favor similar phenotypes, sexual selection can bolster adaptation and potentially help populations track environmental change; when they conflict, sexually selected traits may reduce viability or even increase extinction risk (Candolin, 2019; Petrie, 2021; Rowe & Rundle, 2021).

At macroevolutionary scales, sexual selection contributes to phenotypic diversity but its role in diversification is nuanced (Păsărin & Petrescu-Mag 2011). Large comparative datasets show that sexually selected traits and mechanisms (e.g., female choice, male competition) are concentrated in clades such as vertebrates and evolve rapidly, yet broad-scale effects on speciation and species richness are modest (Janicke *et al.*, 2025; Bora *et al.*, 2025; Păpuc *et al.*, 2025; Popescu & Păpuc, 2025; Januario *et al.*, 2024; Dearborn *et al.*, 2022; Candolin, 2019). A meta-analysis of comparative studies finds a consistent but small positive association between proxies of sexual selection and species diversity, implying that sexual selection is one contributor, but not the dominant driver, of speciation across animals (Dearborn *et al.*, 2022; Januario *et al.*, 2024).

Sexual selection also has ecological and eco evolutionary consequences. In vertebrates, sexually selected traits can shape trophic interactions, behavior, and demography, with feedbacks on community structure and ecosystem processes (Giery & Layman, 2019). Their expression and intensity are strongly context dependent: abiotic factors such as temperature modulate mating success, trait expression and the opportunity for sexual selection in both sexes, suggesting that climate change may alter sexual selection regimes and, indirectly, vertebrate population viability (García-Roa *et al.*, 2020; Candolin, 2019; Owen & Lahti, 2020). Genetic targets of pathogen-mediated and sexual selection, such as MHC genes, show widespread polymorphism and signatures of positive selection across fish, amphibians, birds and mammals, illustrating how mate choice and disease jointly shape vertebrate immune diversity.

Modern syntheses of the sexual selection literature highlight persisting biases (toward males, birds, and certain mechanisms) but also an expanding appreciation of female competition, post copulatory processes and ecological context (Pollo *et al.*, 2024; Fromonteil *et al.*, 2023; Hare & Simmons, 2018).

CAROTENOID RED COLORATION AS A SIGNAL OF MATE QUALITY IN VERTEBRATES

Carotenoid pigments, although not synthesized de novo in the bodies of vertebrates, are widely distributed across both the plant and animal kingdoms, where they fulfill a broad spectrum of physiological and ecological functions (Darsiani *et al.*, 2023; Thinh *et al.*, 2023; Prayitno *et al.*, 2024; Doan *et al.*, 2025; Marzuqi *et al.*, 2025). In photosynthetic organisms such as plants and algae, as well as in certain bacteria and fungi, carotenoids are biosynthesized endogenously and play essential roles in light harvesting and photoprotection (Nurafifah *et al.*, 2023; Tran *et al.*, 2024; Batubara *et al.*, 2025). In contrast, vertebrates lack the metabolic pathways necessary for carotenoid biosynthesis and therefore rely entirely on dietary intake for their acquisition; nevertheless, these compounds are prevalent in animal tissues due to their transfer and accumulation through trophic interactions. Once assimilated, carotenoids contribute to key physiological processes, including functioning as precursors of vitamin A and as antioxidants that mitigate oxidative stress. They also play important ecological roles, particularly in coloration, where they are involved in camouflage, warning signals, and sexual selection. Across vertebrates, red carotenoid-based external coloration—manifested in structures such as skin, bills, combs, irides, plumage, scales, or fins—is widely used in mate choice and social interactions; because carotenoids must be obtained from the diet and are closely linked to physiological condition, the expression of such coloration can act as an honest signal of individual vigor, health status, and reproductive potential.

