frontiers in Endocrinology

MINI REVIEW
published: 23 July 2020
doi: 10.3389/fendo.2020.00468

A Teleost Fish Model to Understand Hormonal Mechanisms of Non-breeding Territorial Behavior

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Aggressive behaviors occurring dissociated from the breeding season encourage the search of non-gonadal underlying regulatory mechanisms. Brain estrogen has been shown to be a key modulator of this behavior in bird and mammal species, and it remains to be understood if this is a common mechanism across vertebrates. This review focuses on the contributions of *Gymnotus omarorum*, the first teleost species in which estrogenic modulation of non-breeding aggression has been demonstrated. *Gymnotus omarorum* displays year-long aggression, which has been well characterized in the non-breeding season. In the natural habitat, territory size is independent of sex and determined by body size. During the breeding season, on the other hand, territory size no longer correlates to body size, but rather to circulating estrogens and gonadosomatic index in females, and 11-ketotestosterone in males. The hormonal mechanisms underlying non-breeding aggression have been explored in dyadic encounters in lab settings. Males and females display robust aggressive contests, whose outcome depends only on body size asymmetry. This agonistic behavior is independent of gonadal hormones and fast acting androgens. Nevertheless, it is dependent on fast acting estrogenic action, as acute aromatase blockers affect aggression engagement, intensity, and outcome. Transcriptomic profiling in the preoptic area region shows non-breeding individuals express aromatase and other steroidogenic enzyme transcripts. This teleost model reveals there is a role of brain estrogen in the control of non-breeding aggression which seems to be common among distant vertebrate species.

Keywords: ***Gymnotus omarorum*, non-breeding aggression, fadrozole, natural spacing, estrogen**

Edited by:
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Specialty section:
This article was submitted to Neuroendocrine Science, a section of the journal Frontiers in Endocrinology

Received: *01 March 2020*
Accepted: *15 June 2020*
Published: *23 July 2020*

Citation:
Silva AC, Zubizarreta L and Quintana L (2020) A Teleost Fish Model to Understand Hormonal Mechanisms of Non-breeding Territorial Behavior. Front. Endocrinol. 11:468. doi: 10.3389/fendo.2020.00468

INTRODUCTION

The study of territoriality can provide insight into how animals integrate social and environmental cues with their physiological context to produce behavioral responses. Steroid hormones are key in this integration, affecting behavior through the modulation of brain areas belonging to the social behavior network (1–3). Territoriality occurs when animals defend spatially associated resources against competing individuals, and it is frequently mediated by agonistic encounters (4–6). Animals will only defend resources when the benefits exceed the costs of defense, and this is key to understanding how spacing, mating, and social systems have evolved (7). Pioneering studies in the field of behavioral ecology (8) have shown that optimal cost-benefit balance in territorial defense occurs when animals compete for mating opportunities, while the defense of resources unrelated to reproduction is less often observed. Nonetheless, in a few species territorial defense is present year-round (9–11), which may ensure access to foraging areas or protection from predators across seasons (4). Territorial aggression may thus occur in these unconventional cases uncoupled from a breeding physiology and independently from gonadal hormones.

Aggressive behaviors which occur dissociated from the breeding season, encourage the search of non-gonadal underlying regulatory mechanisms (12, 13). Early reports in wild birds established the independence of non-breeding aggression from circulating androgens (14–16). Many studies have shown that aggression may occur when gonads are regressed and even after castration in some species of birds, mammals, reptiles and fish (9, 11, 17–25). In addition, it has also been reported that territorial challenges during the non-breeding season do not affect circulating testosterone (22, 26, 27). Brain estrogens have been shown to have a forefront role in the regulation of non-breeding aggression. This was first postulated by pioneer research showing that estrogens promote aggression in non-breeding song sparrows (18, 28, 29) and in California mice subjected to a short photoperiod (30, 31). Aromatase, which converts androgens into estrogens, is present in brain regions related to aggression, and may display seasonal changes in activity (32, 33). This raises the question: is the role of brain estrogen underlying non-breeding aggression a general strategy across vertebrates?

