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BEHAVIORAL PLASTICITY, HONEST SIGNALING, AND PARENTAL INVESTMENT IN *BETTA SPLENDENS*: AN INTEGRATIVE REVIEW ACROSS ENVIRONMENTAL AND EVOLUTIONARY CONTEXTS

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Abstract: This review examines behavioral plasticity, visual signaling, and parental strategies in *Betta splendens* as an integrative model of context-dependent behavior. Adaptation to hypoxic and turbid environments, supported by the labyrinth organ, enables energetically costly behaviors such as aggression and courtship, while environmental and developmental factors shape behavioral variation. Social context and domestication further drive divergence in aggression and stress responses. Visual displays and coloration function as condition-dependent signals with measurable energetic costs, consistent with honest signaling theory, and are strongly influenced by environmental conditions such as turbidity and light. Male parental care, expressed through bubble nesting or mouthbrooding, reflects adaptive trade-offs between current and future reproduction. Overall, *Betta* illustrates how environmental, physiological, and evolutionary processes interact to generate flexible life-history strategies.

Keywords: visual communication, parental care, sexual conflict, phenotypic plasticity, fish behavior, evolutionary ecology.

AIM OF THE STUDY

The aim of this review is to integrate current empirical and theoretical insights on behavioral plasticity, visual signaling, and parental investment in *Betta splendens*, in order to elucidate how environmental conditions, developmental history, and evolutionary processes interact to shape behavior and life-history strategies in this model species.

BEHAVIORAL PLASTICITY IN *BETTA* FISHES ACROSS CONTRASTING ENVIRONMENTS

Betta species inhabit shallow, often hypoxic and turbid waters and have been intensively domesticated, providing a good system to discuss phenotypic plasticity in behavior. The available work on *Betta splendens* and closely related anabantoids, plus comparative fish studies, shows that oxygen, social environment, turbidity, and domestication all shape aggression, exploration, and stress-coping styles.

ENVIRONMENTAL OXYGEN AND THE LABYRINTH ORGAN

The labyrinth organ allows anabantoids to extract oxygen from air and persist in hypoxic and polluted water, which has "a dramatic influence" on territorial, mating and parental behaviors (Tate *et al.*, 2017; Szabó *et al.*, 2023). Air breathing supports energetically costly activities (aggressive displays, courtship) in habitats where dissolved oxygen is low (Tate *et al.*, 2017). Labyrinth development itself is plastic: in paradise fish, preventing surface access delays vascularization and lamella development, which then "catches up" once air access is restored, indicating environment dependent organ ontogeny (Szabó *et al.*, 2023). More generally, fish in fluctuating do regimes use behavioral strategies such as habitat avoidance, redistribution, or reduced activity to balance oxygen acquisition with other demands (Fulford *et al.*, 2024; Blewett *et al.*, 2022; Earhart *et al.*, 2022).

WATER QUALITY AND BEHAVIOR

Across fishes, low dissolved oxygen and poor water quality alter swimming, schooling, feeding, aggression, and exploration, often inducing avoidance and anxiety like behaviors (Fulford *et al.*, 2024; Zhang *et al.*, 2024; Blewett *et al.*, 2022; Earhart *et al.*, 2022). These responses are classic examples of reversible phenotypic plasticity modulating exposure to hypoxic patches (Fulford *et al.*, 2024; Blewett *et al.*, 2022).

SOCIAL ENVIRONMENT, DENSITY AND AGGRESSION/EXPLORATION

In *Betta splendens*, rearing environment strongly shapes aggression. Fish raised from hatching in socially and physically enriched groups show much lower adult aggression than those isolated in poor environments; the timing of isolation (juvenile vs. subadult) produces distinct threat vs. fight profiles and sex specific effects, and also alters cortisol and sex steroid levels (Iwata *et al.*, 2021). This parallels enrichment studies in other fishes where complex/low density environments reduce aggression and risk taking and enhance anti predator behavior and cognitive traits, mediated via HPI-axis activity and neurogenesis (Zhang *et al.*, 2022; Zhang *et al.*, 2020). Density effects on aggression and exploration are also evident in crayfish and social fishes, where higher density tends to produce bolder, more exploratory and more

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aggressive phenotypes, again interpreted as environmentally induced personality shifts (Herczeg *et al*., 2015; Su *et al*., 2024; Salas *et al*., 2022; Asriyana *et al*., 2023).

