



Ready for a fight? The physiological effects of detecting an opponent's pheromone cues prior to a contest



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HIGHLIGHTS

- Mangrove rivulus (*Kryptolebias marmoratus*) can detect a competitor's pheromone cues.
- Detection of pheromone cues elicited a significant rise in androgen levels.
- Physiological responsiveness to pheromones is a trait conserved among lineages.
- Pheromones and physical competition influenced androgen levels equally.

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ABSTRACT

Reception of pheromone cues can elicit significant physiological (e.g. steroid hormone levels) changes in the recipient. These pheromone-induced physiological changes have been well documented for male–female interactions, but scarcely in same-sex interactions (male–male and female–female). We sought to address this dearth in the current literature and examine whether mangrove rivulus fish (*Kryptolebias marmoratus*) could detect and, ultimately, mount a physiological response to the pheromone signature of a potential, same-sex competitor. We examined steroid hormone levels in mangrove rivulus exposed to one of three treatments: 1) isolation, 2) exposure to pheromones of a size-matched partner, and 3) pheromone exposure to a size-matched opponent followed by a physical encounter with the opponent. We found that exposure to a competitor's pheromone cues elicited a significant increase in testosterone levels. Increases in testosterone were similar across genetically distinct lineages derived from geographically distinct populations. Further, testosterone levels were similar between individuals only exposed to pheromone cues and individuals exposed to both pheromone cues and a subsequent physical encounter. Our findings led us to generate a number of testable predictions regarding how mangrove rivulus utilize pheromone signals in social interactions, the molecular mechanisms linking social stimuli and hormonal responses, and the possible adaptive benefits of hormonal responsiveness to receiving a potential competitor's pheromone cues.

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1. Introduction

Pheromones can have significant influences on the expression of social behaviors (e.g. mate choice; reviewed in [1]). The composition, routes of production and release, and phenotypic (i.e. behavioral and physiological) effects of pheromones have been documented in a number of animal taxa including invertebrates (e.g. crayfish, *Orconectes rusticus*; [2–3]), amphibians (e.g. red-legged salamander, *Plethodon shermani*; [4]), fish (e.g. Mozambique tilapia, *Oreochromis mossambicus*; [5]), and small and large mammals (e.g. Syrian hamsters, *Mesocricetus auratus*; [6]). A significant amount of research has focused on the behavioral effects pheromones have on male–female interactions (reviewed

in [1,7]). A classic example is the male house mouse (*Mus musculus*), which produces and deposits pheromones around its territory that act to both attract and induce receptivity in females [1]. Male terrestrial salamanders (*Plethodon jordani*) release pheromones during courtship, which increase female receptivity and reduce courtship duration [8]. Furthermore, female goldfish (*Carassius auratus*) release pheromones at spawning sites, which signals to nearby males the location of the receptive female [9–11]. Research examining the effects pheromones have on same sex interactions (e.g. male–male contests) has received considerably less attention. Male crayfish produce pheromones during agonistic interactions; pheromone production increases as contest intensity increases, and eventual winners often produce higher quantities of pheromones during agonistic interactions compared to eventual losers [2–3]. At the conclusion of agonistic interactions, dominant male crayfish continue to produce pheromones and claim upstream territories while subordinate males cease pheromone production and are

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relegated to downstream territories [3]. By doing so, subordinate individuals are constantly exposed to pheromones produced by dominant individuals, which potentially reinforces subordinate status. During agonistic interactions between male Mozambique tilapia, both opponents frequently urinate and, as a result, release pheromones into the surrounding water [5,12]. Contest winners and dominant males tend to urinate more frequently, in greater quantities, and with greater potencies compared to eventual losers and subordinate individuals [5]. Pheromone production during these interactions is thought to provide both combatants with information regarding asymmetries in fighting ability between the contestants and often leads to contests settling without the use of physical aggression [12]. Surgically impeding the contestants' abilities to urinate causes increased use of physical aggression during agonistic interactions and protracted fights [12].

Pheromones also can elicit significant physiological responses [4, 7,13], which may mediate adaptive behavioral changes [14–18]. Pheromone-induced neuroendocrine changes have been well documented in mice and principally for male–female interactions [7]. Female mice exposed to the pheromones of dominant males rapidly enter into and synchronize their estrous cycles (Whitten effect) but exposure to an unfamiliar male's pheromone signature can interrupt this cycle and cause females to abort their current pregnancy (Bruce effect; reviewed in [1,7]). Exposure to female pheromones elicits significant increases in male androgens (testosterone) and luteinizing hormone, a peptide hormone that regulates spermatogenesis, in male Syrian hamsters [6] and glucocorticoid levels (corticosterone – a stress-related steroid hormone) in male red-legged salamanders [4]. Furthermore, exposure to androstenedione, an androgen and a component of male sweat, elicited a significant elevation in stress hormone (cortisol) levels in human females [13]. Prior investigations have focused heavily on pheromone-induced neuroendocrine responses elicited during male–female interactions but, to the best of our knowledge, there has only been a single study that has investigated pheromone-induced neuroendocrine changes elicited by same sex interactions. O'Connell et al. [19] found that when a male cichlid fish (*Astatotilapia burtoni*) was both visually and chemically exposed to a potential competitor it exhibited a significant increase in androgen levels. We sought to further expand upon this work by examining whether mangrove rivulus fish (*Kryptolebias marmoratus*) could detect and mount a physiological response to the pheromone signature of a potential same-sex competitor.