Fish are an ideal group to approach this question as they are evolutionarily early vertebrates, they display diverse and elaborate social behaviors, brain areas related to social behavior are conserved, and they exhibit extraordinarily high levels of brain aromatase activity (34–38).

This review focuses on the contributions from a teleost fish model on the hormonal modulation of non-breeding territorial behavior, to better understand different mechanisms underlying aggression. South American weakly electric fish of the Order Gymnotiformes, constitute a highly diverse group. They produce electric organ discharges (EOD) that are used for active sensing and communication [reviewed in (39)], and their well-known electrogenic system is composed of discrete nuclei in the brainstem and spinal cord and a peripheral electric organ. This system has been shown to be hormone-sensitive in many of its components frequently producing sexually dimorphic communication signals, making these fish well established models to study steroid action on neural circuits underlying behavior (40–49). *Gymnotus omarorum* occurs naturally at the southern boundary of gymnotiform distribution in South America (Uruguay). It is a seasonal breeder, yet it displays year-round territoriality in both males and females (50). It allows the analysis of territorial aggression in the natural habitat as well as the exploration of its proximate mechanisms in lab settings. The fact that this behavior occurs when gonads are regressed and circulating sex steroids are low, puts the spotlight on brain synthesis of steroid hormones. This is the first teleost model that contributes to revealing common estrogenic roles in the control of non-breeding aggression, broadening the perspective of the current state of knowledge currently based mostly on bird and mammal models.

YEAR-LONG SPACING IN THE NATURAL HABITAT

The spacing patterns of *G. omarorum* in the natural habitat likely reflect year-long territorial defense in both males and females. Territorial defense, usually associated with breeding males, has been proposed to follow two general principles: (1) territory size depends on body size as it is the universal indicator of physical strength and resource holding power (51–53); and (2) territory size depends on individual reproductive state and may be related to circulating androgen levels (54–56). Sexual dimorphism in territory size during breeding can also be expected even in species in which both sexes display territoriality, as males and females may have asymmetries in their motivation and/or their fighting ability. This is the case of red squirrels (*Sciurus vulgaris*), for example, in which males often hold larger territories than females (57) or in the striped plateau lizard (*Sceloporus virgatus*), in which females are more territorial than males (58).

During the breeding season (corresponding to the austral spring-summer, from December to February), this sexually monomorphic species displays similar patterns of spatial arrangement for males and females (59). In resting diurnal conditions, both males and females are found occupying individual spots, distanced at least a meter away from their closest neighbor. A close analysis shows that sex is relevant in spatial arrangements, as animals are more likely to have an opposite-sex than a same-sex closest neighbor. Although males and females hold same-sized territories, when the size of each territory is normalized to its owner's body size, sexual dimorphism arises as females hold relatively larger territories. This interesting difference is probably due to sex-biased reproductive requirements associated to anisogamy, which may lead to higher metabolic requirements in females and thus the need for larger foraging grounds. In male *G. omarorum* gonadosomatic index (GSI) did not show correlation to territory sizes, but circulating 11-ketotestosterone (11-KT, the main bioactive androgen in teleost fish) marginally predicted territory size (59). This data falls in line with the well documented relationship between androgens and male territorial behavior (60–62). In contrast, both female GSI and circulating estradiol show high predicting power on territory size, which constitutes the first report to associate circulating estradiol and territory size in a vertebrate species (59). In the light of the evidence that estradiol promotes female aggression (63–65), ovarian estradiol is likely involved in the modulation of breeding territorial aggression in this species. In summary, during the breeding season, sexually dimorphic individual traits seem to influence motivation toward territory defense in *G. omarorum* impacting on individual spacing in the wild in a sex-dependent manner.

During the non-breeding season (corresponding to the austral autumn-winter, from June to August), adults of *G. omarorum* occupy individual spots in the wild separated at least one meter from the closest neighbor. Sex of individuals does not bias spacing, as closest neighbors are randomly opposite-sex or same-sex. Body size, but not sex, correlates positively with territory size (59). Motivation to maintain territories in the non-breeding season may be related to the fact that these fish continuously produce electric signals as a means of communicating and imaging their world. Electrogeneration is an energetically expensive process which has been associated with high basal metabolic requirements (39, 66) and most likely imposes high year-long foraging demands. Equally sized territories between males and females may reflect the same energetic requirements in both sexes.