DOMESTICATION, INVASIVE VS DOMESTIC *BETTA*

Domesticated “fighter” *Betta* strains are more aggressive than wild types and show a proactive coping style: lower cortisol responses to novel environments, rapid immobility under confinement, and altered stress physiology (Verbeek *et al*., 2008; Tate *et al*., 2017). In a recent invasion, wild *Betta splendens* descended from ornamental lines differ behaviorally from domestic conspecifics: invaders are more active, eat fewer prey items, and show different repeatability and trait correlations in foraging and activity, indicating rapid behavioral divergence in a novel environment (Brand *et al*., 2021). As has also been observed in other animal groups (Nursyahran *et al*., 2023; Polishchuk *et al*., 2025), domestication in anabantoids has also radically altered morphology and aggression, raising questions about correlated changes in air breathing behavior and energetics (Tate *et al*., 2017; Brand *et al*., 2021).

TURBIDITY AND SENSORY/EXPLORATORY PLASTICITY

Work in zebrafish shows that chronic or periodic turbidity drives sensory plasticity: fish with turbid experience down weight vision and rely more on olfaction in foraging, while aggression and shoaling depend more on immediate context than on prior turbidity history (Bhat *et al*., 2015; Suriyampola *et al*., 2018; Singh & Bhat, 2026). Long term turbidity exposure changes variance–covariance structures and increases behavioral flexibility under sensory uncertainty, especially in aggression–boldness links (Singh & Bhat, 2026). Turbidity and suspended solids also modify depth use and can cause mortality via respiratory impairment in other fishes (Kang *et al*., 2025). These data suggest that *Betta* in naturally turbid, shallow habitats may flexibly adjust exploration and cue use, while relying on air breathing to mitigate oxygen constraints.

DISCUSSION ON BEHAVIORAL PLASTICITY

Across studies, *Betta splendens* fits a broader pattern where behavior is a highly plastic phenotype tuned by oxygen regime, habitat structure, social density, and domestication state. The labyrinth organ is both a product and an enabler of plasticity: its development is environmentally modulated (Szabó *et al*., 2023), and its function underpins aggressive and territorial behaviors in hypoxic habitats (Tate *et al*., 2017). Social and physical enrichment in early life can canalize lower adult aggression and alter endocrine profiles (Iwata *et al*., 2021; Zhang *et al*., 2022; Zhang *et al*., 2020), while domestication and invasion rapidly reshape coping styles, activity, and foraging (Verbeek *et al*., 2008; Brand *et al*., 2021; Tate *et al*., 2017). Turbidity and other water quality factors add a sensory and metabolic dimension, restructuring variance and trait covariances rather than just shifting mean behavior (Bhat *et al*., 2015; Suriyampola *et al*., 2018; Singh & Bhat, 2026; Zhang *et al*., 2024; Blewett *et al*., 2022). Taken together, *Betta* behavioral strategies can be interpreted as context dependent expressions of a flexible behavioral phenotype, constrained and guided by respiratory morphology, developmental history, and current ecological conditions (Syarif *et al*., 2023; Khairul *et al*., 2024; Saputra *et al*., 2024; Pertiwi *et al*., 2025) (Table 1).

Table 1.

Environmental drivers of behavioral plasticity in fishes, including *Betta splendens* (Consensus, 2025)

Factor / context	Main behavioral effects (generalized)	References
Hypoxia / low DO	Increased air-breathing, habitat shifts, reduced activity, altered territoriality	(Fulford *et al*., 2024; Tate *et al*., 2017; Szabó *et al*., 2023; Blewett *et al*., 2022; Earhart *et al*., 2022)
Early social enrichment	Lower adult aggression, modified stress hormones, group-housing possible	(Iwata *et al*., 2021; Zhang *et al*., 2022; Zhang *et al*., 2020)
High density / crowding	More exploration and aggression, bolder phenotypes in several taxa	(Herczeg *et al*., 2015; Su *et al*., 2024; Salas *et al*., 2022)
Turbidity / sensory noise	Shift from visual to olfactory cues, flexible aggression–boldness covariation	(Bhat *et al*., 2015; Suriyampola *et al*., 2018; Singh & Bhat, 2026; Kang *et al*., 2025)
Domestication / invasion	Heightened aggression, proactive coping, altered activity/foraging	(Tate *et al*., 2017; Verbeek *et al*., 2008; Brand *et al*., 2021).

VISUAL SIGNALLING AND EVOLUTIONARY COSTS IN *BETTA SPLENDENS*

Siamese fighting fish are a classic model for studying how conspicuous visual signals (flaring, fin spreading, intense colour) mediate aggression and how these signals might be constrained by metabolic costs, sensory environments and mechanisms of honest signalling.