MECHANISMS LINKING CAROTENOID RED TO PHYSIOLOGICAL CONDITION

Carotenoid pigments are acquired from food and then transported, transformed (often into red ketocarotenoids) and deposited in external tissues. This requires coordinated uptake, metabolism and tissue-specific gene expression, frequently under hormonal control (Khalil *et al*., 2020; Khalil *et al*., 2023; Blas *et al*., 2016; McCoy *et al*., 2023). In red-backed fairywrens, testosterone upregulates the ketolase gene CYP2J19 and other carotenoid-processing and transporter genes in liver and feather follicles, directly driving red plumage production (Khalil *et al*., 2020; Khalil *et al*., 2023). Similar links between carotenoid metabolism, cellular respiration and red ketocarotenoid production have been proposed to tie ornament expression to mitochondrial efficiency and lifespan (Cantarero *et al*., 2019; Hill *et al*., 2023; Hill, 2022). Red coloration can also depend on the availability of specific dietary carotenoids and on the individual's ability to manage oxidative stress during biotransformation; in red-legged partridges, particular carotenoid substrates plus mild oxidative stress produce redder bare-part ornaments but at measurable oxidative costs, supporting a costly "biotransformation" component of the signal (Cantarero *et al*., 2019; Blas *et al*., 2016). Experimental work in sticklebacks and zebra finches shows that non-carotenoid antioxidants (vitamins C and E, melatonin) enhance redness when carotenoids are held constant, indicating that red ornaments can signal the availability of broader antioxidant defences rather than carotenoids alone (Pike *et al*., 2007; Bertrand *et al*., 2006). Immune activation and reduced food intake rapidly dull carotenoid-based bare parts in zebra finches, highlighting how these signals track short-term physiological condition and resource trade-offs (Pike & Lindholm, 2017; Cantarero *et al*., 2025).

EVIDENCE THAT RED CAROTENOID TRAITS PREDICT REPRODUCTIVE PERFORMANCE AND "VIGOUR"

In male red-legged partridges, initial redness of bill and eye rings predicts both longevity (up to seven years) and lifetime reproductive output (offspring number and hatching success), directly linking a carotenoid-based ornament to core fitness components (Cantarero *et al*., 2019). In great black backed gulls, more intense red/yellow carotenoid coloration of bill, gape and eye-ring correlates with better male body condition and, in females, with larger clutches and eggs, as well as higher lymphocyte density, suggesting that red carotenoid traits reflect general quality and immune status (Kristiansen *et al*., 2005). In three spined sticklebacks, females prefer males with more intense red nuptial coloration, and experimental manipulations show that high-antioxidant diets increase redness and female preference, while female perception is tuned to discriminate males based specifically on carotenoid allocation to the signal (Pike *et al*., 2007; Pike & Lindholm, 2017). Moreover, in sticklebacks, males with more intense red breeding coloration have faster, more linear sperm, linking the ornament to fertilization ability and supporting phenotype linked fertility (Mehlis *et al*., 2013). In guppies, carotenoid-based orange spots influence female mate choice, and male investment in the carotenoid–pteridine mix of these patches reflects carotenoid availability in nature, suggesting that orange/red patterning encodes information about foraging success and perhaps parasite resistance (Grether *et al*., 2001; Lozano, 1994).

HONEST SIGNALING, TRADE-OFFS AND CONSTRAINTS

Two main frameworks explain why carotenoid red remains informative. Resource based "handicap" models emphasize trade-offs between using carotenoids as pigments versus for immunity and antioxidant defence; only high-quality individuals can afford to allocate enough pigment to become conspicuously red (Pike *et al*., 2007; Lozano, 1994; Kristiansen *et al*., 2005). Index models instead propose that redness is intrinsically tied to vital metabolic pathways (e.g. mitochondrial function, carotenoid oxygenases such as CYP2J19 or BCO2), making "cheating" physiologically difficult (Hill *et al*., 2023; Khalil *et al*., 2023; Blas *et al*., 2016; Lu *et al*., 2024; Hill, 2022). Experimental manipulations support both resource allocation costs and biochemical constraints: carotenoid scarcity, oxidative challenges and limited non-pigmentary antioxidants all restrict red signal expression (Pike *et al*., 2007; Blas *et al*., 2016; Bertrand *et al*., 2006); interference with steroid metabolism can decouple ornament intensity from longevity and fecundity, destroying signal reliability (Cantarero *et al*., 2019). Recent work also shows that structural effects (changes in light path length through pigment layers) can redshift carotenoid colours independent of pigment concentration, potentially weakening honesty if microstructural elaboration allows redder appearance without greater carotenoid investment (McCoy *et al*., 2023). Meta-analytic comparisons of carotenoid vs. melanin ornaments suggest that, despite biochemical differences, both pigment classes can act as condition-dependent sexual signals, indicating that strong condition dependence is not unique to carotenoids (Griffith *et al*., 2006).