GONAD-INDEPENDENT AGONISTIC BEHAVIOR MEDIATES NON-BREEDING TERRITORIAL BEHAVIOR

G. omarorum is one of the few teleost species in which the hormonal regulation of non-breeding aggression has been studied [see also damselfish, (22, 27, 67)], and the only teleost species in which the determinants of natural non-breeding spacing have been explored in the field (59).

The acquisition and defense of territories in non-breeding *G. omarorum* have been empirically shown to be mediated by agonistic encounters in laboratory settings (68). When staging dyadic agonistic encounters using a neutral plain arena, all fish engage in rapid escalated conflicts in which the dominant-subordinate status is achieved in <5 min. Subordinates end the struggle when they decide to stop attacking and retreat. In addition, they further signal their surrender electrically: first interrupting their EOD to hide from the dominant, then emitting transient electric submission signals, and finally, adopting a lower post-resolution EOD basal rate (69, 70). The intensity of submission signals emitted by the subordinate individual is correlated to the aggression levels displayed by the dominant (71). Body size is the only predictor of contest outcome, while individual sex has no significant influence (69). After resolution, dominants monopolize the acquired territory and actively exclude subordinate fish to the periphery of the tank (68). Laboratory evidence falls in line with what is observed in the wild, where non-breeding territory sizes are determined by body size and are unrelated to sex. Several pieces of evidence support that the non-breeding agonistic behavior of *G. omarorum* is independent of gonadal hormones. First, intra and intersexual non-breeding agonistic contests are indistinguishable (69, 72). Secondly, aggressive challenges do not have an effect on circulating 11-ketotestosterone (72). Moreover, the clearest evidence of gonadal independence of non-breeding aggression in *G. omarorum* is that agonistic behavior persists unchanged after castration. Gonadectomized and control dyads do not differ in contest outcome, dynamics, aggression levels, nor submissive displays (21), demonstrating that the low levels of non-breeding circulating gonadal hormones are not necessary for the occurrence of this behavior.

NON-GONADAL ESTROGENS MODULATE NON-BREEDING AGONISTIC BEHAVIOR

Brain estrogens are critical regulators of non-breeding aggression. In the absence of high circulating testosterone, brain derived estrogens may be synthesized from circulating adrenal dehydroepiandrosterone (DHEA), proposed to have a key role underlying non-breeding aggression in mammals and birds. DHEA is reported to have higher plasmatic levels in the non-breeding season in birds (26, 73), its levels may respond to social challenges in birds and mammals (26, 74, 75) and it can be metabolized in the brain into active androgens and estrogens (76, 77). In contrast to the breeding season, in non-breeding mammalian and avian models estrogens exert rapid effects upon aggression which reflect non-genomic mechanisms (30, 31, 78, 79). In turn, aggressive interactions can produce changes in steroid hormone levels in specific brain areas of the songbird model (76, 80).

In *G. omarorum* the influence of gonadal hormones in the non-breeding aggression has been ruled out by castration experiments (21), and the role of extra-gonadal steroid hormones has been tested via pharmacological manipulations. Short term involvement of androgens and estrogens was explored focusing on the effects these hormones have on the rapid dynamics of conflict and resolution. Acutely impeding aromatase action by administration of its inhibitor (Fadrozole, 60 min pre contest) in intrasexual dyads had a profound effect in non-breeding agonistic encounters of *G. omarorum*. Overall, results from both male-male and female-female contests show that the inhibition of estrogen synthesis causes a decrease in aggressive displays revealed by an important delay in initiating overt aggression. In addition, it decreases aggression levels and prevents potential winners (larger fish) from achieving dominance (21, 81). Direct short-term effects of androgens were ruled out, since acute treatment with androgen receptor antagonists showed no influence upon conflict engagement, aggression dynamics nor the establishment of dominant-subordinate status (81). If androgens were directly involved in the modulation of non-breeding aggression in *G. omarorum*, their action may be evinced in a longer time frame, as has been observed in other non-breeding territorial fish in which chronic androgen receptor blocking decreases aggression (22).

