Acta Limnologica Brasiliensia

Publication of the Brazilian Association of Limnology

Original Article
Acta Limnologica Brasiliensia, 2023, vol. 35, e30
https://doi.org/10.1590/S2179-975X6023
ISSN 2179-975X on-line version

From the pond to the creek many years ago: life-history dynamics of feral poeciliids in Brazil

Do tanque de piscicultura para o córrego muitos anos atrás: dinâmicas da história de vida de poecilídeos ferais no Brasil

André Lincoln Barroso Magalhães[1]*, Eneida Maria Eskinazi-Sant'Anna[1], Mário Luís Orsi[2], Dilermando Pereira Lima Junior[3], Jean Ricardo Simões Vitule[4] and Fernando Mayer Pelicice[5]

[1]Programa de Pós-graduação em Ecologia de Biomas Tropicais, Departamento de Biodiversidade, Instituto de Ciências Exatas e Biológicas, Universidade Federal de Ouro Preto – UFOP, Rua Diogo de Vasconcelos, 122, 35400-000, Ouro Preto, MG, Brasil

[2]Laboratório de Ecologia de Peixes e Invasões Biológicas, Universidade Estadual de Londrina – UEL, Rodovia Celso Garcia Cid, PR 445, Km 380, CP 10.011, Campus Universitário, 86057-970, Londrina, PR, Brasil

[3]Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos, Universidade Federal do Mato Grosso – UFMT, Rodovia MT-100, Km 3,5, Setor Universitário, 78698-000, Pontal do Araguaia, MT, Brasil

[4]Laboratório de Ecologia e Conservação, Departamento de Engenharia Ambiental, Setor de Tecnologia, Universidade Federal do Paraná – UFPR, Rua Franscisco H. dos Santos 210, Centro Politécnico, Setor de Tecnologia, CP 19.011, Jardim das Américas, 81531-970, Curitiba, PR, Brasil

[5]Núcleo de Estudos Ambientais, Universidade Federal do Tocantins – UFT, Rua 03, Quadra 17, Jardim dos Ipês, 77500-000, Porto Nacional, TO, Brasil

*e-mail: andrebiomagalhaes@gmail.com

Cite as: Magalhães, A.L.B. et al. From the pond to the creek many years ago: life-history dynamics of feral poeciliids in Brazil. *Acta Limnologica Brasiliensia*, 2023, vol. 35, e30.

Abstract: Aim: We investigated trophic and reproductive traits of feral guppy *Poecilia reticulata* and southern platyfish *Xiphophorus maculatus* in a headwater creek located in the Paraíba do Sul River basin, southeastern Brazil. **Methods:** Fish were collected bimonthly from January to December 2017 using sieve in Lopes Creek. Stomach items were analyzed and developmental stages of females were classified as 1 (Non-gravid), 2 (Yolked ova), 3 (Eyed embryos), and 4 (Mature embryos). The mean values of fecundity and population structure for each developmental stage were determined for females using six length classes. Bimonthly mean values of gonadosomatic index of females were overlayed with average bimonthly rainfall, water level/temperature, and the sex ratio was calculated. The juvenile-to-adult proportion was calculated bimonthly, and the phenotype (ornamental-type × wild-type) was also analyzed. **Results:** The guppy and southern platyfish fed, primarily, on detritus, and both species showed reproductive activity during all the sampling period. The mean fecundity of *P. reticulata* and *X. maculatus* was high and the smallest gravid female of guppy measured 0.8 cm SL, and southern platyfish 1.0 cm. The GSI of both species showed peaks coinciding with the highest rainfall, water level/temperature, and females were significantly more frequent than males. Juveniles were found during all the sampling period, and both species were represented by wild-type forms. **Conclusions:** *P. reticulata* and *X. maculatus* presented opportunistic feeding, long reproductive period, high fecundity and early maturity. The year-round presence of reproductive females, juveniles and wild-type phenotypes suggests establishment of populations in the study area. We hypothesize that the introduction of both species has occurred several years ago, and the continued exposure to predation seems to have molded their life-history traits and phenotype.

Keywords: aquaculture; biological invasions; diet; livebearers; reproduction.

Resumo: Objetivo: Investigamos as características tróficas e reprodutivas de populações do guppy *Poecilia reticulata* e plati *Xiphophorus maculatus* ferais em um riacho de cabeceira localizado na bacia do rio Paraíba do Sul, sudeste do Brasil. **Métodos:** Exemplares foram coletados bimestralmente de janeiro a dezembro de 2017 utilizando-se peneira no riacho Lopes. Os itens alimentares foram analisados e os estágios de desenvolvimento embrionário de fêmeas foram classificados como 1 (Não grávida), 2 (Ovo), 3 (Embrião com olhos) e 4 (Embrião formado). Os valores médios da fecundidade e estrutura populacional para cada estágio de desenvolvimento embrionário foram determinados para as fêmeas usando seis classes de comprimento. Os valores médios bimestrais do Índice Gonadossomático de fêmeas foram associados com a precipitação média bimestral, nível/temperatura da água e a razão sexual foi calculada. A proporção juvenil-adulto foi calculada bimestralmente, e os fenótipos ornamental/selvagem também foram analisados. **Resultados:** O guppy e plati se alimentaram especialmente de detritos, e ambas espécies apresentaram atividade reprodutiva durante todo o período amostral. A fecundidade média de *P. reticulata* e *X. maculatus* foi alta e a menor fêmea grávida de guppy mediu < 1,0 cm e plati 1,0 cm CP. O IGS de ambas as espécies apresentaram picos coincidindo com maior precipitação, nível/temperatura da água, sendo as fêmeas mais numerosas que machos. Juvenis foram encontrados durante todo o período amostral, e ambas as espécies foram representadas pelo fenótipo selvagem. **Conclusões:** *P. reticulata* e *X. maculatus* apresentaram alimentação oportunista, longo período reprodutivo, alta fecundidade e maturidade precoce. A presença de fêmeas reprodutivas, juvenis e do fenótipo selvagem durante todo o período amostral sugere estabelecimento das espécies na área de estudo. Hipotetizamos que a introdução do guppy e plati ocorreu há vários anos, e que a contínua exposição à predação parece ter moldado aspectos de sua história de vida e fenótipo.

Palavras-chave: aquicultura; invasões biológicas; dieta; ovovivíparos; reprodução.

