Gasterosteus aculeatus as a model for instinctive behavior and fixed action patterns

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Abstract. The three-spined stickleback (*Gasterosteus aculeatus*) represents a cornerstone model in ethology for investigating instinctive behavior and fixed action patterns. Originating from Niko Tinbergen's seminal work on innate releasing mechanisms, research on this species has provided foundational insights into how simple sign stimuli—such as red nuptial coloration or female body morphology—trigger highly stereotyped behavioral sequences including aggression, courtship, and parental care. This review synthesizes classical and contemporary findings, highlighting how these instinctive responses are not rigid reflexes, but are modulated by genetic architecture, hormonal regulation, developmental processes, and ecological context. Modern approaches extend the stickleback model into the domains of behavioral syndromes and animal personality, revealing consistent correlations between traits such as boldness and aggression that vary across environmental gradients, particularly predation pressure. Furthermore, advances in neurobiology and genomics have linked behavioral outputs to conserved molecular pathways, while cognitive and social studies demonstrate the integration of learning processes—such as individual recognition—into instinctive frameworks. At the group level, individual behavioral variation influences collective dynamics, including leadership and shoaling behavior. Overall, *G. aculeatus* provides a uniquely integrative system bridging classical ethological theory with contemporary interdisciplinary research, offering critical insights into the organization, plasticity, and evolution of instinctive behavior.
Key Words: aggression, animal personality, behavioral genetics, behavioral syndromes, ecology, ethology, evolution, innate releasing mechanisms, neurobiology, sign stimuli, social behavior, stickleback, territoriality.

Introduction. The study of fish ethology, defined as the systematic investigation of behavior in aquatic organisms under both natural and controlled conditions, represents a fundamental component of contemporary animal biology and applied aquatic sciences. Behavioral traits in fish are not merely descriptive attributes; they are integrative expressions of physiological processes, ecological interactions, and evolutionary adaptations (Petrescu-Mag 2023ab; Zanghi & Ioannou 2025). As such, ethological research provides essential insights into how fish perceive, respond to, and modify their environment, thereby contributing to a deeper understanding of aquatic ecosystems and the organisms that inhabit them (Petrescu & Mag 2006; Storm et al 2025).

One of the primary reasons for the importance of fish ethology lies in its direct connection to survival and fitness (Petrescu-Mag 2025abc). Behaviors such as foraging, predator avoidance, reproduction, and social interaction are critical determinants of individual success and population dynamics. For instance, feeding strategies reflect both environmental resource availability and species-specific adaptations, while anti-predator behaviors reveal complex decision-making processes involving risk assessment and energy trade-offs. Reproductive behaviors, including courtship displays, nest building, and parental care, are often highly specialized and sensitive to environmental cues, making them valuable indicators of ecological stability and habitat quality (Bourne & Sammons 2008; Bourne & Watson 2009).

From an ecological perspective, fish behavior plays a central role in structuring aquatic communities. Movement patterns, habitat selection, and territoriality influence species distribution and interspecific interactions, ultimately shaping biodiversity and ecosystem function. Ethological studies contribute to the identification of critical habitats, migration corridors, and spawning grounds, which are essential for effective conservation and management strategies (Petrescu-Mag & Gavriloaie 2023). In the context of global environmental change, including climate warming, pollution, and habitat degradation, behavioral responses often constitute the first line of adaptation or stress signaling. Therefore, monitoring behavioral changes can provide early warning indicators of ecosystem disturbance.

In aquaculture, the relevance of fish ethology is particularly pronounced. Understanding behavioral needs and stress responses is crucial for optimizing rearing conditions, improving welfare, and enhancing production efficiency (Cui et al 2025). Abnormal behaviors, such as aggression, stereotypies, or reduced feeding activity, often signal suboptimal environmental conditions or poor management practices. By integrating ethological knowledge into system design and husbandry protocols, producers can reduce mortality, improve growth performance, and ensure compliance with increasingly stringent welfare standards. Moreover, selective breeding programs may benefit from incorporating behavioral traits associated with robustness and adaptability.

Fish ethology also holds significant value in fisheries science, where behavior influences catchability, gear selectivity, and stock assessment accuracy. Behavioral avoidance of fishing gear, diel activity patterns, and schooling dynamics all affect the efficiency and sustainability of fishing practices (McDonald et al 2026). Incorporating behavioral data into fisheries models can lead to more precise estimates of stock abundance and exploitation rates, thereby supporting evidence-based management decisions.