To date, the expression pattern of brain aromatase has been identified in several teleost species (82–89); including a recent study in the weakly electric fish *Apteronotus leptorhynchus* (90), which also exhibits territorial aggression in non-breeding conditions (43, 91). Aromatase mRNA was mapped in non-breeding male and female *A. leptorhynchus* in the telencephalon, preoptic area, hypothalamus, and pituitary gland, showing a high degree of regional conservation with previous reports in teleosts. Reports of the presence of high levels of aromatase in the social behavior network strongly suggest these neural circuits are affected by local estrogen production. Moreover, testosterone aromatization has reported effects in social behavior electric displays in *Apteronotus* (42, 92). The first transcriptomic study carried out in *G. omarorum* during the non-breeding season shows that aromatase, as well as other steroidogenic enzymes are expressed in the preoptic area (93). This node of the social brain has a well-documented role in aggressive behavior (1, 94–97). Moreover, it has already been shown that preoptic area neuropeptides have a status-dependent role in the modulation of non-breeding aggression in *G. omarorum* (70, 98). The analysis of local brain synthesis of estrogens and androgens in this region regulating non-breeding aggression is currently underway.

Overall, research in *G. omarorum* point to brain estrogen as an important modulator of non-breeding aggression acting in regions of the social brain through rapid mechanisms.

STATE OF THE ART AND PERSPECTIVES: NEUROSTEROIDS UNDERLYING NON-BREEDING AGGRESSION

Currently, *G. omarorum* is the strongest teleost model to approach neuroendocrine mechanisms underlying non-breeding aggression. Contributions in this model demonstrate that brain estrogens are key regulators of non-breeding aggression in a much broader sense than previously reported. Revised evidence, brought together from both laboratory and natural settings, shed light on the sequence of events and underlying mechanisms leading to territory acquisition and spatial distribution in the wild (**Figure 1**). Fish contenders competing for territory display a short evaluation time and engage in escalated conflicts from which a clear dominant-subordinate status emerges. Males and females show no difference in aggressive behavior, but outcome is biased by body size: the larger fish wins and acquires the disputed territory. Agonistic behavior is independent of gonadal hormones and fast acting androgens, although it is strongly dependent on estrogenic action, revealed by the rapid and dramatic effect of blocking estrogen synthesis upon conflict engagement, aggression intensity and establishment of dominance. Agonistic behavior is a key element for the non-breeding distribution of fish in the wild in which animals hold sexually monomorphic territories and body size is the strongest determinant for territory size.

The year-long territorial behavior of *G. omarorum* opens exciting avenues of research on steroid modulation of aggression, and in particular, the yet unexplored role of both circulating and brain-derived steroids in breeding territorial aggression. We have two hypotheses on potential seasonal plasticity in the role of steroids regulating aggression, which are leading our current research. First, we understand that non-breeding contests produce a fast rise in brain estrogen in regions of the social behavior network. This estrogen peak has a rapid, non-genomic effect, promoting aggressive behavior, the fast establishment of dominance, and ultimately, at least in a short time scale, it correlates to the size of the acquired territory in the natural habitat. In absence of high circulating sex steroids, we propose this brain hormonal signature is important in enabling stable territory distributions in natural populations. Secondly, based on the correlation between GSI and territory size in the breeding season, and the independence of aggression from