VISUAL SIGNALLING AND INFORMATION CONTENT IN *BETTA*

Male *Betta* uses stereotyped flare displays (opercular gill cover erection, fin spreading, lateral displays) as ritualized aggression; individuals that flare less typically surrender, and display phases can escalate to biting, showing that displays convey information about fighting motivation and likely outcome (Everett *et al*., 2025; Castro *et al*., 2006). *Betta* is strongly visually driven: aggressive displays can be elicited purely by visual stimuli such as mirrors, models or animations, and the visual image of a displaying male functions as a powerful reinforcer for operant behaviour (Everett *et al*., 2025; Thompson & Sturm, 1965; Thompson, 1963). *Betta* integrates shape and motion into holistic percepts, showing complex visual analysis of socially relevant signals (Neri, 2019). Colour also carries information: blue finned males, a wild type phenotype, are more aggressive and perform longer lateral displays, likely because blue travels better in the murky waters they inhabit (McGoran *et al*., 2020).

ARE *BETTA* SIGNALS "HONEST"?

Game theoretical models of honest signalling show that honesty can be maintained by high potential costs of cheating, not necessarily by high realized handicaps for honest signallers (Számadó, 2011; Higham, 2013). Signals may honestly reflect multiple underlying qualities via multi component displays (Johnstone, 1995) or evolve as discrete "all or nothing" stereotyped displays under perceptual error, as seen in many ritualized displays (Johnstone, 1994). Empirical work in other fish shows that dynamic colour signals (e.g. facial stripes) can honestly indicate aggressive intent and dominance, with honesty enforced by social punishment of cheaters rather than intrinsic metabolic cost (Bachmann *et al*., 2017). In *Betta*, display duration predicts contest outcome and display performance is measurably costly (Castro *et al*., 2006), supporting the idea that flaring and fin displays are at least partly honest signals of current condition or motivation under a costly signalling framework (Castro *et al*., 2006; Everett *et al*., 2025; McGoran *et al*., 2020).

METABOLIC AND ENERGETIC COSTS OF DISPLAYS AND COLOUR

In *Betta*, oxygen consumption rises with time spent erecting gill covers and spreading the dorsal fin during mirror stimulation, demonstrating direct metabolic costs of aggressive display (Castro *et al*., 2006). Winners and losers do not differ in metabolic rate during the fight, but winners show higher oxygen consumption during the following night, indicating delayed physiological costs of intense display and winning (Castro *et al*., 2006). Lateral displays are described as less energetically costly than opercular flaring, suggesting multiple display types may trade off intensity versus cost (McGoran *et al*., 2020).

Work on other fish indicates that colour change itself can be energetically expensive: guppies that darken to match backgrounds increase food intake to cover the energetic costs while maintaining growth, and post change they select habitats and shoals that match their coloration, implying both energetic and opportunity costs of maintaining or altering colour (Rodgers *et al*., 2013). Theoretical models of warning coloration show that pigments and chemical defences can compete for shared resources (energy, antioxidants), making bright colour a handicap-like honest index of underlying toxicity or condition when resources are limiting (Blount *et al*., 2008). These frameworks support the idea that maintaining intense *Betta* coloration and performing repeated flares can be energetically and physiologically costly, helping to stabilize signal honesty (Castro *et al*., 2006; Rodgers *et al*., 2013; Blount *et al*., 2008; Számadó, 2011; Higham, 2013).

ILLUSTRATIVE OVERVIEW OF COSTS AND HONESTY

Illustrative overview of costs and honesty are presented in Table 2.

Table 2.

Energetic, ecological, and social costs underlying visual signal honesty (Consensus, 2025)

Aspect of signal	Evidence in *Betta* / fish	Link to honesty / handicap	References
Flaring & fin spread	Raise oxygen consumption; winners show elevated post-fight metabolism	Realized energetic costs make intense display harder to sustain for low-condition males	(Castro ***et al***., 2006; Everett ***et al***., 2025; mcgoran ***et al***., 2020)
Colour & pattern	Blue fins linked to higher aggression in murky habitats; strong colour discrimination	Colour likely tuned to maximize range and detectability; may correlate with aggressiveness/condition	(McGoran ***et al***., 2020; Neri, 2019; Thompson & Sturm, 1965; Thompson, 1963)
Dynamic colour change	Background-matching colour change in guppies increases food intake needs	Colour maintenance/change has energetic and opportunity costs, supporting handicap-like honesty	(Rodgers ***et al***., 2013; Blount ***et al***., 2008)
Social enforcement	Retaliation maintains honesty of dynamic facial signals in cichlids	Honesty via social costs rather than large intrinsic metabolic handicaps	(Bachmann ***et al***., 2017; Számadó, 2011; Higham, 2013).