VARIATION, LIMITS AND ALTERNATIVE EXPLANATIONS

Although red carotenoid traits often function as signals of vigour, their role is not universal. In a marine copepod, red carotenoid coloration is condition dependent yet males do not consistently prefer redder females once diet is controlled, implying that the same pigment can serve primarily protective rather than sexual signalling roles in some taxa (Powers *et al*., 2020). In lizards and fish, similar hues can arise from endogenously synthesized pteridines whose red patches may signal quality (for example in male Guinan toad headed lizards) but are genetically and biochemically distinct from carotenoid reds (Lu *et al*., 2024; Xiao *et al*., 2024). Conceptually, several authors have argued that carotenoid-based coloration may signal access to uncoloured antioxidant resources, overall oxidative balance, or proper functioning of shared biochemical pathways, rather than simply "antioxidant wealth" in carotenoids themselves (Hill *et al*., 2023; Pike *et al*., 2007; Hartley & Kennedy, 2004; Bertrand *et al*., 2006; McCoy *et al*., 2023; Hill, 2022).

PTERIDINIC RED AND OTHER PIGMENTS AS SENSORY TRAPS IN SEXUAL SELECTION

Pigment-based sexual signals often exploit how receivers' sensory systems are tuned to food, predators, or habitat light, potentially creating "sensory traps" where attractive cues in nonsexual contexts are co opted in mate choice (Petrescu-Mag & Proorocu 2022). The literature links pteridine based reds and other pigments to honest signaling, compensation for carotenoid limits, and to broader sensory drive and sensory trap frameworks in sexual selection across fishes, lizards, insects, spiders, and vertebrates**.**

MECHANISMS OF PTERIDINE AND OTHER PIGMENTARY REDS

Pteridines (especially drosopterins) generate bright yellow orange red colors in skin and scales of fishes and reptiles, and in butterfly wings, often alongside carotenoids and structural components (Weiss *et al*., 2012; Grether *et al*., 2001; Morehouse *et al*., 2007; Steffen & McGraw, 2009; Stuart-Fox *et al*., 2021; Erritouni *et al*., 2018). In female striped plateau lizards, orange reproductive color is entirely explained by drosopterin levels, not carotenoids (Weiss *et al*., 2012). Male guppies' orange spots contain both carotenoids and red drosopterins; pterin use increases where carotenoids are more abundant, shaping hue and potentially female preferences via pigment ratios rather than carotenoid amount alone (Grether *et al*., 2001). In brown anoles and other anoles, red–yellow dewlap and body coloration is partly or wholly pterin based, with sex specific pigment effects on spectral properties (Steffen & McGraw, 2009; Erritouni *et al*., 2018). Agamid lizards show a clear ecological partition: pteridine concentrations increase and carotenoids decrease in low productivity environments, and color among species is driven mainly by pteridines (Stuart-Fox *et al*., 2021). In pierid butterflies, pterin granules both scatter light and selectively absorb UV/visible wavelengths, producing highly chromatic wing patterns and sexual dichromatism important in mating (Morehouse *et al*., 2007). Pterin based red in Guinan toad headed lizards is produced by multiple pterins in xanthophores and genetically linked to pterin synthesis loci; carotenoids and pterins jointly underlie complex sexual coloration (Lu *et al*., 2024; Xiao *et al*., 2024) (Table 1).

Table 1.