1. Introduction

In Brazil, aquatic invasions have been recognized as one of the most serious environmental problems since the last two decades (Pelicice et al., 2017; Vitule et al., 2019; Geller et al., 2020). Invasive aquatic organisms have spread over different habitats, causing multiple ecological disturbances and costs to Brazilian society (Adelino et al., 2021; Magalhães et al., 2021).

One of the major pathways by which invasive aquatic species are introduced and spread throughout Brazil is the aquarium trade (Magalhães & Jacobi, 2017; Vitule et al., 2019; Geller et al., 2020). With the growing pursuit of fish keeping, several aquarium fish species have recently been documented in inland waters, all of which are directly associated with aquarium dumping (Magalhães et al., 2017 and references therein) or escapes from fish farms (Magalhães et al., 2019, 2020, 2021). Some records are diagnosed as occasional, e.g., the translocated blackline tail tetra *Moenkhausia costae*, bristlemouth catfish *Ancistrus multispinis* (Magalhães et al., 2019); whereas some others, including the exotic zebra fish *Danio rerio* and oriental wheather loach *Misgurnus anguillicaudatus*, have established viable populations in several waterways (Abilhoa et al., 2013; Magalhães & Jacobi, 2013a; Magalhães et al., 2021).

The family Poeciliidae (Cyprinodontiformes) includes 42 genera and roughly 356 species, and is distributed naturally in Africa and the Americas [see Nelson et al. (2016)]. Many poeciliids, especially the guppy *Poecilia reticulata* and the southern platyfish *Xiphophorus maculatus*, are well known among Brazilian hobbyists, commonly sold in pet shops and raised in some ornamental fish farms (Magalhães & Jacobi, 2013b; Geller et al., 2020; Magalhães et al., 2021; Luduvice & Brito, 2023). As a consequence, they have been frequently released by hobbyists (i.e., aquarium dumping or pet release) from home aquaria and/or escaped from ornamental fish farms, and registered in all five Brazilian geopolitical regions (Oliveira & Bennemann, 2005; Montag et al., 2011; Krinski & Camera, 2018; Magalhães et al., 2021; Luduvice & Brito, 2023). Despite several populations of guppies and platies have been introduced to different Brazilian drainages, reliable studies related to their trophic and reproductive ecology are still incipient (Ferreira & Casatti, 2006; Rocha et al., 2009; Silva et al., 2012; Alves et al., 2016; Magalhães & Jacobi, 2017; Ganassin et al., 2020; Luduvice & Brito, 2023). When it comes to life-history aspects and evolution (i.e., phenotypic changes) of feral populations in response to shifts in ecological conditions (e.g., predation), studies are non-existent.

In this paper, we investigated ecological aspects of *P. reticulata* and *X. maculatus* introduced into a small creek in the region of Muriaé Ornamental Aquaculture Center, Minas Gerais State, with a special focus on life-history aspects of feral populations. In particular, this study investigated: (i) the trophic and reproductive dynamics of these fish (i.e., developmental stages, population structure for each developmental stage, gonadosomatic index and the association with environmental variables), (ii) the sex ratio, (iii) the possible establishment/evolution of feral populations (i.e., presence of young and alteration of phenotype ornamental-type to wild-type), and (iv) suggested management strategies to avoid new introductions of feral guppies and platies in the area affected by the largest ornamental aquaculture center in Brazil.

2. Materials and Methods

2.1. Study area

This study was conducted at an ornamental aquaculture center in the Muriaé region, located in the "Zona da Mata" of the Minas Gerais State, Brazil. The Muriaé Ornamental Aquaculture Center, the largest establishment in Brazil since 1979 [*sensu* Vidal Júnior & Costa (2000)], comprising 350 fish farms and 4,500 production ponds bordering small creeks located in an Atlantic Forest region. Most of the ponds are drained eight times a year, resulting in more than 30,000 release events per year (Magalhães et al., 2020). The majority of these ponds do not have devices to prevent the escape of non-native fish. As a result, fish escapes have been routine, and several small-sized ornamental fish have invaded and established populations in different creeks of the region (Magalhães & Jacobi, 2013a, 2017; Magalhães et al., 2020, 2021).

2.2. Field collections

One headwater creek was surveyed in this study, belonging to the Paraíba do Sul River basin. This creek runs across an ornamental fish farm with more than one hundred production ponds that cultivate many varieties of *P. reticulata* (e.g., snakeskin, dragon, Moscow, half-black) and *X. maculatus* (e.g., tuxedo, Mickey Mouse, wagtail, sunset). It is a slow-flowing habitat with an average width/depth of 100/48 cm respectively, muddy bottom devoid of aquatic macrophytes and their banks are covered by non-native grasses *Urochloa* spp. (Magalhães & Jacobi, 2017). According to local fish farmer, guppies and platies have been cultivated since 2001: fish escapes have occurred since then (Magalhães, pers. obs.). The native ichthyofauna is composed of only four native species: "lambaris" *Psalidodon parahybae* and *Deuterodon janeiroensis*, cascarudo *Callichthys callichthys*, suckermouth catfish *Hypostomus affinis* and the spot-sided livebearer *Poecilia vivipara*. Native invertebrates such as fishing spiders (Pisauridae), diving beetles (Dysticidae), water boatmen (Corixidae), water striders (Gerridae), dragonfly nymphs (Libellulidae), and water bugs (Belostomatidae) are also found. Currently, this headwater creek has been invaded by fifteen species of non-native fish such as rosy barb *Pethia conchonius*, "acará" *Cichlasoma dimerus* and several poeciliids such as black molly *Poecilia sphenops*, sailfin molly *Poecilia velifera*, green swordtail *Xiphophorus hellerii*, and variable platyfish *Xiphophorus variatus* (Figure 1) (Magalhães et al., 2022).

Fish were collected every two months, from January to December 2017, in Lopes Creek (20°50'16.5"S; 42°13'48.9"W), municipality of Vieiras, Minas Gerais State, southeastern Brazil (Figure 2). Juveniles (*P. reticulata*: 91, *X. maculatus*: 165) and adults (*P. reticulata*: 658 females, 402 males, *X. maculatus*: 364 females, 36 males) were collected from margins and channel bed, with a rectangular sieve measuring 95 cm long × 25 cm high and 0.3 mm mesh. The sieve was hauled 50 times along a 100 m-long transect during 2 h in Lopes Creek at daytime. The fishes were anesthetized on an ice slurry (IACUC, 2002) and soon after, sacrificed by immersion in Eugenol (Griffiths, 2000): then, the material was sorted by site collection, packed in plastic bags, fixed in 10% formalin, and subsequently transferred to 70% alcohol. Voucher specimens are deposited under their respective catalogue numbers in the Universidade Federal de Sergipe fish collection (CIUFS): *P. reticulata* CIUFS 2244, *X. maculatus* CIUFS 2260. The samplings were carried out under authorization from the Chico Mendes Institute for Biodiversity Conservation-ICMBio, granted through the System of Authorization and Information on Biodiversity-SISBIO, nº 61740. In the laboratory, all fish were measured (total and standard lengths, cm), weighted (g) and eviscerated to remove the stomach and gonads.