At a broader scientific level, fish serve as important model organisms for studying fundamental principles of neurobiology, cognition, and social behavior (Gavriloaie 2023). Research on learning, memory, communication, and decision-making in fish has challenged traditional assumptions about the cognitive capacities of aquatic vertebrates. These findings not only enrich comparative ethology, but also contribute to interdisciplinary fields such as behavioral ecology, evolutionary biology, and neuroscience.

The study of fish ethology is indispensable for advancing both theoretical knowledge and practical applications across multiple domains. By elucidating the behavioral mechanisms underlying ecological interactions, physiological regulation, and evolutionary processes, ethological research enhances our capacity to manage aquatic resources sustainably, improve animal welfare, and respond effectively to environmental challenges.

Aim of the Review. The three-spined stickleback, *Gasterosteus aculeatus*, is one of the classic vertebrate models in ethology, originating with Niko Tinbergen's work on innate releasing mechanisms and fixed action patterns. Modern research extends this role, linking its instinctive, stereotyped behaviors with genetics, neurobiology, and evolutionary ecology (Huntingford & Ruiz-Gómez 2009; Foster 2018; McKinnon et al 2019; Norton & Gutiérrez 2019).

The aim of this review is to critically examine the role of *G. aculeatus* as a model organism for understanding instinctive behavior and fixed action patterns, integrating classical ethological concepts with recent advances in behavioral ecology, neurobiology, and evolutionary biology, in order to elucidate the mechanisms, plasticity, and adaptive significance of innate behavioral responses.

Historical and Conceptual Role in Instinct Research. Tinbergen chose sticklebacks because they are small, robust, easy to keep, and show behavior that is simple enough to analyze, yet rich enough to be interesting (Huntingford & Ruiz-Gómez 2009; Foster 2018). Ethological studies on territoriality, courtship, and parental care provided early, influential demonstrations of innate, stimulus-bound responses and helped frame Tinbergen's four questions: causation, development, function, and evolution (Huntingford & Ruiz-Gómez 2009; Foster 2018). Work on sign stimuli and dummies, including red nuptial coloration and female body shape, directly elaborated Tinbergen's classic experiments and extended the analysis of fixed action patterns and releasing stimuli (Sevenster & Rowland 1985; Bolyard & Rowland 1996).

Innate Aggression, Territoriality and "Red Belly" Stimuli. Breeding males develop a bright red throat and belly coloration and become strongly territorial; they attack rival males and defend a carefully built nest (Norton & Gutiérrez 2019). Aggressive encounters include stereotyped displays, chases, bites, and eventual retreat of the subordinate male (Norton & Gutiérrez 2019). Tinbergen's original finding that red ventral coloration triggers attack has been refined: males respond aggressively to male-like dummies and video images, but responses depend on context and stimulus properties. Males in their own territories attack brighter red images more strongly than males in neutral tanks, consistent with interacting aggression–fear processes (Bolyard & Rowland 1996). Re-examinations of sign stimuli show that posture and female abdominal distension can also act as powerful releasers, sometimes even "supernormal" when exaggerated (Sevenster & Rowland 1985).

Habituation experiments reveal that repeated exposure to an intruder reduces attack over time even when biting is physically prevented, indicating that habituation can occur as a function of stimulus exposure rather than response execution (Peeke & Veno 2010). Behavior-genetic work demonstrates substantial heritability of intra-specific aggression across multiple contexts (juvenile, territorial, courtship, dominance), with shared and distinct genetic components for different aggressive patterns and links to hormonal systems, including androgens and gonadotropic hormones (Bakker 1986) (Table 1).

