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AGGRESSION, SEXUAL SELECTION, AND NEUROENDOCRINE REGULATION IN *BETTA SPLENDENS*: AN INTEGRATIVE MINI-REVIEW

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Abstract: The genus *Betta* comprises a diverse group of Southeast Asian freshwater fishes exhibiting remarkable variation in ecology, reproductive strategies, and behavior. Among them, *Betta splendens* has emerged as a key model for studying aggression and sexual selection. This mini-review synthesizes current knowledge on the behavioral, endocrine, and genetic mechanisms underlying aggression in *B. splendens*, emphasizing its role as both a territorial and sexually selected trait. Evidence indicates that aggression is modulated by environmental conditions, developmental context, and domestication history, with strong links to endocrine pathways involving cortisol and 11-ketotestosterone. Artificial selection for fighting has further shaped aggressive phenotypes, revealing shared genetic architectures across sexes and highlighting the plasticity of this trait. Additionally, aggression is intricately connected to courtship and mate choice, where females prefer males exhibiting optimal combinations of dominance, coloration, and controlled aggression. Genomic and transcriptomic studies support a polygenic basis for aggression, involving neuroactive signaling and steroid-related pathways. Overall, *B. splendens* represents a powerful model for understanding the co-evolution of aggression and sexual selection across multiple biological levels, from gene expression to complex behavior.

Keywords: aggression, neuroendocrinology, cortisol, 11-ketotestosterone, artificial selection, domestication, mate choice, behavioral ecology, genomics.

INTRODUCTION

The genus *Betta* comprises small freshwater fishes in the gourami family (Osphronemidae), best known globally through the Siamese fighting fish *Betta splendens* (Petrescu-Mag *et al*., 2013), but actually including over 70 species distributed across Southeast Asia. Many species are localized endemics inhabiting fragile wetlands, peat swamps, blackwater streams, and even brackish habitats, and are increasingly threatened by habitat loss, over-collection, and urbanization (Helmizuryani *et al*., 2026; Panijpan *et al*., 2020; Nur *et al*., 2022; Khanati *et al*., 2024; Khairul *et al*., 2024; Fahmi *et al*., 2020).

Taxonomically, *Betta* is diverse and still being revised. Species are grouped based on morphology, coloration, and reproductive mode; examples include the splendens, coccina, waseri, and pugnax groups, among others (Helmizuryani *et al*., 2026; Panijpan *et al*., 2020; Kowasupat, 2012; Fahmi *et al*., 2020). DNA barcoding and multilocus phylogenetic work have revealed cryptic diversity, such as multiple lineages within the *Betta smaragdina* complex and overlooked species related to the *B. splendens* group in Thailand and Indonesia (Kowasupat *et al*., 2014; Sriwattanarothai *et al*., 2010; Kowasupat, 2012; Fahmi *et al*., 2020). Some new species (e.g., *B. siamorientalis*, *B. mahachaiensis*, *B. stiktos*) have been described in the last decades, and further hidden diversity is likely (Kowasupat *et al*., 2014; Sriwattanarothai *et al*., 2010; Kowasupat, 2012; Fahmi *et al*., 2020; Syarif *et al*., 2023; Saputra *et al*., 2024; Pertiwi *et al*., 2025).

Betta species show striking variation in reproductive strategies. Two major forms of paternal care are recognized: bubble-nest builders, which construct floating nests in shallow, stagnant waters (Pop & Petrescu-Mag 2004ab), and mouthbrooders, in which males (and in some cases females) incubate eggs in the mouth (Panijpan *et al*., 2020; Nur *et al*., 2022; Budi *et al*., 2025; Fahmi *et al*., 2020). These strategies correlate with life history traits and have been key to understanding the evolution of parental care within the genus (Nur *et al*., 2022; Budi *et al*., 2025; Fahmi *et al*., 2020).