ENVIRONMENTAL CONTEXT: TURBIDITY, LIGHT AND VISUAL ECOLOGY

Betta naturally inhabits murky, shallow waters, and there is evidence that blue fin coloration, common in wild type males, is favoured because blue wavelengths propagate better through such turbid habitats, enhancing visibility of signals (McGoran *et al*., 2020). Studies in other fish show how light environment shapes both sensory systems and signalling traits. In centrarchids, opsin expression (sensory side) is relatively robust across contrasting light environments, whereas body reflectance (signalling side) is more flexible and species specific, suggesting signalling traits often evolve more readily than receptors

(Bertinetti *et al.*, 2025). In East African crater-lake cichlids, rapid ecological divergence along depth/light gradients involves shifts in cone opsin expression alongside changes in male colour signals (e.g. deeper red egg spots) that match visual models of signal efficiency in new light environments (Carruthers *et al.*, 2025).

Turbidity alters luminance, hue, chroma and contrast in water, and different turbidity sources (algae vs minerals) have distinct effects on ambient light, implying that the selective landscape for visual signals is highly source and level dependent (Garcia *et al.*, 2025). Behaviourally, adult fish exposed to periodic turbidity can shift reliance from visual to olfactory cues in foraging, while high turbidity reduces movement efficiency in visually guided reef fish (Suriyampola *et al.*, 2018; Newport *et al.*, 2021). Developmentally, turbidity can induce plastic changes such as larger eyes and optic tecta in cichlids, particularly in young fish, indicating that visual systems and possibly signalling can adjust to degraded light environments within a lifetime (Tiarks *et al.*, 2024). For a highly visual, display driven species such as *Betta*, these findings suggest that hydrological changes (turbidity, colour of water, depth, background) will strongly influence which colours, patterns and movement components are effective signals and thus how visual signals evolve or lose reliability (Neri, 2019; Everett *et al.*, 2025; McGoran *et al.*, 2020; Bertinetti *et al.*, 2025; Tiarks *et al.*, 2024; Garcia *et al.*, 2025; Carruthers *et al.*, 2025; Newport *et al.*, 2021; Suriyampola *et al.*, 2018).

DISCUSSION ON VISUAL SIGNALLING AND EVOLUTIONARY COSTS

Taken together, work on *Betta splendens* and comparative fish systems indicates that *Betta*'s flamboyant flare displays and intense colours fit well within honest signalling theory, but not necessarily in the strict classic sense of large permanent handicaps. In *Betta*, aggressive visual displays are energetically costly in real time and leave detectable physiological traces after contests, and display effort predicts contest outcome, consistent with signals that reflect current condition and motivation (Castro *et al.*, 2006; Everett *et al.*, 2025). The existence of a cheaper lateral display alongside more expensive opercular flaring supports the idea of multi component signals that map onto different aspects of quality (e.g. stamina vs escalation willingness) as modelled in multi signal games (Johnstone, 1995; McGoran *et al.*, 2020). Theories emphasizing potential rather than realized costs of cheating, and social enforcement of honesty, highlight that honest *Betta* signalling may be maintained by a combination of metabolic costs, physical constraints, and social retaliation, rather than by large, continuous handicaps alone (Számadó, 2011; Johnstone, 1994; Higham, 2013; Bachmann *et al.*, 2017).

Environmentally, *Betta*'s visual system and blue biased fin colours appear tuned to murky, shallow habitats, echoing broader patterns where visual signals evolve to maximize contrast and detectability in local light environments (McGoran *et al.*, 2020; Bertinetti *et al.*, 2025; Carruthers *et al.*, 2025). Variability in turbidity and light spectra can change how signals propagate and are perceived, favouring certain hues (e.g. short wavelengths) and potentially driving divergence in both sensory tuning and signalling traits (Garcia *et al.*, 2025; Tiarks *et al.*, 2024; Carruthers *et al.*, 2025; Newport *et al.*, 2021; Suriyampola *et al.*, 2018). Plasticity in eyes and brains in response to turbidity implies that *Betta* populations could respond developmentally to changing conditions, but reliance on visual aggression also makes them vulnerable to anthropogenic shifts that degrade underwater visibility.

