

Behavioral interactions between sexes in the critically endangered annual killifish *Leptopanchax itanhaensis* (Cyprinodontiformes, Rivulidae)

João Henrique Alliprandini da Costa^{1*} , Victor Monteiro Zanette² , Ana Giulia Stefanelli Biussi³ , Amanda Selinger³ 
*Contato principal

¹ Universidade Estadual Paulista “Júlio de Mesquita Filho”/UNESP, Instituto de Biociências, Programa de Pós-Graduação em Biodiversidade de Ambientes Costeiros/PPGBAC, São Vicente/SP, Brazil. < jh.costa@unesp.br >.

² Universidade Santa Cecília/UNISANTA, Laboratório de Biologia de Organismos Marinhos e Costeiros/LABOMAC, Santos/SP, Brazil. < zanettevictor81@gmail.com >.

³ Universidade Estadual Paulista “Júlio de Mesquita Filho”/UNESP, Instituto de Biociências, Núcleo de Estudos sobre Poluição e Ecotoxicologia Aquática/NEPEA, São Vicente/SP, Brazil. < ana.gs.biussi@unesp.br, amandaselinger@gmail.com >.

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ABSTRACT – We provide the first quantitative description of intersexual behavioral interactions in the critically endangered annual killifish *Leptopanchax itanhaensis*, aiming to characterize its behavioral repertoire, sex-specific expression of behaviors, and variation associated with couple size. Behavioral observations were conducted on seven couples sampled from a roadside ditch in the coastal Atlantic Forest of southeastern Brazil. Behavioral frequencies were recorded during standardized observation periods, converted to relative proportions, and analyzed using generalized linear mixed models to test for sex differences in total behavioral activity and behavioral diversity while accounting for couple identity. Behavioral composition varied markedly among couples and across size classes. Resting in the bottom was the most frequent behavior in both sexes, while courtship-related behaviors were more prevalent in larger couples. Total behavioral activity and behavioral diversity did not differ significantly between sexes. However, males more frequently exhibited courtship and harassing behaviors, whereas females more frequently exhibited being courted and escape behaviors. These findings provide the first behavioral baseline for this critically endangered species and highlight the importance of behavioral studies for understanding *habitat* use and reproductive interactions in annual killifishes.

Keywords: Atlantic Forest; intersexual behavior; courtship; mate choice; body size.

Interações comportamentais entre sexos no killifish anual criticamente em perigo *Leptopanchax itanhaensis* (Cyprinodontiformes, Rivulidae)

RESUMO – Apresentamos a primeira descrição quantitativa de interações comportamentais intersexuais no killifish anual *Leptopanchax itanhaensis*, criticamente em perigo, com o objetivo de caracterizar seu repertório comportamental, a expressão de comportamentos específicos de cada sexo e a variação associada ao tamanho do casal. Observações comportamentais foram realizadas em sete casais amostrados em uma vala de estrada na Mata Atlântica costeira do sudeste

do Brasil. As frequências comportamentais foram registradas durante períodos de observação padronizados, convertidas em proporções relativas e analisadas utilizando modelos lineares mistos generalizados para testar diferenças entre os sexos na atividade comportamental total e na diversidade comportamental, levando em consideração a identidade do casal. A composição comportamental variou consideravelmente entre os casais e entre as classes de tamanho. Repousar no fundo foi o comportamento mais frequente em ambos os sexos, enquanto os comportamentos relacionados ao cortejo foram mais prevalentes em casais maiores. A atividade total e a diversidade de comportamentos não diferiram significativamente entre os sexos. No entanto, os machos exibiram com mais frequência comportamentos de cortejo e assédio, enquanto as fêmeas exibiram com mais frequência comportamentos de cortejo e fuga. Essas descobertas fornecem a primeira base comportamental para essa espécie criticamente ameaçada de extinção e destacam a importância de estudos comportamentais para a compreensão do uso do *habitat* e das interações reprodutivas em peixes anuais.

Palavras-chave: Mata Atlântica; comportamento intersexual; cortejo; escolha de parceiro; tamanho corporal.