Major pigment classes and their sexual signaling roles (summarized by Consensus 2026)

Pigment class / system	Main role in red/yellow signaling and selection context	References
Pterins (drosopterins) in lizards, fishes, butterflies	Endogenous reds/oranges, often linked to quality and ecological gradients; can relax or reshape carotenoid trade-offs, influence male competition and female signals	(Weiss *et al*., 2012; Lu *et al*., 2024; Xiao *et al*., 2024; Grether *et al*., 2001; Morehouse *et al*., 2007; Steffen & McGraw, 2009; Stuart-Fox *et al*., 2021; Erritouni *et al*., 2018)
Carotenoids in fishes, birds, lizards	Classic environmentally limited signals of condition; interact with pterins and melanin; linked to foraging and health and to sensory biases for orange/red	(Grether *et al*., 2001; Somjee *et al*., 2025; Grether *et al*., 2005; Griffith *et al*., 2006; Stuart-Fox *et al*., 2021)
Melanin (eumelanin, pheomelanin)	Dark or reddish traits with genetic and pleiotropic links to condition and behavior; may function as honest or context-dependent signals	(Roulin, 2016; Griffith *et al*., 2006)
Mixed pigment–structural systems	Combined structural scattering and pigment absorption shape chroma and UV contrasts important in mate recognition	(Somjee *et al*., 2025; Morehouse *et al*., 2007; Glenszczyk *et al*., 2021)

HONEST SIGNALS, CONDITION DEPENDENCE, AND ECOLOGICAL MODULATION

Indicator models predict that bright coloration remains honest when constrained by costs. Carotenoid based traits are classically constrained by dietary supply and physiological use (Grether *et al*., 2001; Somjee *et al*., 2025; Griffith *et al*., 2006). Pteridines, being synthesized de novo, might be cheaper, yet several studies suggest nontrivial costs or tight physiological links: pteridines are involved in immune and antioxidant functions, so allocation to ornaments may still trade off with other functions (Weiss *et al*., 2012; Xiao *et al*., 2024; Stuart-Fox *et al*., 2021; Erritouni *et al*., 2018). In striped plateau lizards, pterin based female orange reliably indicates reproductive quality despite not being carotenoid limited, potentially relaxing direct egg pigment trade offs while still tying signal expression to physiological state (Weiss *et al*., 2012). In Guinan toad headed lizards, pterin based red intensity predicts male–male contest success but not size, bite force, or testosterone, implying a cryptic quality axis, possibly metabolic or immunological (Xiao *et al*., 2024). Across Australian agamids, pteridines compensate for low carotenoid environments, but sexual dimorphism and sexual selection indices do not predict pigment concentrations, challenging strict carotenoid honesty paradigms and highlighting ecological productivity as a key driver (Stuart-Fox *et al*., 2021). Reviews of melanin based and carotenoid based signals show that melanic traits can also correlate with body condition via production, maintenance, or pleiotropic genetic links, undermining simplistic pigment specific honesty dichotomies (Roulin, 2016; Griffith *et al*., 2006). Novel pterin based orange body morphs in brown anoles show little effect on immune or performance traits and no strong female preference, but may reduce avian detectability, suggesting natural rather than sexual selection can maintain such traits (Erritouni *et al*., 2018).

SENSORY DRIVE, SENSORY BIASES, AND SENSORY TRAPS

The concept of a sensory trap—signals that mimic nonsexual cues to exploit pre existing receiver biases—is well developed for pheromones and courtship signals and provides a framework for pigment evolution as sensory traps (Popescu *et al*., 2025). In sea lampreys, males release a pheromone mimicking larval cues; females initially use this cue to locate spawning streams, then a pheromone antagonist (PZS) allows discrimination between larvae and males, turning a deceptive sensory trap into reliable sexual communication (Fissette *et al*., 2024; Buchinger *et al*., 2020). Theory and empirical work show that mimetic courtship signals can become exaggerated supernormal stimuli, limited by viability costs or reduced responsiveness at extremes; preferences originate from selection on responses to model cues, not directly on courtship signals (Christy, 1995). Sensory drive extends this logic to visual signals: in Lake Victoria cichlids and threespine sticklebacks, ambient light and visual sensitivity coevolve with male nuptial red/blue coloration and female preferences; divergence in photic environments produces correlated divergence in male color, female visual tuning, and mating preferences, contributing to reproductive isolation (Maan *et al*., 2006; Boughman, 2001). In guppies, female preference for orange male spots is genetically linked to a sensory bias for orange objects, probably connected to foraging on orange fruits; both the mate preference and the underlying bias are plastic with respect to carotenoid availability, implying that sexual selection has modified an ancestral foraging bias (Grether *et al*., 2005). These studies collectively illustrate how pigments like carotenoids and pterins can act as sensorial traps by aligning with sensory channels tuned by ecology (food color, habitat light), then being reshaped by sexual selection into mating signals. Similar sensory mismatches occur in visual systems: in the jumping spider *Saitis barbipes*, females lack a red photoreceptor and cannot distinguish male red from black patches chromatically; red and black instead generate achromatic contrast against backgrounds, so human perceived red ornamentation may not exploit a "red channel" but a contrast channel in spider vision (Glenszczyk *et al*., 2021). Wing pigmentation in damselflies and butterflies interacts with thermoregulation and UV signaling, indicating that pigment evolution is simultaneously shaped by physical environment, performance, and mate choice, consistent with sensory drive rather than purely arbitrary choice (Somjee *et al*., 2025; Morehouse *et al*., 2007; Svensson & Waller, 2013).