Finally, metabolic studies and comparative work on colour costs in other species show that maintaining or adjusting intense pigmentation can draw on limited energetic and biochemical resources, creating trade-offs that can stabilize honest signalling under a handicap-like logic when resources are limiting (Castro *et al.*, 2006; Rodgers *et al.*, 2013; Blount *et al.*, 2008). In *Betta*, where colour, movement and motivation are tightly coupled to contest outcomes, these energetic and ecological constraints likely interact to maintain the reliability of their dramatic visual "language" of aggression.

PARENTAL STRATEGIES AND NATURAL SELECTION IN *BETTA* FISHES

Parental care in *Betta* offers an excellent case study for parental investment theory: males invest heavily in eggs and larvae (bubble nests or mouthbrooding), trading current offspring survival against future mating opportunities and survival (Rüber *et al.*, 2004; Gross, 2005; Budi *et al.*, 2025; Nasir *et al.*, 2025; Nagasawa *et al.*, 2025; Perrone & Zaret, 1979). These strategies are shaped by energetic costs, sexual conflict and adaptive decisions to continue or abandon care (Goldberg *et al.*, 2020; Barta *et al.*, 2002; Webb *et al.*, 2002; Webb *et al.*, 1999; Székely, 2014; Wojczulanis-Jakubas, 2021).

FORMS OF PARENTAL CARE IN *BETTA* AND THEIR EVOLUTIONARY CONTEXT

Within *Betta*, males either build bubble nests and guard eggs/larvae at the water surface or practice paternal mouthbrooding, incubating eggs in the buccal cavity (Budi *et al.*, 2025; Rüber *et al.*, 2004; Nasir *et al.*, 2025). Phylogenetic analysis shows recurrent transitions between bubble nesting and mouthbrooding, with mouthbrooders producing significantly larger offspring but no consistent differences in egg volume, clutch size or brood-care duration, challenging simple "safe harbor" predictions that brooding always entails higher investment and reduced fecundity (Rüber *et al.*, 2004). More broadly in fishes, male-only care is common and is explained by Williams's principle and the relative value theorem: males care when the cost to their future fitness is lower relative to females, and when caring increases the value of current offspring versus future breeding (Gross, 2005; Perrone & Zaret, 1979).

Comparative work across fish shows egg care strategies are often evolutionarily irreversible, associated with genomic loss of egg hardening genes; *Betta splendens* shows such gene loss, implying a genetic "lock-in" of parental egg care (Nagasawa *et al.*, 2025). Domestic *B. splendens* and related wild species retain these male-focused strategies under captivity, and understanding their ecology and care forms is central to conservation breeding design (Budi *et al.*, 2025; Nasir *et al.*, 2025).

BETTA STRATEGIES IN A WIDER CARE-DIVERSITY FRAMEWORK

Across vertebrates, parental care evolves along axes of who cares, how long, and how complex the adaptations are (Gross, 2005; Goldberg *et al.*, 2020; Furness & Capellini, 2019). Amphibian comparative work shows that simple egg attendance can be gained and lost quickly, while more complex brooding forms tend to be evolutionarily stable and hard to reverse (Furness & Capellini, 2019).

Analogously, *Betta* mouthbrooding represents a more specialized, “brooding” form likely closer to the high investment end of the spectrum than surface guarding in bubble nesters (Rüber *et al.*, 2004). Yet in *Betta*, life history correlates are surprisingly weak: care form consistently tracks only offspring size, not duration or egg number (Rüber *et al.*, 2004), suggesting strong selection specifically on offspring phenotype rather than a wholesale shift in parental time budgets. At a broader teleost scale, extended care and large egg size are tightly coupled to higher total energetic cost of care (Cooke *et al.*, 2006), so the larger offspring of mouthbrooding *Betta* imply higher energetic and opportunity costs for males despite mixed life history signals (Rüber *et al.*, 2004; Cooke *et al.*, 2006). Meta-analysis across amphibians also demonstrates that biparental care is evolutionarily unstable, with many lineages reverting to uni- or no care (Furness & Capellini, 2019), consistent with the predominance of male only care in *Betta*.