Interacciones comportamentales entre sexos en el killifish anual críticamente amenazado *Leptopanchax itanhaensis* (Cyprinodontiformes, Rivulidae)

RESUMEN – Presentamos la primera descripción cuantitativa de interacciones comportamentales intersexuales en el killifish anual *Leptopanchax itanhaensis*, críticamente amenazado, con el objetivo de caracterizar su repertorio comportamental, la expresión de comportamientos específicos de cada sexo y la variación asociada al tamaño de la pareja. Las observaciones comportamentales se realizaron en siete parejas muestreadas en una zanja de carretera en la Mata Atlántica costera del sudeste de Brasil. Las frecuencias comportamentales fueron registradas durante períodos de observación estandarizados, convertidas en proporciones relativas y analizadas mediante modelos lineales mixtos generalizados para evaluar diferencias entre los sexos en la actividad comportamental total y en la diversidad comportamental, considerando la identidad de la pareja. La composición comportamental varió considerablemente entre las parejas y entre las clases de tamaño. Descansar en el fondo fue el comportamiento más frecuente en ambos sexos, mientras que los comportamientos relacionados con el cortejo fueron más prevalentes en parejas de mayor tamaño. La actividad comportamental total y la diversidad comportamental no difirieron significativamente entre los sexos. Sin embargo, los machos mostraron con mayor frecuencia comportamientos de cortejo y acoso, mientras que las hembras mostraron con mayor frecuencia comportamientos de cortejo y de huida. Estos hallazgos proporcionan la primera base comportamental para esta especie críticamente amenazada de extinción y destacan la importancia de los estudios comportamentales para comprender el uso del hábitat y las interacciones reproductivas en peces anuales.

Palabras clave: Mata Atlántica; comportamiento intersexual; cortejo; elección de pareja; tamaño corporal.

Rivulidae are a diverse family of Neotropical killifishes that includes both annual and non-annual species. Annual killifishes usually inhabit temporary pools, dynamics environments characterized by extreme fluctuating environmental conditions and seasonal *habitat* desiccation [1]. Moreover, they exhibit pronounced sexual dimorphism where males are intensively colored while females are more cryptic [2]. These differences extend beyond color patterns in Rivulidae, as behavioral studies have demonstrated intersexual differences in avoiding competition and predation risk [3]. Ethological studies in the family have also evaluated social and reproductive behavior [4], courtship [5, 6, 7], sound production during the courtship [8], and even intersexual differences in rhythmic locomotion and reproductive activity [9]. However, these behavioral investigations are scarce compared with other studies within the clade, highlighting a gap that still needs to be filled for many taxa [10], representing one of the least explored dimensions of killifish biology.

Intersexual behavioral differences in annual killifish play an important role in territory defense and mate choice [2,7]. Nevertheless, differences between sexes were also reported regarding feeding preferences [4] and even predator avoidance. In fact, sex-specific coloration is a key factor influencing the demographic of annual killifishes, since predators preferentially target the more colorful sex [11]. Previous studies have also shown that antagonistic interactions may occur between males and females, although less frequently than within the same sex [4], that males frequently perform lateral and sigmoid courtship displays [6,7], and that females typically spend longer periods in quietness during courtship, probably representing an evaluation phase before mating [6,7]. Despite their biological relevance, these intersexual behavioral studies remain restricted to a few species, such as *Simpsonichthys boitonei* Carvalho, 1959 [4], *Argolebias nigripinnis* (Regan, 1912) [7], and *Garcialebias reicherti* (Loureiro & García, 2004) [6,9], highlighting the need for comparable studies across the diversity of Rivulidae.

Leptopanchax itanhaensis (Costa, 2008) is a small annual killifish endemic to the Preto River sub-basin in Itanhaém, São Paulo, Brazil, that inhabits lowland forest pools with low volume characterized by acidic and hypoxic blackwaters. The species is currently listed as critically endangered [12, 13] and belongs to a genus composed of six valid species, most of which are either rare and highly threatened or possibly extinct [14,15]. Despite its recent records after years without confirmed occurrences [16], little is known about its distribution, ecology, and biological traits, and filling these knowledge gaps is essential for improving our understanding of the species' biology and conservation needs.

Here, we provide a preliminary quantitative assessment of the behavioral repertoire of *L. itanhaensis* couples, focusing on (i) the relative frequency of behaviors across observed couples, (ii) variation associated with couple size, and (iii) differences in behavioral activity and diversity between sexes. By documenting these patterns, we aim to provide an initial characterization of the species' behavioral repertoire and sex-specific behavioral expression, establishing a preliminary baseline for future behavioral studies while helping to fill an important gap in the ecology of this highly threatened species.