2.3. Feeding habits

Stomach items were analyzed under a stereoscopic microscope and, when possible, identified to the

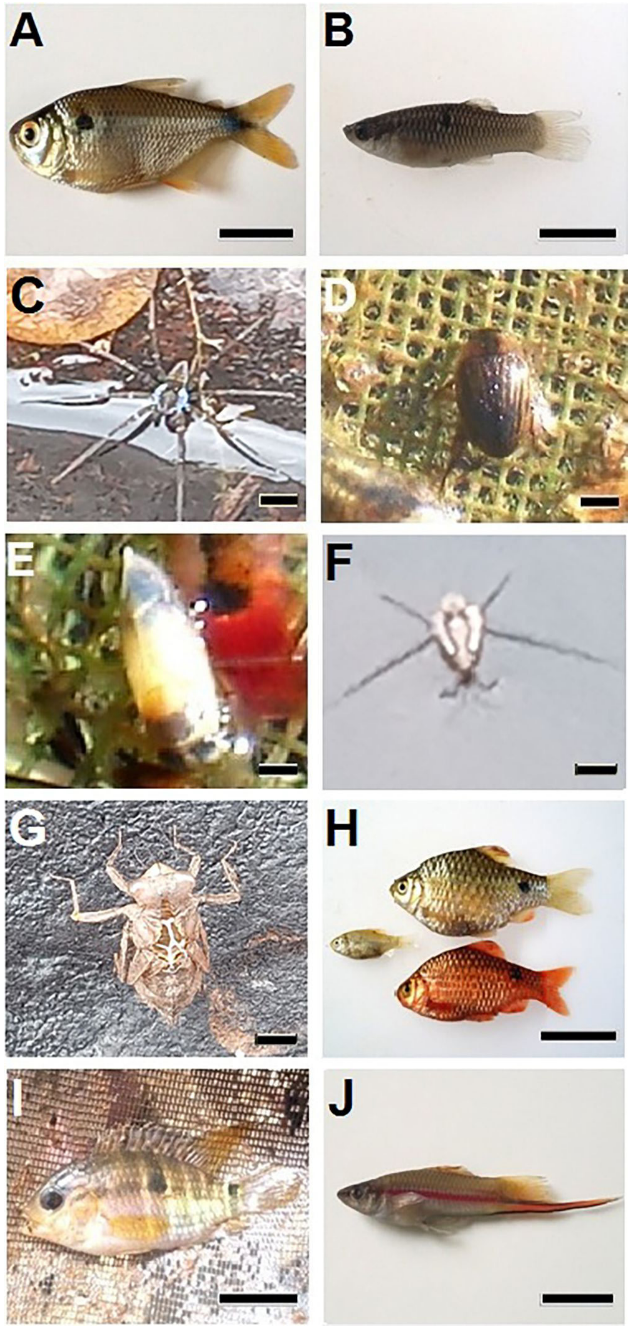

Figure 1. Aquatic predators found in Lopes Creek, municipality of Vieiras, Minas Gerais State, southeastern Brazil. Natives: (A) *Deuterodon janeiroensis*, (B) *Poecilia vivipara*, (C) fishing spider of the family Pisauridae, (D) diving beetle of the family Dysticidae, (E) water boatman of the family Corixidae, (F) water strider of the family Gerridae, (G) exuvia of a dragonfly nymph of the family Libellulidae. Non-natives: (H) *Pethia conchonius*, (I) *Cichlasoma dimerus*, and (J) *Xiphophorus hellerii*. Scale bars: 1 cm (fish), 1 mm (spider/insects).

lowest taxonomic level. The relative importance of each food item was calculated applying the Feeding Index (Kawakami & Vazzoler, 1980) described as: $IAi = ((Fi \times Vi)/(\Sigma \text{ Fi} \times Vi)) \times 100$, where $i = 1, 2, \ldots$ n are the food items, Fi is the frequency of occurrence of item i, Vi is the relative volume of item I, and Vi is the relative volume of item i.

2.4. Developmental stages

We adapted the methods of Haynes (1995) to determine the developmental stages of adult females. We classified as non-gravid those females without a conspicuously enlarged ventral region, absence of eggs, embryos, or gravid spot near the base of the anal fin. Females were classified as gravid when they

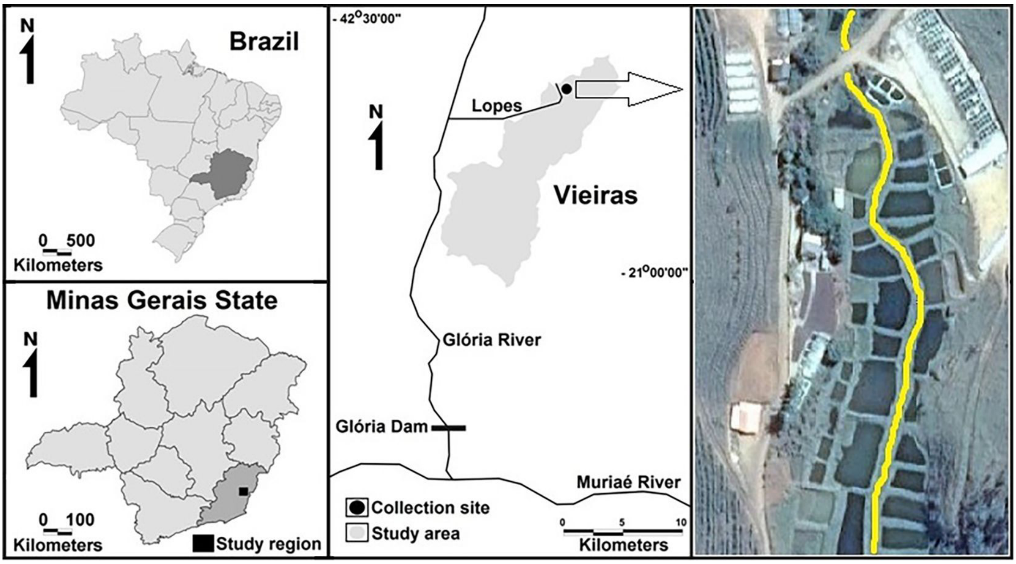

Figure 2. Map showing the Lopes Creek, municipality of Vieiras, Minas Gerais State, Brazil, where feral populations of *Poecilia reticulata* and *Xiphophorus maculatus* were monitored. In the satellite image, the section of the Lopes Creek (yellow) is surrounded by more than 40 production ponds stocked with many varieties of guppies and platies.