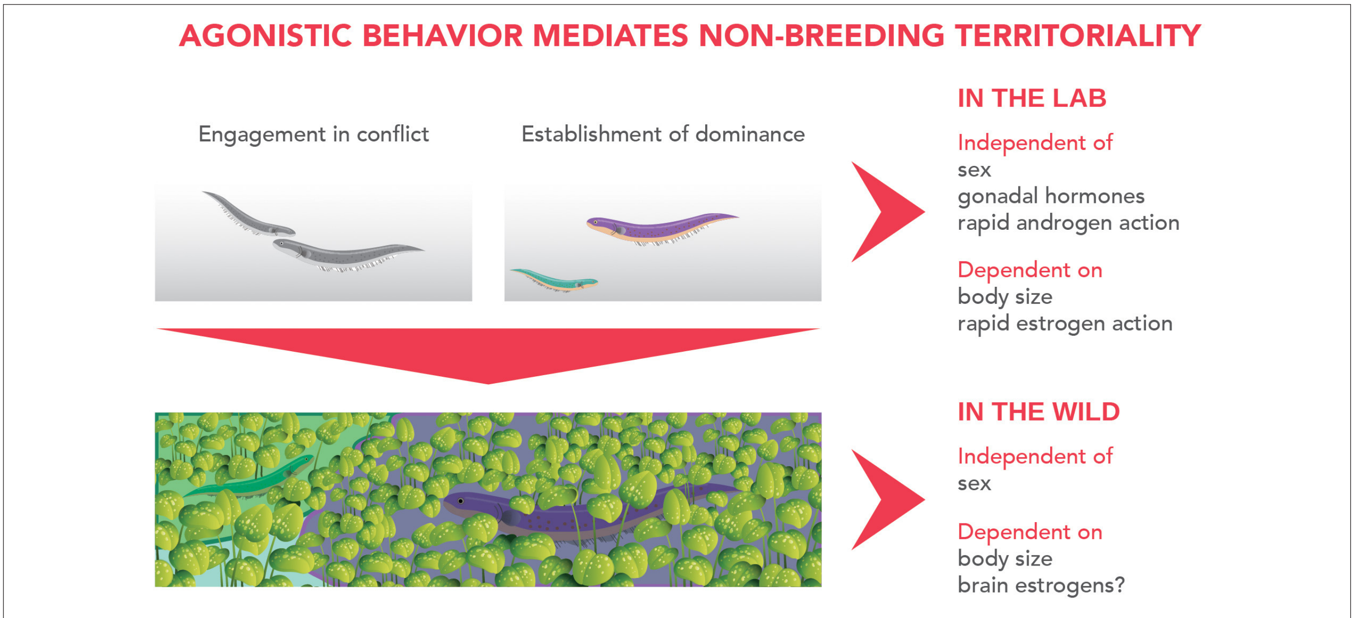

FIGURE 1 | Events and underlying mechanisms of non-breeding territoriality in *Gymnotus omarorum*. Laboratory evidence shows that agonistic behavior mediates territory acquisition, as after conflict resolution dominant animals monopolize the territory and actively exclude subordinate fish to the periphery of the tank. Body size, but not sex, is a strong predictor of conflict outcome. Aggression is maintained even in gonadectomized animals, indicating its independence of gonadal hormones. Behavioral pharmacology evinces aggression is also independent of rapid actions of androgens, although strongly dependent on rapid estrogenic action, as an aromatase inhibitor greatly influences conflict engagement, aggression intensity and establishment of dominance. This evidence suggests that brain-derived estrogens play a key role in agonistic behavior. Agonistic behavior most probably underlies territorial spacing in the natural habitat. Territory sizes are not sex-biased, but do depend on body size, and we propose that at least in the short-term after dominance establishment, they also correlate to brain estrogen levels.

gonads in the non-breeding season, we postulate that regulation of aggression varies seasonally. We hypothesize that estrogens and androgens maintain key roles as modulators, but their main sources alternate from the brain (in the non-breeding season) to the gonads (in the breeding season). In addition, we propose that non-breeding aggression depends exclusively upon brain-derived steroids, either produced *de novo* or from circulating precursors. Studies testing these two hypotheses are underway.

The contributions of *G. omarorum*, a teleost fish with persistent aggression uncoupled from seasonal breeding, expand concepts based on mammal and bird models to further understand the breadth of estrogenic regulation of aggression. Fish are the oldest and most diverse class of vertebrates. Thus, common regulation strategies suggest either a very strong conservation of the trait, or an independent evolution path arriving at the same solution, both underscoring the relevance and extensive impact of estrogens upon aggression.

AUTHOR CONTRIBUTIONS

AS and LQ conceived the general organization of the manuscript. AS, LZ, and LQ wrote the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

Funding agencies: Agencia Nacional de Investigación e Innovación Grant ANII_ FCE 136381; Comisión Sectorial de Investigación Científica, Universidad de la República, Uruguay, Grant Grupos I+D (#883158). Programa de Desarrollo de las Ciencias Básicas.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.