In January 2026, 14 individuals of *L. itanhaensis*, seven males and seven females (Figure 1), were sampled from a roadside ditch (24°11'23.1"S, 46°54'25.5"W) using hand nets (50 × 40 cm frame, 1 mm mesh). Sampling was conducted in the Preto River sub-basin, part of the Itanhaém River basin, located in the coastal Atlantic Forest of São Paulo State, Brazil. This lowland floodable area is characterized by sandy-clay soils, remnant restinga vegetation, and blackwater systems with acidic and hypoxic conditions resulting from the decomposition of lignin-rich organic matter [16]. The sampled ditch had a maximum length of 8.46 m, a maximum width of 3.42 m, and a maximum depth of 0.33 m, with a measured pH of 6.97, dissolved oxygen concentration of 3.24 mg L⁻¹, and water temperature of 23.74 °C, at the time of sampling. Specimens were identified following recent occurrences [16], since it's the only annual killifish with records within this sub-basin.

After capture, fish were temporarily maintained in a field station located near the sampling site (< 500 m distance). Each individual was kept separately in aerated containers containing 300 mL of water collected from the sampling site and maintained at room temperature (20 – 25 °C) for two days following capture. Subsequently, individuals were paired into seven couples (one male and one female) and transferred to glass aquaria measuring 29 cm in length, 19 cm in width, and 18 cm in height, filled with a 14 cm water column. The aquaria were maintained inside the field station under natural daylight, ambient temperature, protected from direct sunlight and human disturbance. Couples were formed based on similar body size, with individuals measured and assigned to one of three size classes according to standard length: < 1.5 cm (N = 1), 1.5–2.0 cm (N = 2), and 2.0–2.5 cm (N = 4). All individuals were adults, and the size classes therefore represented variation in adult body size rather than differences in ontogenetic stage. Each couple was maintained in the aquarium for two hours prior to behavioral observations, under standardized conditions and in the absence of external stimuli. Because this study was designed as a preliminary field assessment and all individuals were released back into their original *habitat*

immediately after the trials, we opted to minimize the time spent under experimental conditions rather than maintaining fish in captivity for prolonged acclimation. To mimic natural conditions, 5 g of leaf litter was placed at the bottom of each aquarium, allowing fish to hide if desired, similar to the litter-covered substrate of forest pools inhabited by the species. All litter used in the trials was collected from the same ditch where fish were sampled.

After the acclimation period, the behavior of both individuals in each couple was recorded for 30 min as a preliminary behavioral assessment, following the observation time adopted by García et al. [6]. All trials were conducted by the same observer, positioned approximately one meter away and hidden from the fish's view. Aquaria were placed on a table at a height above the seated observer to avoid alignment with the fish's line of sight. Behavioral events were recorded for each sex as the frequency of occurrence of predefined behavioral categories. During each trial, one observer continuously identified and verbally reported the behaviors of both individuals, while a second researcher simultaneously recorded each behavioral event separately for males and females, minimizing the risk of missed observations. Behavioral categories were adapted from Domínguez-Castanedo and Reichard [2] and included (Table 1): 1) territoriality; 2) harassing other sex; 3) chasing other sex; 4) attacking other sex; 5) escaping other sex; 6) courtship; 7) courtship and spawning; 8) being courted; 9) breeding in bottom; 10) maintenance; 11) feed; 12) rest in the bottom; 13) rest in the surface; 14) dive into the bottom; 15) patrol the bottom; 16) patrol the surface; 17) hide. After behavioral trials, all individuals were released at the original sampling site. All procedures were conducted in accordance with ethical approval – Comissão de Ética no Uso de Animais, Instituto de Biociências, Câmpus do Litoral Paulista (CEUA-IB/CLP) no. 15/2023 and under Sistema de Autorização e Informação em Biodiversidade (Sisbio) collecting license (no. 90241-3).



Figure 1 – Photographs of *Leptopanchax itanhaensis* individuals; (A) male, and (B) female. Pictures taken by Amanda Selinger.

Table 1 – Behavioral categories recorded for *Leptopanchax itanhaensis* during observations.