Table 1

Core innate behaviors and their triggers in sticklebacks (summarized by Consensus, 2026)

Behavioral system	*Key innate trigger features*	*Notes and context of expression*	*Citations*
Male territorial aggression	Presence of conspecific male, red nuptial coloration, rival posture/orientation (e.g. horizontal body)	Occurs in breeding males defending nest and territory	(Sevenster & Rowland 1985; Bakker 1986; Bolyard & Rowland 1996; Norton & Gutiérrez 2019)
Courtship towards females	Female silver, distended abdomen (gravid or supergravid), specific body orientation	Triggers zig-zag dance, leading to nest, and spawning sequence	(Sevenster & Rowland 1985; Norton & Gutiérrez 2019)
Anti-predator boldness/fear	Predator models (pike, bird skull strike), novel risks	Boldness–aggression syndromes link predator response and social aggression	(Huntingford 1976; Bell 2004; Bell & Sih 2007; Tulley & Huntingford 2010)

From Fixed Action Patterns to Behavioural Syndromes and Personality. Modern work treats the classic instinctive responses as part of broader behavioral syndromes (animal personality). Boldness towards predators is positively correlated with aggression towards conspecifics in some populations, suggesting a shared underlying trait architecture (Huntingford 1976; Bell 2004; Tulley & Huntingford 2010). This bold–aggressive syndrome is expressed or broken apart depending on ecological context: strong predation pressure favors tight correlations, whereas predator-free populations show weaker or absent correlations (Bell 2004; Dingemanse et al 2007). Experimental exposure to real predation can generate or strengthen the boldness–aggression correlation through both selection (predators removing particular behavioral types) and plasticity, demonstrating that "personality" structure is itself environmentally shaped (Bell & Sih 2007).

Comparative studies across multiple populations show that the structure of behavioural syndromes (links among aggression, activity, and exploration) differs predictably with predator regime, supporting an adaptive rather than purely constrained view of covariance between instinctive traits (Dingemanse et al 2007). Behaviour-genetic selection lines confirm that aggressiveness in different contexts can be genetically correlated or partly independent, supporting a modular, but not fully separable, organization of fixed action patterns and their thresholds (Bakker 1986).

Neurobiological, Collective and Cognitive Extensions. The stickleback's instinctive behaviors now serve as entry points into neuroscience. Standardized assays quantify mirror-induced aggression, anxiety-like behavior, boldness, and shoaling; these responses are modifiable by psychoactive drugs such as fluoxetine and buspirone, opening translational links to human psychiatric models (Norton & Gutiérrez 2019). At the molecular level, territorial aggression in sticklebacks shares neuromolecular signatures with social challenge responses in mice and honey bees, including hormone signaling, G-protein–coupled receptor pathways, and conserved transcription factor networks associated with neural plasticity and energy metabolism (Rittschof et al 2014).

Instinctive tendencies also scale up to group-level patterns. Individual differences in sociability and boldness predict leadership, spatial positioning, and foraging performance in shoals; faster, less sociable fish tend to lead groups and shape collective movement dynamics (Jolles et al 2017). High-resolution movement tracking has enabled biologically realistic models of stickleback locomotion that live fish treat as indistinguishable from real conspecific movement, allowing precise experimental manipulation of social stimuli while preserving naturalistic kinematics (Pike & Burman 2023).

Cognition overlays these instinctive mechanisms. Territorial sticklebacks can recognize familiar individuals by facial cues and adjust aggression according to "dear enemy" relationships, even when red nuptial color is controlled, implying that learned social information can modulate innate sign-stimulus driven aggression (Sogawa et al 2024).

Broader Significance as a Model of Instinct and Evolution. *Gasterosteus aculeatus* has evolved from a purely behavioral model into a "supermodel" spanning ethology, behavioral ecology, evolution, and environmental science (Huntingford & Ruiz-Gómez 2009; Foster 2018; McKinnon et al 2019). Its postglacial radiation, with repeated benthic–limnetic ecotypes, links classic instinctive displays to adaptive divergence in feeding, courtship, cannibalism, and aggression, including ecotype-specific aggressive patterns and plasticity in how aggression is incorporated into courtship (Scotti & Foster 2007; Foster 2018). Across this work, the same fundamental idea remains: clearly defined releasing stimuli (color, shape, orientation, intruder presence) trigger organized, often stereotyped response chains, but the expression, thresholds, and correlations among these fixed action patterns are shaped by genetics, hormones, development, social experience, and ecology (Huntingford 1976; Bakker 1986; Bell & Sih 2007; Dingemanse et al 2007; Scotti & Foster 2007; Huntingford & Ruiz-Gómez 2009; Norton & Gutiérrez 2019) (Table 2).