had enlarged belly, presence of gravid spot, eggs or embryos. Developmental stages were then classified as follows: Non-gravid (stage 1 - ovarian tissue without ovum and/or embryos), Yolked ova (stage 2 - ovum in the process of yolking), Eyed embryos (stage 3 - eyes pigmented, head enlarged compared to trunk, caudal and pectoral fin buds present), Mature embryos (stage 4 - yolk sac mostly or completely absorbed, pectoral fins elongated, embryo resembling a small adult) (Figure 3). After determining the developmental stages, the bimonthly absolute and relative frequencies of females were calculated.

2.5. Fecundity

We calculated the bimonthly and total mean values of fecundity (number of embryos in stages 3 and 4 per female). Only embryos were used as a measure of fecundity because ova development and fertilization are not discernible with a dissecting microscope (Haynes, 1995).

2.6. Population structure for each developmental stage

The population structure associated with developmental stages was determined for females using six standard length classes (0.5 cm intervals) (Hojo et al., 2004). We calculated the number of fish within each length class for each developmental stage.

2.7. Gonadosomatic index and environmental factors

The gonadosomatic index (GSI) (Hernández et al., 2004) was calculated bimonthly for females using the formula: $GSI = (GW/BW \times 100)$, where GW is the gonad weight, and BW is the body weight. We grouped the bimonthly mean values of GSI of females which were then overlayed with the average bimonthly rainfall (mm), and the water level (cm) in the Lopes Creek for identification of potential trends between biotic (GSI) and abiotic factors (rainfall, water level/temperature). Rainfall data was obtained from the database of the weather station A517 located in the municipality of Muriaé (INMET, 2020), water level was measured using a 2-m-long pole marked every 10 cm and water temperature was obtained with a mercury-in-glass thermometer to the scale 0º to 50ºC.

2.8. Sex ratio

The sex ratio (Pope et al., 2010) was calculated from the bimonthly and total number of females and males of *P. reticulata* and *X. maculatus* collected in the Lopes Creek. Chi-square (χ^2) goodness-of-fit test was used to check whether significant differences were present in the sex ratio (Sokal & Rohlf, 1995). Differences were significant when $p < 0.05$. The analysis was performed using the Paleontological Statistics-Past software (3.25 version) (Hammer et al., 2001).

2.9. Establishment and feral status

The adult-to-juvenile relative frequencies (Pope et al., 2010), were calculated bimonthly for *P. reticulata* and *X. maculatus* collected in

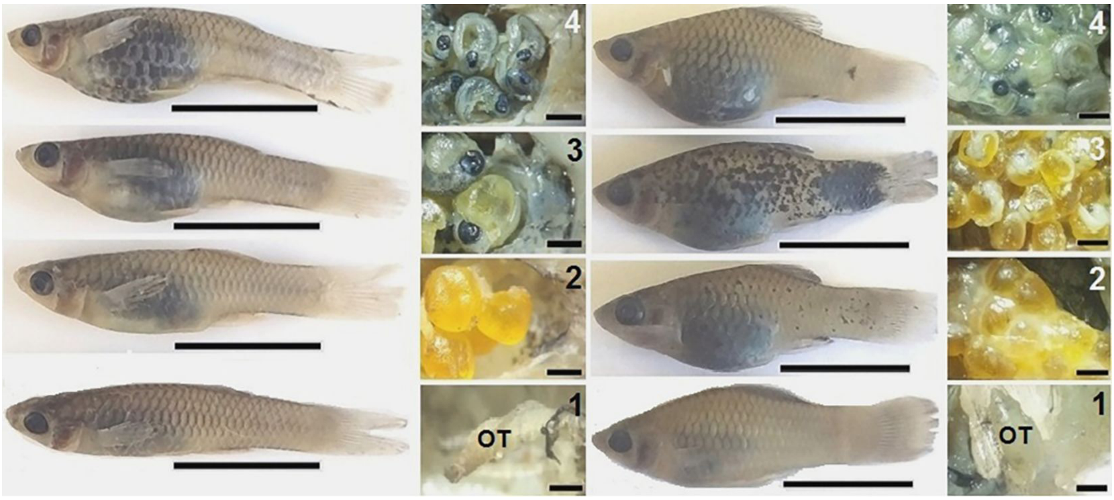

Figure 3. Macroscopic and mesoscopic developmental stages of feral *Poecilia reticulata* (left column) and *Xiphophorus maculatus* (right column) females captured in Lopes Creek, Minas Gerais State, Brazil. Developmental stages: 1) Non-gravid (OT: ovarian tissue without ovum or embryos), 2) Yolked ova, 3) Eyed embryos, 4) Mature embryos. Scale bars (macroscopic: 1 cm, mesoscopic: 20 ×).

the Lopes Creek. The phenotype of females and males of guppies and platies was also analyzed (i.e., in percentages) to verify variations in color patterns. Two color patterns were considered as basic phenotypic categories: (i) ornamental-type and (ii) wild-type. Ornamental-type are colorful forms cultivated on the ornamental fish farm that surrounds Lopes Creek: guppy females are plainer in color and have a smaller colorful tail, while males are brighter and have colorful tails with various shapes such as round, flag, delta, or half-moon. In southern platyfish, both females and males express bright color patterns including yellow/red pigmentation (Figure 4A, 4B, 4C, 4D). Wild-type guppy females are dull brown, males contained pale orange stains and small black spots on the anterior/posterior lateral part of the body and a translucent small tail. Southern platyfish females and males are beige with or without melanic/speckled patches on the body and presence or absence of black spots on the caudal peduncle (Figure 4E, 4F, 4G, 4H). Each captured fish was assigned as ornamental or wild-type.

3. Results

3.1. Feeding habits

The guppy and southern platyfish fed primarily on detritus (unspecified organic and inorganic material), followed by aquatic insects (i.e., dragonfly nymphs, true fly larvae) and zooplankton. Both species also consumed food resources of allochthonous origin such as ants and flies (Table 1).