Behavioral category	Definition
Territoriality	Stationary or active defense of a particular area against the other individual.
Harassing other sex	Repeated close approaches or persistent following of the opposite sex without immediate physical attack.
Chasing other sex	Rapid pursuit of the opposite sex through the aquarium.
Attacking other sex	Physical aggressive interaction involving direct contact or biting attempts.
Escaping other sex	Rapid swimming away from the opposite sex in response to its approach or aggression.
Courtship	Courtship display directed toward the opposite sex, including lateral and/or sigmoid displays and fin movements.
Courtship and spawning	Courtship behavior immediately followed by spawning.
Being courted	Remaining receptive or relatively immobile while receiving courtship displays from the opposite sex.
Breeding in bottom	Reproductive activity performed on or within the bottom substrate.
Maintenance	Self-maintenance behaviors such as body cleaning or fin adjustments, not directly related to social interactions.
Feed	Searching for, capturing, or ingesting food items.
Rest in the bottom	Remaining motionless or nearly motionless on or immediately above the bottom substrate.
Rest in the surface	Remaining motionless or nearly motionless close to the water surface.
Dive into the bottom	Rapid movement from the water column toward the bottom.
Patrol the bottom	Active swimming while exploring the bottom region of the aquarium.
Patrol the surface	Active swimming while exploring the surface region of the aquarium.
Hide	Remaining concealed beneath leaf litter or other available shelter.

For each couple and couple-size class, behavioral frequencies were converted to proportions (%). Total behavioral activity (behavior counts) and behavioral diversity were quantified for each individual. Behavioral diversity was measured using the Shannon index (H'), because it integrates both the number of behavioral categories and their relative frequencies. Sex differences were tested using generalized linear mixed models, with sex as a fixed effect and couple identity as a random intercept. Activity counts were modeled using a negative binomial distribution with a log link, whereas Shannon diversity was modeled using a Gamma distribution with a log link. Model residuals were evaluated using the *DHARMa* package. Analyses were conducted in R version 4.4.3 using *vegan* (for Shannon index), *glmmTMB* (for mixed models), and *DHARMa* (residual evaluation) R packages; figures were produced using *ggplot2*.

Considering all fish together, the most common behaviors for males were rest in the bottom (27.4%), courtship (20.5%) and harassing other sex (16.4%), meanwhile, for females were rest in the bottom (32.8%),

being courted (22.4%) and escape other sex (14.9%). Behavioral composition varied markedly among couples and sexes, with no single behavioral profile dominating all observations (Figure 2A). Resting in the bottom was frequent across all couples, while courtship-related behaviors, harassment and hiding showed strong inter-couple variability. Behavioral profiles also differed across couple size classes (Figure 2B). Smaller couples exhibited higher relative frequencies of patrolling, hiding, and feeding, whereas larger couples showed increased proportions of courtship.

Total behavioral activity did not differ significantly between sexes (Figure 2C; negative binomial generalized linear mixed model, $z = 0.51$, $p = 0.61$). Similarly, behavioral diversity, measured by the Shannon index, showed no significant difference between males and females (Figure 2D; Gamma generalized linear mixed model, $z = 0.05$, $p = 0.96$). These results indicate that males and females expressed comparable levels of both behavioral activity and behavioral diversity. Even so, radar plots revealed clear sex-specific behavioral patterns (Figure 3). Males exhibited higher frequencies of rest in the bottom, courtship, harassment, and feeding, whereas females showed higher frequencies of rest in the bottom, being courted, escape, and hiding. Resting in the bottom was the most frequent behavior of both sexes.