PIGMENT BASED SIGNALS WITHIN BROADER SEXUAL SELECTION AND ENERGETICS

Integrative work emphasizes that carotenoid and pterin signals reflect underlying cellular and metabolic processes, linking ornament expression to mitochondrial function, hormonal regulation, and energetic capacity (Somjee *et al*., 2025). Sexually selected traits (e.g., dewlaps, nuptial colors, enlarged structures) are embedded in networks of behavior, physiology, and environment, with pigment systems as one layer in a multiscale energetic phenotype (Roulin, 2016; Somjee *et al*., 2025; Svensson & Waller, 2013). In many taxa, sexual dimorphism in pterin deposition (e.g., male pierid wings richer in pterin granules than females, sex specific pigment contributions to anole dewlaps) underscores sex specific selection regimes and the potential for female ornaments (e.g., pterin based orange in *S. virgatus* females) to evolve under mate choice or social competition (Weiss *et al*., 2012; Morehouse *et al*., 2007; Steffen & McGraw, 2009; Svensson & Waller, 2013; Erritouni *et al*., 2018). At the same time, phylogenetic and comparative analyses in damselflies and lizards show that sexually selected pigmentation can elevate both speciation and extinction rates and need not increase ecological adaptation or species longevity, reinforcing that some pigment based "sensory traps" are evolutionarily labile and potentially risky (Svensson & Waller, 2013; Stuart-Fox *et al*., 2021).

COEVOLUTION OF MATE CHOICE AND PREDATOR PRESSURE

Mate choice and predation are tightly linked: traits that attract mates often also attract predators. The coevolutionary question is how preferences and signals evolve when sexual selection and predator pressure act simultaneously and feed back on population dynamics (Petrescu-Mag & Păsărin 2025).

CONCEPTUAL AND THEORETICAL FRAMEWORKS

Classical sexual selection theory predicts a trade-off: more conspicuous sexual signals increase mating success but also predation risk, so natural selection should cap signal elaboration (Zuk & Kolluru, 1998; Heinen-Kay *et al*., 2015). A recent quantitative genetic and population model explicitly embeds predator–prey dynamics in the evolution of sexual displays and shows that density dependent predation generates eco evolutionary cycles in sexually selected traits, maintains polymorphisms in displays, and alters prey cycles (Lerch & Servedio, 2023). This work demonstrates that predation does not just impose a static cost; predator–prey feedbacks continually reshape both display evolution and population dynamics (Lerch & Servedio, 2023). A broad meta analysis confirms that predators and parasitoids often prefer sexual signals in forced choice tests and that signaling increases realized predation in the wild, especially for acoustic and olfactory signals, whereas visual signals are more variable in cost (White *et al*., 2022). These findings support a general framework in which mate choice and predator pressure coevolve through shifting balances between attractiveness and detectability (Zuk & Kolluru, 1998; White *et al*., 2022; Heinen-Kay *et al*., 2015).