3.2. Developmental stages

Females of *P. reticulata* (n = 525) and *X. maculatus* (n = 219) were found in several reproductive stages (i.e., stages 2, 3, 4) during the sampling period in Lopes Creek. Females in stages 3 and 4 were found in all months for *P. reticulata*, and between September and April for *X. maculatus* (Figure 5).

3.3. Fecundity

The mean fecundity of guppy and southern platyfish was greater than 27 and 30 embryos per brood respectively in each bimester; considering the total period, it was greater than 32 and 34 embryos per brood respectively (Figure 6).

3.4. Population structure for each developmental stage

We observed wide variation in the proportion of developmental stages within length classes. Virtually all stages were recorded in each length class; stages 2 and 3 predominated across length classes for *P. reticulata*, while stages 1 and 2 predominated for *X. maculatus*. In Lopes Creek, the smallest gravid female of guppy measured 1.4 cm TL (0.8 cm SL) and southern platyfish measured 1.5 cm TL (1.0 cm SL). The largest *P. reticulata* females were 3.9-4.4 TL (3.3-3.8 cm SL) and *X. maculatus* 4.5-5.0 TL (4.0-4.5 cm SL) (Table 2).

3.5. Gonadosomatic index and environmental factors

For both species, GSI of females showed peaks coinciding with the highest rainfall, and water level/temperature values (Figure 7).

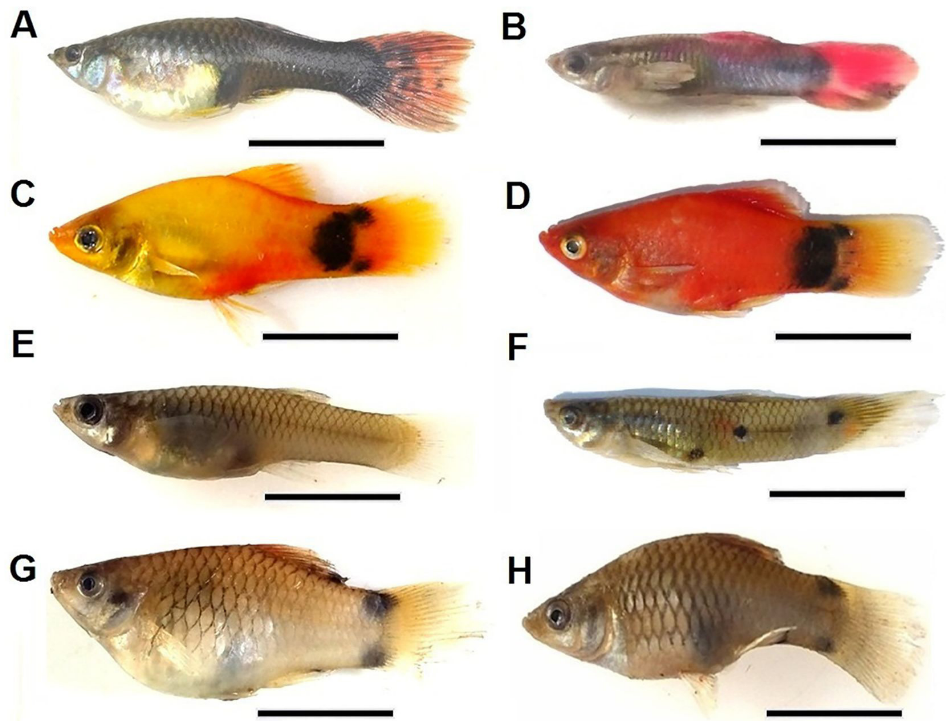

Figure 4. Ornamental and wild-type phenotypes of *Poecilia reticulata* and *Xiphophorus maculatus* reared in an ornamental fish farm bordering Lopes Creek and collected in the aforementioned creek, Minas Gerais State, Brazil. (A, B) Ornamental-type female/male of *P. reticulata* (red mosaic round-tail variety), (C, D) ornamental-type males of *X. maculatus* (yellow/red Mickey Mouse varieties), (E, F) wild-type female/male of *P. reticulata*, (G, H) wild-type females of *X. maculatus*. Scale bar: 1 cm.

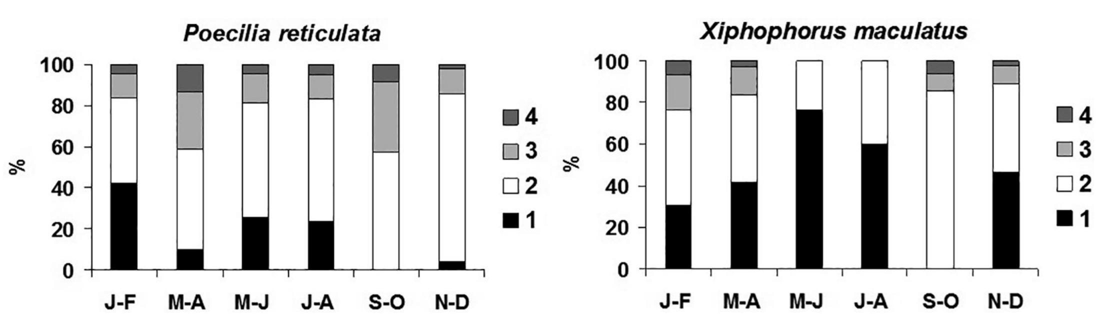

Figure 5. Relative bimonthly frequency of developmental stages in feral poeciliid females captured in Lopes Creek, between January and December 2017, Minas Gerais State, Brazil. Bimonths: J-F (January-February), M-A (March-April), M-J (May-June), J-A (July-August), S-O (September-October), N-D (November-December). Developmental stages: 1) Non-gravid, 2) Yolked ova, 3) Eyed embryos, 4) Mature embryos.

Table 1. Food items found in stomachs of feral poeciliids (values represent the feeding index, % *IAi*) captured in Lopes Creek, Minas Gerais State, Brazil.

Taxon	Food items	Origin	*Poecilia reticulata* (n = 211 stomachs)	*Xiphophorus maculatus* (n = 147 stomachs)
Crustacea	Ostracoda	Autochthonous	4.52	6.94
Insecta	Diptera (Larvae)	Autochthonous	5.08	8.10
Insecta	Odonata (Nymphs)	Autochthonous	5.06	15.07
Insecta	Hemiptera	Autochthonous	2.12	3.00
Eukaryota	Algae	Autochthonous	1.50	1.52
-	Detritus	Autochthonous	77.11	61.40
Insecta	Diptera (Adults)	Allochthonous	1.53	1.94
Insecta	Formicidae	Allochthonous	3.08	2.03

3.6. Sex ratio

Overall, females were significantly more frequent than males in guppy (χ^2=61.82; 1.6:1; d.f.=1; $p < 0.05$) and southern platyfish (χ^2=268.96; 1.9:1; d.f.=1; $p < 0.05$) (Table 3).