Beyond their ornamental importance, bettas are emerging genomic and behavioral models. High-quality genomes for *B. splendens* and several congeners enable studies of species radiation, aggression, coloration, and conservation genetics across the genus, supporting efforts to manage declining wild populations and design breeding programs for endangered species (Helmizuryani *et al*., 2026; Srikulnath *et al*., 2021; Zhang *et al*., 2021; Kwon *et al*., 2022; Nguyen *et al*., 2025; Fahmi *et al*., 2020).

The aim of this mini-review is to integrate current behavioral, endocrine, and genomic evidence to elucidate the mechanisms underlying aggression in *Betta splendens* and to examine how this trait interacts with sexual selection, environmental factors, and domestication processes.

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AGGRESSION AND SEXUAL SELECTION IN BETTA FISH (*BETTA SPLENDENS*)

Aggression in *Betta splendens* is both a territorial strategy and a sexually selected trait tightly linked to courtship, mate choice and reproductive success (see more about sexual selection in Petrescu-Mag, 2025). Recent work combines behavioral, endocrine and genetic approaches, showing how domestication, environment and sex-specific factors shape this link.

AGGRESSION, ENVIRONMENT, AND SEXUAL MATURATION

Bettas raised in enriched social groups show markedly lower adult aggression than fish isolated in poor environments, and the timing of isolation (juvenile vs. subadult) alters both aggressive patterns and sexual maturity indices (gonadosomatic index, sex steroids) in a sex specific way (Iwata *et al*., 2021). Cortisol and 11 ketotestosterone (11 KT) covary with aggression and reproductive state, supporting a physiological bridge between stress, aggression and sexual development (Iwata *et al*., 2021; Agues-Barbosa *et al*., 2022). Long term fluoxetine exposure reduces aggressive motivation and movement, indicating serotonergic modulation of aggressive arousal rather than just motor output (Greene & Szalda-Petree, 2021).

DOMESTICATION, ARTIFICIAL SELECTION AND ENDOCRINE CORRELATES

Centuries of artificial selection for staged fights produced "fighter" strains that are more aggressive than wild type males and show distinct fight display structure and higher activity (Ramos & Gonçalves, 2019). This selection also co elevates female aggression and reveals strong cross sex correlations in aggressive behavior, implying shared genetic and physiological bases (Ramos & Gonçalves, 2019). Endocrinologically, fighter males exhibit lower baseline and post fight cortisol, but comparable or higher post fight 11 KT relative to wild types, consistent with a combination of high androgens and low corticosteroids in highly aggressive lines (Ramos & Gonçalves, 2022). Genomic and transcriptomic studies identify polygenic signals and sex biased expression in neurotransmitter and steroid related genes implicated in aggression and sex differences (Zhang *et al*., 2021; Yang *et al*., 2018).

LINKS BETWEEN SELECTION, AGGRESSION AND ENDOCRINE TRAITS

Synthetic data on comparative patterns linking aggression, hormones and selection in *Betta splendens* are shown in Table 1.

Table 1.

Comparative patterns linking aggression, hormones and selection in *Betta splendens* (Consensus 2025)

Comparison / context	Aggression pattern	Key hormones / genes	References
Fighter vs. wild-type males	Fighters more aggressive, higher activity	Lower cortisol, higher post-fight 11-KT	(Ramos & Gonçalves, 2019; Ramos & Gonçalves, 2022)
Group-raised vs. isolated (timing of isolation)	Isolation increases adult aggression	Cortisol, 11-KT, estradiol differ by group	(Iwata *et al*., 2021)
Nest-builder vs. non-builder males	Non-builders most aggressive	Higher cortisol; variable 11-KT	(Agues-Barbosa *et al*., 2022)
Genomic / transcriptomic sex differences	Sexual dimorphism in aggression potential	Sex-biased htr, drd, gabr, steroid genes	(Zhang *et al*., 2021; Yang *et al*., 2018).