ENERGETIC COSTS OF MALE CARE AND LINKS TO PARENTAL INVESTMENT THEORY

Parental investment theory predicts that parents should allocate care until the marginal benefit to current offspring equals the marginal cost in reduced survival or future reproduction (Gross, 2005; Cooke *et al.*, 2006; Webb *et al.*, 2002; Goldberg *et al.*, 2020; Perrone & Zaret, 1979). Across fishes with male-only care, empirical work on centrarchids shows large variation in duration and intensity of nest-guarding, with energetic cost rising with both species body size and egg size; larger eggs require more total parental effort, and species with extended care show stage-specific modulation of activity and expenditure that fits theoretical predictions of dynamic investment (Cooke *et al.*, 2006). Experimental manipulation of caring male smallmouth bass confirms that nest guarding is energetically and physiologically costly: caring males cease foraging, suffer immune shifts and oxidative damage, and are prone to nest abandonment when condition is poor, while supplemental feeding reduces abandonment and oxidative injury and increases reproductive success (Zolderdo *et al.*, 2016).

A meta-analysis of paternal care in fish, however, finds that across species there is little evidence that care systematically depresses male condition; instead, care often enhances mating success because females prefer males already caring for broods, particularly where males increase effort for larger broods (Goldberg *et al.*, 2020). This means that in many fishes, including *Betta*, male care is shaped not only by survival–reproduction trade-offs but also by sexual selection for caring males (Gross, 2005; Justus & Mendelson, 2018; Goldberg *et al.*, 2020; Petrescu-Mag, 2025).

In *B. splendens*, males pay substantial costs beyond sperm—territory defense, bubble nest construction, courtship and care—so overall mating and care may be more expensive for males than females, and males show stronger preference for conspecific females than females do, an inversion of classical expectations where females are choosier due to higher gamete cost (Justus & Mendelson, 2018). Integrating these findings with the relative value theorem, *Betta* males should elevate care when: (1) brood size and expected survival gain are high; (2) their own reserves remain sufficient to protect future breeding; and (3) caring boosts their attractiveness for additional matings or multiple spawning events within the same territory (Gross, 2005; Justus & Mendelson, 2018; Goldberg *et al.*, 2020; Cooke *et al.*, 2006; Webb *et al.*, 2002; Zolderdo *et al.*, 2016; Perrone & Zaret, 1979).

CONDITION-, TIME- AND ENVIRONMENT-DEPENDENT CARE DECISIONS

Dynamic models treating parental care as an adaptive decision show that whether a parent continues care or deserts depends on its energetic reserves, time in the breeding season, and prospects of remating (Barta *et al.*, 2002; Webb *et al.*, 2002; Webb *et al.*, 1999; Wojczulanis-Jakubas, 2021). When remating opportunities exist and care is costly, optimal strategies involve state-dependent thresholds: parents in poor condition or late in the season are more likely to desert, whereas those in good condition or early in the season should extend care (Barta *et al.*, 2002; Webb *et al.*, 2002). These models also show that changing care costs can have non intuitive effects, lengthening care at some times and shortening it at others, because the decision is jointly shaped by reserve dynamics and seasonal time horizon (Webb *et al.*, 2002; Webb *et al.*, 1999).

In fishes, males commonly adjust care effort dynamically to brood size, genetic relatedness and alternative mating opportunities—core components of Williams’s principle and parental investment theory (Gross, 2005). For nest-guarding species, including bubble nesters, increased energetic support (as in supplemental feeding) stabilizes care and reduces abandonment (Zolderdo *et al.*, 2016); conversely, environmental harshness that pushes males close to their “parental capacity” will magnify the survival cost of care and favor earlier desertion or reduced guarding intensity (Cooke *et al.*, 2006; Zolderdo *et al.*, 2016; Wojczulanis-Jakubas, 2021).

The recent “parental capacity” framework argues that care is only very costly when performed near the limits of an individual’s abilities; under more benign conditions, sexual conflict over who cares may be less intense than often assumed (Wojczulanis-Jakubas, 2021). Still, the genetic “dead-end” associated with egg hardening gene loss in *B. splendens* and other egg care fishes indicates that once a lineage has committed to parental egg care, ecological changes that undermine the feasibility of care (e.g. habitat degradation affecting nest stability or oxygen levels) can drastically reduce fitness because reversion to broadcast spawning is constrained (Nagasawa *et al*., 2025). For wild *Betta* in fragile blackwater habitats, ex-situ breeding must therefore carefully mimic environmental conditions that allow energetically sustainable male care, especially in mouthbrooders with long incubation times (Budi *et al*., 2025; Nasir *et al*., 2025).