The mangrove rivulus is a small fish endemic to mangrove ecosystems [20]. Populations of mangrove rivulus can be found as far north as Central Florida, U.S.A. to as far South as Venezuela and Rio de Janeiro [20]. Mangrove rivulus are known to be highly aggressive towards conspecifics and have become a model system for investigating aggressive behaviors [21], experience-dependent changes in behavior (e.g. winner and loser effects; [22]) and hormonal modulation of aggressive behaviors [23]. Androgens (testosterone and 11-ketotestosterone) and glucocorticoids (cortisol) in mangrove rivulus change as a function of engaging in aggressive contests (duration and escalation; [23–24]). Furthermore, pre-contest androgen and glucocorticoid levels can dictate an individual's probability of initiating, escalating, and winning a contest [23]. Whether mangrove rivulus are responsive (e.g. physiologically) to conspecific pheromones remains unknown. We hypothesized that mangrove rivulus would detect pheromone cues emitted by a conspecific and that they would exhibit significant hormonal changes in response to those cues. We elected to assay two androgens (testosterone and the fish specific 11-ketotestosterone), an estrogen (estradiol), and a glucocorticoid (cortisol) in fish that were exposed, or not, to conspecific pheromones. We chose these steroid hormones based on their connection with aggressive behaviors in the mangrove rivulus (e.g. [23–24]) and because prior research has shown that steroid hormone concentrations (e.g. testosterone and cortisol) can change in response to pheromone cues (e.g. [4,6]). We predicted that pairs of rivulus that are visually, but not chemically, isolated from one another would

exhibit significant increases in hormone levels compared to individuals that receive no chemical cues from a potential adversary. Furthermore, we were interested in whether there was a relationship between pheromone-induced and contest-induced changes in hormones; that is, whether fighting affects hormones more than, less than, or equivalent to olfactory stimulation alone. We predicted that fighting would have an additive effect and that individuals that were both exposed to pheromonal cues and competed in a contest would have higher hormone levels compared to individuals that were only exposed to pheromonal cues.

2. Methods

2.1. Study system

Mangrove rivulus populations are androdioecious; consisting of males and self-fertilizing hermaphrodites [25–26]. While there are documented cases of outcrossing between males and hermaphrodites [27], the most common mode of reproduction for rivulus is self-fertilization. Repeated bouts of selfing can result in completely homozygous individuals capable of producing offspring that are genetically identical to parent and all siblings (isogenic lineages; [28–29]).

Individuals from three distinct, isogenic lineages derived from field-caught individuals collected at various geographic locales (HON9: Utila, Honduras; R2: Roatan, Bay Islands, Honduras; RHL: San Salvador, Bahamas), were utilized in this study. All lineages were confirmed homozygous at 32 highly polymorphic loci [28–30]. Only adult hermaphrodites (>6 months of age) were utilized. All focal individuals were housed in ventilated, 1 l Rubbermaid® containers filled with 25 ppt salt water (Instant Ocean® salt and tap water). All individuals were kept under a 12L:12D photoperiod, a temperature of 26 ± 1 °C, and were fed daily 2 ml of live brine shrimp (*Artemia*) nauplii reconstituted in water. The University of Alabama Institutional Animal Care and Use Committee approved all procedures described herein (IACUC #13-309-1).

2.2. Experimental protocol

All focal individuals were measured (mm) and weighed (g). Average mass of all focal individuals was 0.36 ± 0.08 g (range: 0.2–0.58 g) and average standard length (from snout to caudal peduncle) was 27.38 ± 1.74 mm (range: 23.3–31.8 mm). Afterwards, focal individuals from each lineage were assigned to each of the three treatments based on mass and standard length to keep variance in body size consistent among treatments. In treatment 1, a focal individual was isolated overnight in one compartment of our contest arenas, $31 \times 20 \times 15$ cm Plexiglas containers lined with black corrugated plastic; divided in the center by a black, non-reflective partition. This treatment was used to quantify hormone concentrations of individuals that were not exposed chemically, visually or physically to a potential competitor ($N = 24$; 8 per lineage). In treatment 2, a focal individual and a communal partner were housed overnight in the right and left compartments of the contest arena, respectively. The focal individuals and communal partners were matched by lineage and size ($\leq 10\%$ mass asymmetry). The focal individual and communal partner were visually, but not chemically, isolated by an opaque black partition. This treatment was used to quantify hormone concentrations of individuals that were chemically, but not visually or physically, exposed to a potential competitor ($N = 24$; 8 per lineage). It was confirmed that the partition allowed water to pass between compartments in a pilot study; non-experimental fish, one in each compartment, were placed into the contest arenas, food dye was added to the right-hand side compartment, and at 0800 h the following day, it was found that the dye had been evenly dispersed throughout both compartments. In treatment 3, two focal individuals, matched by lineage and size ($\leq 10\%$ mass asymmetry), were housed overnight in the contest arenas separated by an opaque partition. At 1000 h the following day

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