EMPIRICAL PATTERNS: WHEN PREDATION CONSTRAINS OR REDIRECTS MATE CHOICE

In Bahamas mosquitofish, males in predator free “blue holes” have evolved more orange dorsal fins; field and lab tests show these orange fins are both more attractive to females and more conspicuous to predatory fish, providing direct evidence for a trade-off between natural and sexual selection on a visual signal (Heinen-Kay *et al*., 2015). Strawberry poison frogs exhibit aposematic and cryptic colour morphs; experiments with avian predators show cryptic females incur higher predation risk when associating with conspicuous aposematic males, implying direct selection on female choice that favours assortative mating by colour and can reinforce divergence among populations (Marzal *et al*., 2016). In female ornamented jumping spiders, UV induced fluorescence strongly increases male preference but simultaneously elevates predation by spider eating *Portia*, demonstrating a clear survival cost to a female sexual trait (Zhou *et al*., 2026). Some systems show that relaxed predator pressure permits the evolution of highly conspicuous signals: an Amazonian weakly electric fish living under low electroreceptive predation exhibits permanently conspicuous electric organ discharges whose exaggeration appears unconstrained by predators and is instead shaped by mate choice and intrasexual competition (Cola *et al*., 2025).

BEHAVIOURAL PLASTICITY: MAINTAINING CHOICE UNDER RISK

Predator pressure can change how, but not whether, choosy individuals express preferences. In eastern gray treefrogs, females exposed to simulated predators maintain their preference for attractive calls yet approach preferred males more slowly, with more cautious trajectories and more escape attempts, supporting a “behavioural adjustment” rather than “mate choice flexibility” model (Feagles & Höbel, 2022). In lesser waxmoths, bat calls induce males to temporarily fall silent and females to freeze, and both sexes adjust signalling and preference decisions depending on social context and risk (Edomwande & Barbosa, 2020). A related study in the same species shows that males with more attractive songs resume calling sooner after predator cues, taking greater risks than unattractive males; this suggests that condition, life history costs of attractiveness, or risk taking itself as a sexually selected trait can decouple predictions of simple “asset protection” models (Cordes *et al*., 2014). In túngara frogs, variation in call elaboration and in defensive swatting against eavesdropping midges cascades through the communication network: defensive strategies against micropredators alter how females and frog eating bats rank males, creating context dependent shifts in relative attractiveness and predation risk (Leavell *et al*., 2025). Fiddler crabs provide a contrasting example where predation can actually strengthen mate choice: under higher bird predation risk, females show stronger preference for males with sand “mounds” that guide them quickly into burrows, so the sexual signal yields direct survival benefits to choosy females (Kim *et al*., 2007).

EVOLUTIONARY OUTCOMES: FROM SAFER STRATEGIES TO RISKIER TRAITS

Predator pressure does not uniformly select for “safer” mates or signals across populations. In the field cricket *Gryllus lineaticeps*, both females and parasitoid flies prefer higher chirp rates. Contrary to the antagonistic selection hypothesis, high risk populations (with intense parasitoid eavesdropping) have evolved faster, riskier male songs and stronger female preferences. This pattern is consistent with a “late season parasitism” scenario, where selection favours increased reproductive investment before parasitoid activity peaks, even at the cost of higher risk (Beckers & Wagner, 2018). A large scale meta analysis likewise reveals high variance: although predators often exploit sexual signals, contexts in which signalling does not increase, or even reduces, predation are common, indicating that ecological details (signal modality, habitat structure, predator sensory systems, temporal patterns of risk) strongly mediate coevolutionary trajectories (Zuk & Kolluru, 1998; White *et al*., 2022; Leavell *et al*., 2025; Beckers & Wagner, 2018).

INTERACTION OF MATE CHOICE, PREDATION AND OTHER ECOLOGICAL AXES

Predation interacts with additional ecological factors that themselves coevolve with sexual selection. Work on thermal ecology argues that temperature regimes can shape both the costs and efficacy of sexual traits, while mating interactions can impose selection on thermal physiology, creating reciprocal evolutionary feedbacks between climatic adaptation and sexual signals (Leith *et al*., 2022). Eco evolutionary feedbacks in predator–prey systems more generally can maintain sexual reproduction through Red Queen dynamics, as shown experimentally in a rotifer–algae system where coevolutionary cycles in defense and attack traits maintain high rates of sex in predators (Haafke *et al*, 2016). At a broader conceptual scale, contemporary syntheses of sexual selection stress that mate choice mechanisms can evolve in response not only to benefits or costs tied to sexual traits, but also to direct viability effects such as predation and coercion risk, with choosers adjusting preferences and mating tactics to balance autonomy, safety and reproductive payoff (Rosenthal & Ryan, 2022; Verpooten, 2024) (Table 2).