3.7. Establishment and feral status

Juveniles of *P. reticulata* and *X. maculatus* were found during the entire sampling period in Lopes Creek, although in low proportions (Figure 8).

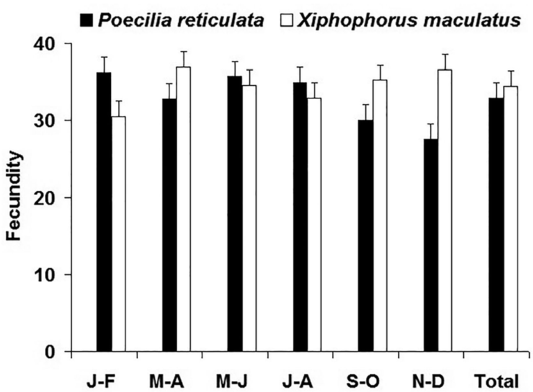

Figure 6. Bimonthly and total fecundity (number of embryos per brood) of feral poeciliid females captured in Lopes Creek, between January and December 2017, Minas Gerais State, Brazil. Bimonths: J-F (January-February), M-A (March-April), M-J (May-June), J-A (July-August), S-O (September-October), N-D (November-December).

For both species, all individuals captured were classified as wild-type forms.

4. Discussion

This study provided information about trophic, reproductive status, and the establishment of feral *P. reticulata* and *X. maculatus* in a small Atlantic Forest creek in Brazil. Both species are popular among fish farmers in the study region, and have been raised in ponds for decades [since 1979, see Vidal Júnior & Costa (2000)], which implies that they have been released in the creeks continuously (Magalhães & Jacobi, 2017; Magalhães et al., 2020, 2021). Our results showed that feral guppies and platies dominate and colonize the studied creek, a probable result of the environmental selection that favors the survival and recruitment of more discrete phenotypes. Moreover, both species colonized successfully the environment, considering they fed on abundant resources and showed prolonged reproductive activity, including early maturity and the presence of young (i.e., recruitment). This is a particular case in which ornamental fish (i.e., colorful patterns) escape from production ponds and rapidly evolve to feral strains (i.e., discrete or cryptic patterns) in the environment.

The analysis of the trophic activity of guppy and southern platyfish demonstrated that detritus dominated the diet of these feral poeciliids in the Lopes Creek. The same tendency occurred with feral *P. reticulata* in streams located in São Paulo and

Table 2. Distribution of total and standard length classes by developmental stages of feral poeciliid females captured in Lopes Creek, Minas Gerais State, Brazil. Developmental stages: 1) Non-gravid, 2) Yolked ova, 3) Eyed embryos, 4) Mature embryos.

Total (TL) and Standard length (SL) classes (cm)	*Poecilia reticulata*				
	1	2	3	4	Total
0.9-1.4 TL (0.3-0.8 SL)	70	69	20	7	166
1.5-2.0 TL (0.9-1.4 SL)	9	44	25	12	90
2.1-2.6 TL (1.5-2.0 SL)	40	86	22	7	155
2.7-3.2 TL (2.1-2.6 SL)	10	25	5	2	42
3.3-3.8 TL (2.7-3.2 SL)	0	62	37	9	108
3.9-4.4 TL (3.3-3.8 SL)	4	79	12	2	97
Total	133	365	121	39	658
Total (TL) and Standard length (SL) classes (cm)	***Xiphophorus maculatus***				
	1	**2**	**3**	**4**	**Total**
1.5-2.0 TL (1.0-1.5 SL)	14	21	8	3	46
2.1-2.6 TL (1.6-2.1 SL)	57	58	18	4	137
2.7-3.2 TL (2.2-2.7 SL)	29	9	0	0	38
3.3-3.8 TL (2.8-3.3 SL)	6	4	0	0	10
3.9-4.4 TL (3.4-3.9 SL)	0	42	4	3	49
4.5-5.0 TL (4.0-4.5 SL)	39	36	7	2	84
Total	145	170	37	12	364

Table 3. Bimonthly and total sex ratio of feral poeciliids collected in Lopes Creek, between January and December 2017, Minas Gerais State, Brazil.

Bimonths/Sex ratio	*Poecilia reticulata*			*Xiphophorus maculatus*		
	Females	Males	Sex ratio	Females	Males	Sex ratio
January-February	166	92	21.22*	46	2	40.34*
March-April	90	47	13.5*	137	0	137.00*
May-June	155	62	39.86*	38	6	23.28*
July-August	42	13	15.28*	10	0	10.00*
September-October	108	130	2.0	49	6	33.6*
November-December	97	58	9.82*	84	22	36.2*
Total/Sex ratio ♀: ♂	658	402	61.82*/1.6	364	36	268.96*/1.9

*Indicates the significant values for sex ratio (Chi-square; $p < 0.05$, $\chi^2_{0.05} = 3.84$; d.f. = 1).

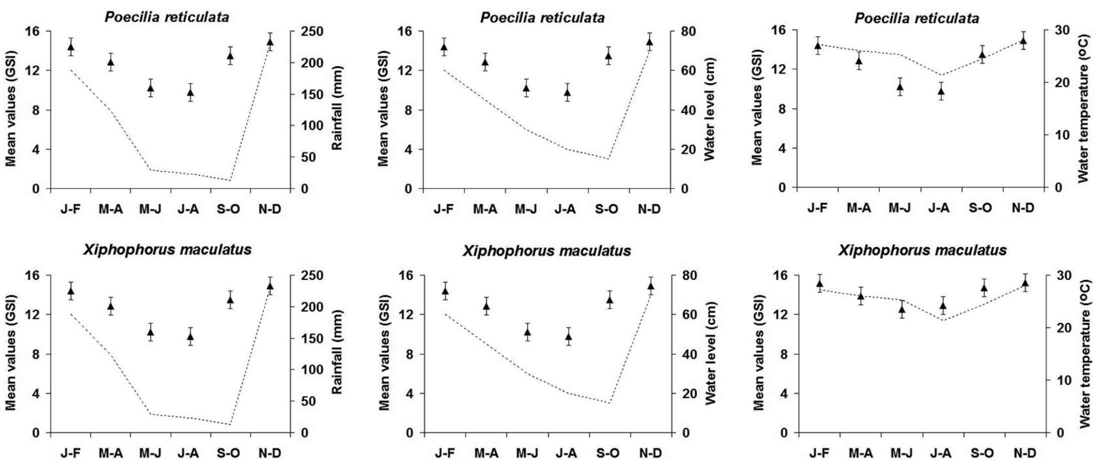

Figure 7. Female gonadosomatic index (GSI) ± SD of feral poeciliids and environmental variables collected in Lopes Creek, between January and December 2017, Minas Gerais State, Brazil. Bimonths: J-F (January-February), M-A (March-April), M-J (May-June), J-A (July-August), S-O (September-October), N-D (November-December). GSI female (black triangle); accumulated rainfall, water level and water temperature (dotted lines).