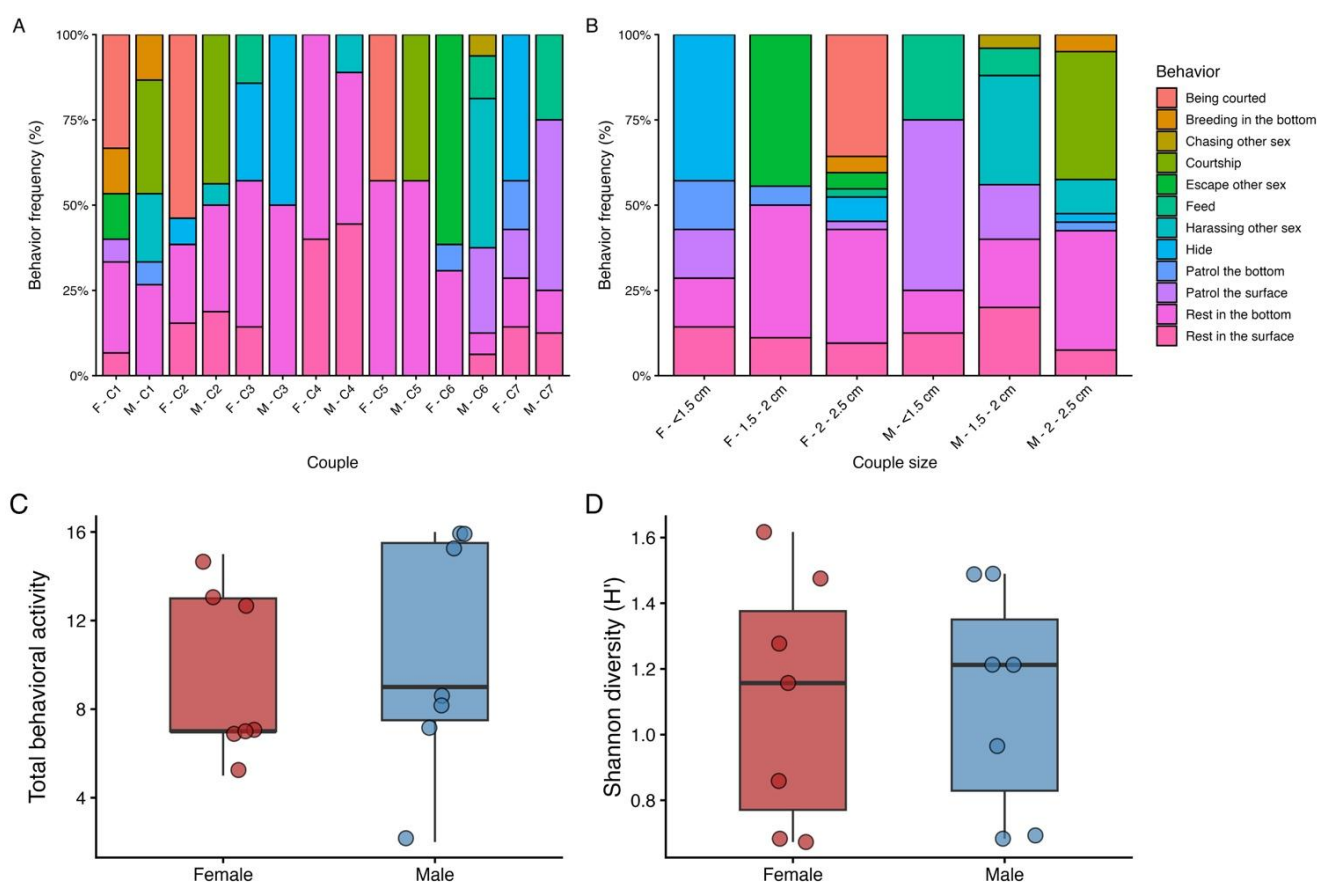


Figure 2 – Behavioral composition and sex-specific behavioral metrics of *Leptopanchax itanhaensis*. (A) Relative frequency (%) of behavioral categories recorded for each couple (C1–C7) and sex (F = females; M = males). (B) Relative frequency (%) of behavioral categories according to couple size classes and sex (F = females; M = males). (C) Total behavioral activity (abundance of behavioral events) per individual for females and males. (D) Behavioral diversity estimated by the Shannon index (H') for females and males.

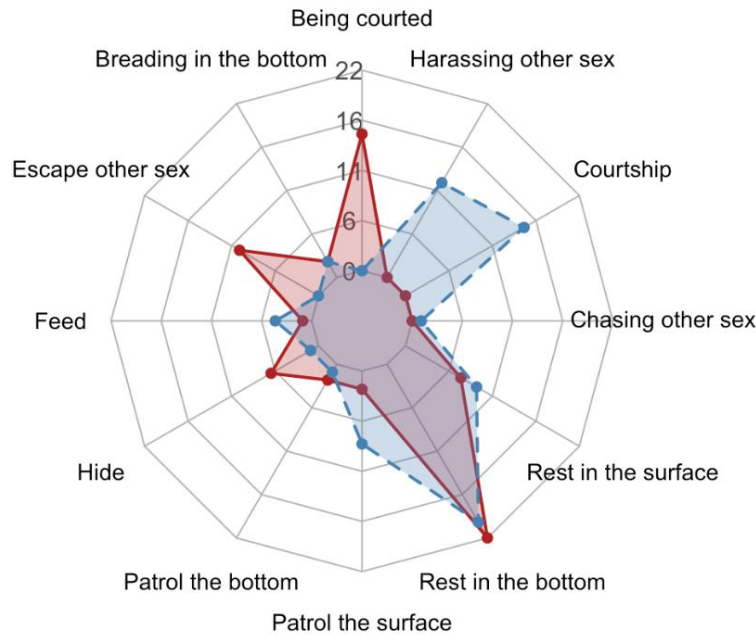


Figure 3 – Sex-specific behavioral profiles of *Leptopanchax itanhaensis*. Radar plot showing the absolute frequency of the most frequent behavioral categories recorded for females (red) and males (blue). Each axis represents a behavioral category, and values correspond to the total number of recorded events per sex, pooled across all couples. Shaded areas indicate the relative magnitude of behavioral expression for each sex.