AGGRESSION, COURTSHIP, AND FEMALE MATE CHOICE

Aggressive and courtship displays are tightly intertwined. Dominant males, established through agonistic interactions, gain better access to space, nest building, females and reproductive opportunities (Bronstein, 1984). Male aggression can conflict with parental and mating effort: intruder males visually stimulate breeder aggression and reduce reproductive efficiency, even though males protect eggs and fry by nest tending and fungus removal (Bronstein, 1982).

Female bettas use both aggression related signals and visual traits when choosing mates. Females eavesdrop on male fights and tend to prefer winners, linking male–male contest outcomes to intersexual selection (Brownell *et al*., 2014). Behavioral profiling shows males score higher on aggression, females on boldness, and both sexes' behavioral types shape mate choice: females prefer bold red and nonaggressive red males, suggesting selection for combinations of conspicuous coloration and moderated aggression, possibly associated with better paternal care potential (Oliveira *et al*., 2021; Brownell, 2014). Female signaling (high contrast vertical barring with slack fins) reduces male attacks and is part of a courtship dialogue where male aggression is "tested" but then modulated to allow spawning (Bronstein, 1982; Rainwater, 1966).

GENETIC AND NEUROENDOCRINE BASES OF SEX-LINKED AGGRESSION

Sexual dimorphism in aggression arises from sex biased brain and endocrine pathways. Transcriptomic analysis reveals thousands of sex biased genes, including serotonin, dopamine and GABA receptors and steroidogenic enzymes, mapped to pathways for neuroactive ligand–receptor interaction, steroid biosynthesis and estrogen signaling, all plausible modulators of aggression and reproductive behavior (Yang *et al*., 2018). Genomic association studies support a polygenic architecture of aggression involving neural genes, set against a complex domestication history with introgression among wild and ornamental forms (Zhang *et al*., 2021). Reviews emphasize *Betta* as a promising model for dissecting sex specific aggression circuits and how artificial selection for fighting has exaggerated male and female

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aggressive phenotypes beyond wild levels (Yue *et al*., 2022; Lichak *et al*., 2022; Pandolfi *et al*., 2021).

CONCLUSIONS

Across *Betta splendens*, aggression emerges as a complex, integrative trait rather than a simple behavioral output. It is deeply embedded in the species' reproductive biology, influencing sexual maturation, access to territories and mates, as well as success in both intra- and intersexual selection contexts. The reviewed evidence consistently shows that aggressive behavior is tightly coupled with endocrine regulation—particularly involving cortisol and 11-ketotestosterone—highlighting a physiological axis that links stress responsiveness, reproductive readiness, and behavioral expression.

Importantly, aggression in this species is highly plastic. Environmental conditions, such as social enrichment or isolation during critical developmental windows, can significantly modulate adult aggression levels and associated reproductive parameters. Pharmacological interventions, such as serotonergic modulation via fluoxetine, further confirm that aggression is not fixed but dynamically regulated by neuroendocrine mechanisms.

At the same time, long-term artificial selection for fighting has led to the genetic consolidation of heightened aggression, producing strains with distinct behavioral, physiological, and endocrine profiles. These domestication-driven changes extend beyond males, affecting females as well, and suggest a shared genetic architecture underlying aggression across sexes. Genomic and transcriptomic data reinforce this view, indicating a polygenic basis involving neural signaling pathways and steroid-related genes.

From a sexual selection perspective, aggression plays a dual and nuanced role. While it enhances male competitive ability and dominance, it must be balanced with courtship and parental investment to maximize reproductive success. Female mate choice reflects this balance: females do not simply prefer the most aggressive males, but rather those exhibiting optimal combinations of coloration, boldness, and controlled aggression. This indicates that excessive aggression may be maladaptive if it interferes with courtship signaling or parental care.

Overall, the synthesis of behavioral, endocrine, and genomic evidence supports a co-evolutionary framework in which aggression and sexual selection are tightly intertwined. In *Betta splendens*, these interactions operate across multiple biological levels—from gene expression and hormone regulation to observable behavior—making this species a powerful model for understanding how complex behavioral traits evolve under both natural and artificial selection pressures.

AUTHORS CONTRIBUTIONS

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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