Table 2.

Examples of mate choice–predation interactions (summarized by Consensus 2026)

System / trait	Effect of predation on signals or choice	Coevolutionary / evolutionary implication	References
Bahamas mosquitofish, orange dorsal fin	Orange fins attract females and predatory fish more than drab fins	Trade-off maintains divergence between high- and low-predation populations	(Heinen-Kay *et al*., 2015)
Strawberry poison frog colour morphs	Cryptic females near aposematic males detected faster by predators	Direct selection on female choice favours colour-assortative mating	(Marzal *et al*., 2016)
Gray treefrog female phonotaxis	Choosiness unchanged; approach becomes slower and less conspicuous	Sexual selection maintained despite high predation risk via behavioural plasticity	(Feagles & Höbel, 2022)
Lesser waxmoth acoustic signalling	Predator cues suppress signalling; female preference lost when risk is higher	Risk-dependent signalling and preferences adjust to predator eavesdropping	(Edomwande & Barbosa, 2020; Cordes *et al*., 2014)
Field cricket with parasitoid fly	High-risk populations evolve faster songs and stronger preference	Seasonal parasitism favours riskier traits (late-season parasitism hypothesis)	(Beckers & Wagner, 2018)
Jumping spiders' UV fluorescence (females)	Fluorescent females preferred by males, but more often attacked by predators	Female ornament coevolves under opposing sexual and natural selection	(Zhou *et al*., 2026)
Fiddler crab sand mounds	Under high predation, mounded males become more attractive	Preference for sexual signal yields direct survival benefits to choosy females	(Kim *et al*., 2007)
Electric fish conspicuous EODs	Low electroreceptive predation allows highly conspicuous electric displays	Relaxed predation enables signal exaggeration driven by mate choice	(Cola *et al*., 2025)
Cross-taxon meta-analysis of signal costs	Predators strongly prefer sexual signals; costs high for acoustic/olfactory, variable for visual	Context-dependent exploitation shapes diversity of signalling strategies	(Zuk & Kolluru, 1998; White *et al*., 2022)

CONCLUSIONS

This review demonstrates that sexual selection in vertebrates is a multifaceted and context-dependent evolutionary force, whose outcomes emerge from the interaction between physiological mechanisms, ecological pressures, and behavioral processes. The synthesis of theoretical and empirical evidence confirms that sexually selected traits, particularly pigment-based signals such as carotenoid- and pteridine-derived coloration, function as informative indicators of individual condition, yet their reliability is maintained through a complex interplay of resource allocation trade-offs, metabolic constraints, and genetic regulation.

A central conclusion is that no single explanatory framework fully captures the evolution of these traits. Both handicap-based and index-based models contribute to understanding signal honesty, while recent findings highlight the importance of broader physiological integration, including links to mitochondrial function, antioxidant systems, and hormonal regulation. Furthermore, the existence of alternative pigment systems, such as pteridines, challenges traditional carotenoid-centered paradigms and underscores the role of ecological context in shaping signal evolution.

Importantly, the review clarifies that sexual selection cannot be disentangled from natural selection, particularly in the presence of predation. The coevolution of mate choice and predator pressure generates dynamic trade-offs between attractiveness and survival, leading to diverse evolutionary outcomes ranging from constrained signal expression to exaggerated traits under relaxed predation. These interactions are further modulated by behavioral plasticity, sensory biases, and environmental factors such as light conditions and temperature, reinforcing the view that sexual selection operates within a broader eco-evolutionary framework.

At macroevolutionary scales, sexual selection contributes to phenotypic diversity but exerts only a modest influence on speciation, acting as one of several interacting drivers rather than a dominant force. Overall, the evidence supports the conclusion that sexual selection in vertebrates is best understood as an integrative process, where signals, preferences, physiology, and ecological context coevolve, shaping both individual fitness and long-term evolutionary patterns in complex and often non-linear ways.

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Ioan Valentin Petrescu-Mag contributed to all aspects of the work.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

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