Here we provide the first description of intersexual behavioral interactions in *L. itanhaensis*. Although we did not detect significant differences between males and females in total behavioral activity or behavioral diversity, despite the high heterogeneity observed among couples, males and females shared a broadly similar behavioral repertoire while differing in the frequency of specific behaviors. In particular, males more frequently exhibited harassment and courtship behaviors, whereas females more frequently displayed escape and hiding behaviors, revealing sex-specific patterns that likely reflect differences in reproductive roles and social interactions. It is worth noting that locomotor activity in Rivulidae is often reduced when individuals are observed in pairs compared to isolation [9], so our results do not necessarily imply that males and females exhibit similar activity or behavioral diversity when isolated or when present with individuals of the same sex [2], an aspect that should be explicitly tested in future studies.

Both males and females exhibited a high frequency of resting in the bottom, a behavior that appears particularly relevant for *L. itanhaensis*, even based only in these preliminary results. Other annual rivulids are known to occupy the lower strata of the water column more frequently than non-annual species [4], and this strategy may be especially advantageous for *L. itanhaensis*, which inhabits temporary forest pools with abundant leaf litter and blackwater conditions [15]. In such environments, the reddish coloration of both males and females may enhance camouflage among decomposing litter, facilitating predator avoidance and benthic foraging, particularly on microcrustaceans (JHAC, author, personal observation based on stomach content analyses of other specimens). In addition, males of annual killifishes commonly establish territories close to the substrate [2], which could further explain the high frequency of bottom-associated behaviors observed here.

The high frequency of courtship behaviors performed by males, often preceded by harassment of females, is consistent with patterns reported for other rivulid species, in which lateral and sigmoid displays are common components of courtship [6]. The “being courted” behavior recorded in this study involved periods of reduced movement by females during courtship, likely reflecting an evaluative phase in which females assess potential

mates, as reported for other annual killifishes [6]. This phase is particularly important because females typically incur higher fitness costs from poor mate choice [7]. During courtship, we frequently observed fin vibrations and undulations of the dorsal and anal fins in *L. itanhaensis* males, which are likely important visual cues for attracting females [7]. However, the effectiveness of vibration frequency, duration, and intensity on reproductive success remains unknown and warrants further investigation. Other complementary signaling modalities, such as sound production [8] and chemical communication [17], may also play a role during courtship in this species, since the integration of multiple signals could enhance female assessment of male condition [18, 7], representing an important avenue for future behavioral studies.

We also detected differences among size classes, with smaller couples exhibiting higher frequencies of hiding behavior and larger couples showing more frequent courtship. However, these patterns should be interpreted with considerable caution because the size classes were represented by very few couples, particularly the smallest and intermediate classes. Consequently, our results should be regarded as preliminary observations rather than evidence of size-related behavioral differences. Although it is possible that body size influences the expression of reproductive behaviors in annual killifishes [19], this hypothesis requires testing with substantially larger sample sizes before any biological interpretation can be made. Moreover, sampling was conducted during the peak rainy season, when most individuals were expected to be relatively older, as they likely hatched early in the flooding period. This limited sample size represents one of the main constraints of our study. Despite this limitation, it is important to emphasize that this work represents a first step toward understanding the behavioral repertoire of *L. itanhaensis*, a critically endangered and extremely rare species [12, 13, 16], for which any new biological information is valuable in helping to fill important knowledge gaps.

Future studies should incorporate intrasexual interactions, which can vary substantially in annual killifishes [2], as well as the role of chemical cues and female mate choice mediated by display frequency and fin undulation during sigmoid displays. By now, improving our understanding of intersexual behavioral interactions for a critically endangered species, such as *L. itanhaensis* [12], even in a preliminary manner, provides essential insights into *habitat* use and courtship dynamics. More broadly, documenting the behavioral repertoire of this species establishes a baseline for future ecological and conservation studies, allowing future studies to understand behavioral responses to *habitat* alteration, and establishing a foundation for studies on its reproductive ecology under natural and captive conditions. Such information may also contribute to the development of *ex situ* conservation initiatives by helping to identify whether pairs of only one male and one female represent an appropriate social unit for captive breeding and reproductive management programs [20].

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