Table 2

Representative research themes involving stickleback instinctive behavior

Theme	*Focus in G. aculeatus research*	*Relation to instinct / fixed patterns*	*Citations*
Classic ethology and sign stimuli	Territoriality, courtship, red coloration, dummy tests	Dissection of key releasing stimuli and fixed response chains	(Sevenster & Rowland 1985; Bolyard & Rowland 1996; Huntingford & Ruiz-Gómez 2009; Peeke & Veno 2010; Foster 2018)
Personality and behavioral syndromes	Boldness–aggression–activity correlations within and across populations	How suites of instinctive traits co-vary and evolve	(Huntingford 1976; Bell 2004; Dingemanse et al 2007; Bell & Sih 2007; Tulley & Huntingford 2010)
Neurobiology and gene networks	Drug-sensitive aggression/anxiety, transcriptomic response to intrusion	Molecular and neural bases of innate social responses	(Rittschof et al 2014; Norton & Gutiérrez 2019)
Collective and cognitive dimension	Leadership in shoals, realistic movement models, facial recognition	How individual-level instincts shape group and social cognition	(Jolles et al 2017; Pike & Burman 2023; Sogawa et al 2024)

Conclusions. *Gasterosteus aculeatus* remains one of the most powerful and enduring model organisms for the study of instinctive behavior and fixed action patterns, providing a rare continuity between classical ethological theory and modern integrative biology. From Tinbergen's foundational demonstrations of innate releasing mechanisms—where simple, well-defined sign stimuli such as red ventral coloration elicit highly stereotyped behavioral sequences—the stickleback has enabled a precise operationalization of instinct as organized, stimulus-bound response systems.

However, the accumulated body of research clearly demonstrates that these behaviors cannot be interpreted as rigid or purely reflexive units. Instead, they represent dynamic phenotypic expressions emerging from the interaction of genetic architecture, endocrine regulation, neural circuitry, ontogenetic processes, and ecological context. Fixed action patterns in sticklebacks are therefore better understood as probabilistic and threshold-dependent systems, whose expression varies with internal state and external environmental conditions.

A major conceptual advance highlighted in this review is the integration of classical instinct theory with the framework of behavioral syndromes and animal personality. Traits such as aggression, boldness, and exploration are not independent; rather, they form structured covariance patterns that can differ among populations and ecological regimes. This demonstrates that instinctive behaviors are embedded within higher-order behavioral architectures that are themselves subject to natural selection, plasticity, and environmental modulation.

At the mechanistic level, *G. aculeatus* has proven instrumental in linking behavior to its neurobiological and molecular substrates. Evidence for conserved neuromolecular pathways underlying social challenge responses across taxa underscores the translational relevance of this model, extending its importance beyond ethology into neuroscience and even biomedical research. At the same time, the incorporation of cognitive processes—such as individual recognition and social learning—reveals that innate releasing mechanisms operate in conjunction with experience-dependent modulation, challenging traditional dichotomies between instinct and learning.

Importantly, the implications of stickleback research extend beyond the individual level. Variation in instinctive tendencies scales up to influence collective behavior, including leadership, coordination, and information flow within groups. This multi-level integration—from genes to individuals to social systems—positions *G. aculeatus* as a uniquely versatile model for studying the organization of behavior across biological hierarchies.

Finally, the species' remarkable evolutionary diversification, particularly in postglacial adaptive radiations, provides compelling evidence that instinctive behavioral systems are evolutionarily labile and tightly coupled with ecological pressures. Differences in predation regime, habitat structure, and resource availability shape not only the expression of individual behaviors, but also the correlations among them, reinforcing the view that instinct is both an adaptive and evolvable trait complex.

In conclusion, the enduring relevance of *G. aculeatus* lies in its ability to unify multiple levels of analysis—proximate and ultimate, mechanistic and functional—within a single, experimentally tractable system. As such, it continues to serve as a cornerstone model for elucidating the organization, plasticity, and evolution of instinctive behavior, while offering critical insights applicable across ethology, behavioral ecology, neuroscience, and evolutionary biology.

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

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Received: 12 March 2026. Accepted: 30 March 2026. Published online: 10 April 2026.
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How to cite this article:
Nowak M., Păpuc T., 2026 *Gasterosteus aculeatus* as a model for instinctive behavior and fixed action patterns. ABAH Bioflux 18(1):48-55.