SEXUAL CONFLICT, NEGOTIATION, AND POST-REPRODUCTIVE STRATEGIES IN BETTA-LIKE SYSTEMS

Sexual conflict over parental care occurs because the fitness optima of males and females differ: each benefits if the partner invests more, while they invest less themselves (Barta *et al*., 2002; Harrison *et al*., 2009; Webb *et al*., 1999; Parker, 2006; Székely, 2014; Wojczulanis-Jakubas, 2021). In uni-parental systems like *Betta*, conflict is largely pre- and immediately post-zygotic: who will end up providing care, and under what conditions desertion becomes adaptive. Classic theory for fishes proposes that sex differences in confidence of parentage, ability to provide care after spawning, and availability of mates structure which sex evolves to care; males are expected to tend eggs when females spawn multiple times per season, male paternity certainty is high, and caring males can potentially attract more mates or tend multiple broods (Gross, 2005; Perrone & Zaret, 1979). These conditions fit bubble-nesting and mouthbrooding *Betta* reasonably well: external fertilization and male nest control give high paternity confidence, females can spawn repeatedly with different males, and a male guarding a nest or brooding could sequentially mate with multiple females (Budi *et al*., 2025; Rüber *et al*., 2004; Nasir *et al*., 2025; Perrone & Zaret, 1979).

Game-theoretical models of sexual conflict over care show that optimal decisions for each sex depend on their own reserves, their mate’s reserves, and social context; for instance, when males decide first, females may strategically reduce their own reserves to “force” males to care, making desertion too risky for the male given his better condition (Barta *et al*., 2002). More general battleground–resolution frameworks emphasize that conflict arises wherever the optimum levels of care differ between sexes, but resolution can range from one sex always caring (as in *Betta*) to biparental care with partial compensation: experimental meta-analysis in birds shows that when one parent reduces effort, the other typically increases care but does not fully compensate, a pattern that stabilizes biparental systems (Harrison *et al*., 2009; Székely, 2014). Negotiation studies in canaries reveal sex-specific rules: males increase provisioning when the female partner is removed, while females adjust more strongly to offspring begging than to male effort, and offspring bear part of the cost of parental conflict (slower growth in biparental broods with lower total care) (Iserbyt *et al*., 2015). These principles extend conceptually to fish: in male-only *Betta* care, females can desert with low direct cost after spawning, while males face a tug-of-war between defending broods and seeking new mates.

Theoretical work on multiple parental patterns shows that when feedback from unmated individuals’ mating prospects is included, mixed strategies (care vs. desert) can be evolutionarily stable and qualitative shifts between uniparental, biparental and no care can occur within a population and season (Webb *et al*., 1999). In this perspective, observed *Betta* male care represents one stable outcome of an underlying care–desert game, shaped by ecological opportunity, paternity certainty, and the relative energetic and opportunity costs of continued nest attendance or mouthbrooding. Sexual conflict theory more broadly stresses that such care strategies are embedded in a larger web of pre- and postcopulatory conflicts—over mating rates, courtship, and fertilization—that can feed back into who ends up providing care (Parker, 2006; Székely, 2014).

In *B. splendens*, where male courtship, territoriality and care are all energetically demanding, the finding that males are choosier about conspecific mates than females implies that male reproductive decisions are strongly constrained by the expected cost of subsequent care; investing in a hybrid or heterospecific brood would squander both current energetic investment and future opportunities (Justus & Mendelson, 2018). *Betta* reproductive biology and conservation practice thus sit at the intersection of parental investment theory, sexual conflict and life history evolution: male care strategies emerge from a continuous decision process balancing reserves, season, mate availability and brood value, all under the shadow of genetic irreversibility in egg care lineages (Gross, 2005; Budi *et al*., 2025; Justus & Mendelson, 2018; Rüber *et al*., 2004; Goldberg *et al*., 2020; Barta *et al*., 2002; Cooke *et al*., 2006; Webb *et al*., 2002; Zolderdo *et al*., 2016; Nasir *et al*., 2025; Webb *et al*., 1999; Nagasawa *et al*., 2025; Perrone & Zaret, 1979; Székely, 2014; Wojczulanis-Jakubas, 2021).

COMPARATIVE FEATURES OF *BETTA* CARE FORMS AND INVESTMENT

Contrasting *Betta* male care forms and costs are shown in Table 3.

Table 3.