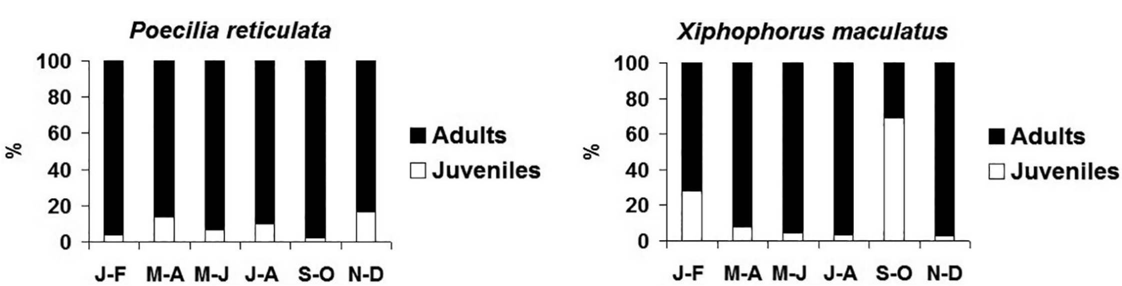

Figure 8. Juvenile-to-adult proportion of feral poeciliids collected in Lopes Creek, between January and December 2017, Minas Gerais State, Brazil. Bimonths: J-F (January-February), M-A (March-April), M-J (May-June), J-A (July-August), S-O (September-October), N-D (November-December).

Paraná states and *X. maculatus* in an Indonesian lake (Green et al., 1978; Rocha et al., 2009; Silva et al., 2012). The opportunistic feeding on a variety of animal resources with a major component of detritus may be the common feeding pattern in feral poeciliids (Green et al., 1978). This is consistent with intestinal morphology, i.e., long and coiled, varying in length from one to two times the standard length (Dussault & Kramer, 1981), an adaptation for digesting detritus (Silva et al., 1980). The high consumption of detritus, which is a resource with low nutritional value, but highly abundant, can indicate a "compensatory feeding strategy" (Yeager et al., 2014, p. 2), a behavior that may facilitate the colonization of non-native poeciliids in new environments (Alves et al., 2016). The increased consumption of detritus by invasive poeciliids can impact nutrient dynamics in streams by mobilizing organic matter by feeding, and releasing nutrients in more liable forms via excretion. Increased nutrient inputs, especially nitrogen, can change stream food web structure and ecological functions such as nutrient cycling and primary production (Vanni, 2002; Holitzki et al., 2013).

We found females of feral guppy and southern platyfish in reproductive activity during the 12 months of the study period. A long reproductive period has also been found for feral *P. reticulata* and *X. maculatus* in five headwater creeks at the Muriaé Ornamental Aquaculture Center and in an Australian stream (Milton & Arthington, 1983; Magalhães & Jacobi, 2017). Frequent reproduction over an extended breeding season is an opportunistic life-history strategy adopted by poeciliids that permit colonization in environments with strong predation pressure (Reznick & Endler, 1982), and this might be the case in the Lopes Creek, which is inhabited by different predators, i.e., aquatic spiders/insects, native and non-native fish (see Figure 1). The fecundity observed for the two feral species was high (> 30 embryos per brood). High fecundity was also found in *X. maculatus* introduced in an Australian stream subjected to high predation pressure (Milton & Arthington, 1983), and conversely, low fecundity was found in *P. reticulata* inhabiting a Brazilian urban reservoir with few predators (Oliveira et al., 2014). High fecundity is a specific trait adopted by native and non-native poeciliids to assure the maintenance of a viable population in an environment with high predation rates (Reznick & Endler, 1982; Sa-nguansil & Lheknim, 2010). Higher fecundity can also give non-native livebearers a competitive advantage over native species, because fry grow more quickly and become adult predators faster, completely dominating the invaded site (Magalhães & Jacobi, 2017).

Our observations showed that adult breeding females of feral *P. reticulata* and *X. maculatus* were found in small sizes (ca. 1.0 cm SL), which can indicate early sexual maturation. This process may be related to size-selective predation performed by a suite of aquatic predators (Figure 1), including native fishing spiders, diving beetles, water boatmen, water striders, dragonfly nymphs, water bugs, native fish *P. parahybae*, *D. janeiroensis*, *P. vivipara* and non-native fish originated from a nearby ornamental fish farm, such as cyprinids, danionids, cobitids, cichlids, characids, and other poeciliids. According to Endler (1982) and Reznick & Endler (1982), the larger the body size, the greater the chance to be visible to the predators and therefore, many animals - including poeciliids - compensate this risk by reducing their body size (and consequently sexual maturation) in order to avoid predation. This is probably the lowest size found in introduced populations of feral *P. reticulata* and *X. maculatus*. In other sites and environments throughout Brazil and the world, the smallest reproductive size of feral guppy and southern platyfish ranged between 1.2-2.0 cm, and 1.7-2.0 cm SL respectively (Milton & Arthington, 1983; Andrade et al., 2008; Montag et al., 2011; Kırankaya & Ekmekçi, 2021; Luduvice & Brito, 2023). In the present study, we also found smallest females of *P. reticulata* and *X. maculatus* measuring 4.4-5.0 cm TL respectively, indicating a feralization process for both species. Previous studies have documented that ornamental strains of guppy and southern platyfish females living in predation free environments (i.e., aquariums) are usually larger, e.g., 6.0 cm TL (Sterba, 1983), than their feral counterparts, e.g., 4.0-5.1 cm TL in *P. reticulata* and *X. maculatus* (Favilli et al., 2018; Kırankaya & Ekmekçi, 2021), likely due to selecting forces such as predation acting upon the body size (Endler, 1982; Reznick & Endler, 1982).