Contrasting *Betta* male care forms and costs (Consensus, 2025)

Care form in *Betta*	Key male investment features	Evolutionary/cost implications	References
Bubble nesting	Territory defence, nest construction at surface, guarding eggs and free-swimming fry for shorter periods; smaller offspring size	Lower offspring size suggests lower per-offspring energetic cost; care form not tightly linked to clutch size or care duration; may allow more frequent spawning and mate attraction while caring	(Budi *et al.*, 2025; Rüber *et al.*, 2004; Cooke *et al.*, 2006; Nasir *et al.*, 2025; Perrone & Zaret, 1979)
Paternal mouthbrooding	Prolonged oral incubation (3–4 weeks in some species), reduced feeding during brooding, larger offspring size at release	Larger offspring imply higher total investment per brood; extended care may reduce remating rate during brooding, but could produce higher-quality juveniles; no consistent change in clutch size or egg volume vs bubble nesters	(Budi *et al.*, 2025; Rüber *et al.*, 2004; Cooke *et al.*, 2006; Nasir *et al.*, 2025).

CONCLUSIONS

This review set out to integrate empirical and theoretical perspectives on behavioral plasticity, visual signaling, and parental investment in *Betta splendens*, with the aim of clarifying how environmental conditions, developmental trajectories, and evolutionary processes interact to shape behavior and life-history strategies. The synthesis of available evidence supports several general conclusions.

First, *Betta splendens* exemplifies a highly plastic behavioral system in which environmental factors act as primary drivers of phenotypic expression. Oxygen availability, mediated through the functional and developmental plasticity of the labyrinth organ, emerges as a central axis linking physiology to behavior. The capacity for air breathing not only enables persistence in hypoxic habitats but also facilitates energetically demanding behaviors such as aggression, courtship, and parental care. At the same time, behavioral adjustments to water quality, turbidity, and oxygen variability demonstrate that *Betta* behavior is not fixed, but dynamically modulated in response to ecological constraints. Social environment and early-life conditions further canalize behavioral phenotypes through endocrine and neurobiological pathways, while domestication and invasion illustrate the rapid evolutionary reshaping of behavioral syndromes under novel selective regimes.

Second, the visual signaling system of *Betta splendens* operates as a flexible yet reliable communication framework shaped by both physiological costs and environmental context. Aggressive displays—particularly opercular flaring and fin spreading—entail measurable energetic and post-contest physiological costs, supporting their role as condition-dependent signals. However, the evidence indicates that signal honesty in *Betta* is maintained not solely through large, fixed handicaps, but through a combination of dynamic energetic costs, structural constraints, and social enforcement mechanisms. The existence of multiple display components with differing costs suggests a multivariate signaling system in which different elements convey distinct aspects of quality, such as motivation, stamina, or escalation potential. Importantly, the efficacy and evolution of these signals are tightly linked to the visual environment: turbidity, light spectra, and habitat structure shape both signal production and perception, reinforcing the idea that signaling systems are context-dependent and evolutionarily labile.

Third, parental strategies in *Betta splendens* reflect the core principles of parental investment theory, while also highlighting the importance of state-dependent decision-making and sexual selection. Male-only care, expressed through bubble nesting or mouthbrooding, represents a stable evolutionary outcome driven by high paternity certainty, repeated mating opportunities for females, and the potential reproductive advantages of caring males. The two care forms differ in their energetic and life-history implications, particularly in relation to offspring size and the temporal constraints imposed on males. Across both strategies, care is not static but dynamically adjusted according to male condition, brood value, environmental conditions, and future reproductive prospects. This aligns with theoretical models predicting that parental care decisions emerge from continuous optimization processes balancing current and future fitness. Furthermore, sexual conflict in *Betta* is largely resolved prior to or immediately after spawning, resulting in a system where male care predominates, yet remains sensitive to ecological and physiological constraints.

Integrating these three domains reveals that behavioral plasticity, signaling systems, and parental investment are not independent traits, but components of a tightly interconnected adaptive framework. Energetic constraints imposed by respiration, environmental variability affecting sensory systems, and reproductive trade-offs jointly shape how individuals allocate effort across aggression, communication, and care. This integrative perspective underscores *Betta splendens* as a model system for understanding how complex behavioral phenotypes emerge from the interaction between proximate mechanisms (physiology, development) and ultimate drivers (natural and sexual selection).

Finally, *Betta splendens* demonstrates that flexible, context-dependent life-history strategies arise from the coupling of environmental heterogeneity, physiological capacity, and evolutionary history. Future research should focus on quantifying the joint effects of these factors—particularly under anthropogenic environmental change—to better understand the limits of plasticity and the potential for adaptive responses in both wild and domesticated populations.

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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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