The gonadosomatic index indicated that feral *P. reticulata* and *X. maculatus* females have the peak of reproduction activity occurring during the austral summer, characterized by warmer temperatures, rainy season and rising water level in Lopes Creek. The main breeding period for many non-native poeciliid species, including guppy and southern platyfish, occurs during periods of heavy rains which lead to the expansion of the littoral zone, thus increasing the availability of food resources for the young (Magalhães et al., 2002; Gómez-Márquez et al., 2016). In addition, warmer water temperatures may increase embryonic development rate and consequently, more broods produced by this group of fish (Snelson, 1989).

We also recorded a higher frequency of females. A similar pattern was found for feral *P. reticulata* and *X. maculatus* introduced into a stream located in Sergipe State and in Australia (Milton & Arthington, 1983; Luduvice & Brito, 2023). The prevalence of females may also be associated with high predation pressure, which may cause differential predation risk between females and males. In poeciliids, males of *P. reticulata* and *X. maculatus* perform prolonged courtship displays (e.g., sigmoidal body curves, lateral displays with erect fins), continuously chasing and mating with females without their consent (i.e., coercive mating), expending a large part of the day in these activities. These behaviors - along with conspicuous colors and ornaments such as larger tails/fins - may expose males to predators, as they become less careful in avoiding predator attacks, biasing the sex ratio toward females (Borowsky & Kallman, 1976; Stoner & Breden, 1988; Snelson, 1989 and references therein).

The proportion of juveniles was lower than adults in the studied populations, contrasting with the high occurrence of gravid females. Again, selective predation may be associated with this pattern. Massive predation events were observed on juveniles of feral poeciliids in the Lopes Creek, performed especially by visually oriented aquatic invertebrates and fish (A.L.B. Magalhães, pers. obs.) (see Figure 1). In spite of the low proportion of juveniles, the year-round presence of reproductive females and juveniles suggests that feral *P. reticulata* and *X. maculatus* are established in the Lopes Creek. The same pattern was found for guppy introduced in a stream in Serbia, and guppy and southern platyfish introduced in an Italian pool (Milenković et al., 2014; Favilli et al., 2018). A strong evidence of local establishment is the alteration of phenotype patterns, in the case, the shift from ornamental-type phenotypes (Figure 4A, 4B, 4C, 4D) available in local fish farm to wild forms. All fish collected in the present study resembled the wild-type (Figures 3, 4E, 4F, 4G, 4H). Similar wild-type phenotypes were found for feral guppy in different localities, including streams in Brazil, Argentina, Serbia and Iran [for examples, see pictures available at Milenković et al. (2014); Mousavi-Sabet & Eagderi (2014); Rosso et al. (2017); and Krinski & Camera (2018)], and feral southern platyfish has been recorded in several water bodies located in the U.S.A., Lesser Antilles and Colombia [for examples, see pictures available at Lawson et al. (2017); Albornoz-Garzón & Villa-Navarro (2017); and Alley et al. (2023)]. The presence of wild forms of feral *P. reticulata* and *X. maculatus* in Lopes Creek may be a result of sixteen years of intermittent escapes and environmental selection, especially shaped by the predation pressure imposed by fishing spiders, numerous aquatic insects and fish (see Figure 1), denoting a rapid selection of life-history traits. This assumption is supported by studies conducted by Endler (1978, 1980) and Milenković et al. (2014) who showed that predation makes poeciliid populations to become cryptic by eliminating the most colorful individuals from the gene pools. Thus, feral populations evolve to become more closely matched with their environment as an anti-predation strategy. The focus of this study was to investigate trophic/reproductive traits and change of phenotypes related to predation. However, we recognize that other natural "forces" may also contribute to the shift in phenotypes observed here such as dominance of wild-type alleles (Fisher, 1930), and sexual selection: gradual decrease of ornamental-type individuals due to a presumably female natural preference for wild-type males (Houde, 1994).

Headwater creeks of Muriaé Ornamental Aquaculture Center are particularly vulnerable to invasion by ornamental non-native species, because this region has low native richness, while it has received intense and constant propagule pressure of ornamental non-native organisms escaping from production ponds (Magalhães & Jacobi, 2013a, 2017; Magalhães et al., 2002, 2019, 2020, 2021, 2022). Negative impacts of non-native *Poecilia* and *Xiphophorus* have been reported elsewhere (Arthington et al., 1983; Courtenay et al., 1988; Englund, 1999; Magalhães et al., 2021 and references therein), but the ecological situation in the region seems especially complicated, considering that the ecological impacts of feral guppy and southern platyfish may be intensified by the invasion of other feral poeciliids, including black molly, sailfin molly, green swordtail, and variable platyfish. Impacts may be especially intense on aquatic insects, zooplankton, *D. janeiroensis*, *P. parahybae*, *P. vivipara*, food web structure and nutrient cycling/primary production.

Modifying human behavior is the key to prevent or minimize the potential ecological impacts of ornamental aquaculture in Brazil [see Magalhães & Jacobi (2017); Lima Junior et al. (2018); Vitule et al. (2019); Luduvice & Brito (2023)]. Therefore, the main management action should include awareness campaigns to educate people who work directly with the ornamental fish industry in the region (Magalhães et al., 2021). Without a change in the behavior of these workers, it will be impossible to avoid fish escaping (i.e., propagule pressure) from production ponds (Magalhães et al., 2019, 2020, 2022). Parallel to education efforts, inspection by environmental authorities is elemental to prevent mismanagement and poor practices that release fish into headwater creeks. Also, Best Management Practices (BMPs) to prevent further introductions from farm ponds should be: (i) to reroute all effluent waters from fish rearing facilities through an above-ground dry well; (ii) to install sand and gravel filter which will allow passage of water but not non-native fish; and (iii) recapture escaped fish in the Lopes Creek, considering that ornamental fish remain in the immediate vicinity soon after the introduction (Magalhães et al., 2021, 2022). Concluding, it is important that future studies focus on possible ecological impacts of feral fishes in the Lopes Creek and other drainages of the region.

Acknowledgements

We thank the ornamental fish farmer Mr. Fábio Lopes who granted access to your property and in particular farmer Jorge Farias for field assistance, and Renata B. Araújo (CIUFS-UFS) for the species catalogue numbers. DPLM, JRSV and FMP thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a Research Productivity fellowship.

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Received: 29 June 2023
Accepted: 11 October 2023

Associate Editor: André Megali Amado.