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Prey selectivity of the invasive largemouth bass towards native and non-native prey: an experimental approach

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Non-native predators are known to cause ecological impacts through heightened consumption of resources and decimation of native species. One such species is *Micropterus salmoides.* Often introduced for sport fishing worldwide; it has been listed by International Union for Conservation of Nature and Natural Resources as one of the 100 of the world's worst invasive species. Whilst impacts conferred towards native prey are well known, its relationship with other non-native species has received much less attention. Therefore, the aim of this study was to experimentally investigate the feeding preference of *M. salmoides* towards native prey (*Geophagus iporangensis*) compared to non-native prey (*Oreochromis niloticus* and *Coptodon rendalli*) using comparative consumption and the Manly-Chesson selectivity index. We found a higher consumption by *M. salmoides* towards the non-native prey and a tendency for this non-native preference to increase when prey availability increased. Our results are in line with the hypothesis that the invasion of the non-native predator can be facilitated by the high abundance and reproductive rate of the non-native prey. This is relevant considering the interaction of multiple invaders in an ecosystem, in particular environments modified by humans. Interspecific relationships are complex and their understanding is necessary for environmental management decision-making.

Keywords: Feeding preference, Invasional Meltdown, *Micropterus salmoides*, Multiple invasions, Tilapia.

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Predadores não-nativos são conhecidos por causar impactos ecológicos com o aumento do consumo de recursos e do declínio das espécies nativas. Uma dessas espécies é *Micropterus salmoides.* Frequentemente introduzida ao redor do mundo para pesca esportiva; essa espécie foi listada pela União Internacional para a Conservação da Natureza como uma das 100 piores espécies invasoras do mundo. Embora os impactos nas presas nativas sejam bem conhecidos, sua relação com outras espécies não-nativas tem recebido muito menos atenção. Portanto, o objetivo deste estudo foi pesquisar experimentalmente a preferência alimentar de *M. salmoides* por presas nativas (*Geophagus iporangensis*) em comparação com presas não-nativas (*Oreochromis niloticus* e *Coptodon rendalli*) comparando o consumo e o índice de seletividade de Manly-Chesson. Encontramos que *M. salmoides* tem um maior consumo de presas não-nativas e uma tendência de aumento de preferência pela presa não-nativa com o aumento da disponibilidade de presas. Nossos resultados são consistentes com a hipótese de que a invasão do predador não-nativo pode ser facilitada pela grande abundância e capacidade reprodutiva de presas não-nativas. Isso é relevante considerando a interação de múltiplos invasores em um ecossistema, particularmente em ambientes modificados pelo homem. Relações interespecíficas são complexas e seu entendimento é necessário para a tomada de decisões de gestão ambiental.

Palavras-chave: Fusão invasora, Invasões múltiplas, *Micropterus salmoides*, Preferência alimentar, Tilápia.

INTRODUCTION

Introductions of non-native species are occurring at a growing rate as a result of human-mediated interests that include transport and trade (Frehse *et al*., 2016; Bezerra *et al*., 2019a,b; Vitule *et al*., 2019; Brito *et al*., 2020; Magalhães *et al*., 2020). Impacts caused by the introduction of non-native species are considered as one of the major causes of biotic change and occur across different levels of biological organization (Vitule *et al*., 2009; Cucherousset, Olden, 2011). Despite the fact that species introductions can often be observed over short time scales (Price *et al*., 2018), the long-term negative impacts can be irreversible, leading to the extinction of native species and the biotic homogenization of once diverse communities (Vitule *et al*., 2012; Bezerra *et al*., 2019b; Magalhães *et al*., 2020). In freshwater ecosystems, the negative impacts of non-native species can be particularly severe (Vörösmarty *et al*., 2000). Freshwater ecosystems are often heavily invaded by multiple species and, due to a high degree of endemism, can experience heightened extinction rates (Ricciardi, Rasmussen, 1999; Hudina *et al*., 2011; Burkhead, 2012; Daga *et al*., 2015). Non-native species are also often introduced for the purposes of aquaculture or sport fishing with many subsequently becoming invasive, especially in environments modified by humans, such as large reservoirs given the construction of dams (Bezerra *et al*., 2019b; Vitule *et al*., 2019; Brito *et al*., 2020).

Brazil is an example of country that has experienced the introduction of a number of highly invasive non-native species for a variety of reasons (Neuhaus *et al*., 2016; Franco *et al*., 2018). A globally invasive fish species is the largemouth bass *Micropterus salmoides* (Lacepède, 1802) of the family Centrarchidae. The native range of this species is from eastern North America to the Rio Grande basin in north-western Mexico (Beltrán Alvarez *et al*., 2013), however it has now been introduced for sport fishing in several continents around the world, including Asia (Ko *et al*., 2017), Europe (García-Berthou, Moreno-Amich, 2000; Costantini *et al*., 2018), Africa (Shelton *et al*., 2008; Ellender *et al*., 2014; Khosa *et al*., 2019), and South America (Garcia *et al*., 2014; Daga *et al*., 2015; Ribeiro *et al*., 2015; Pereira, Vitule, 2019). The largemouth bass usually has considerable impact as a voracious predator, demonstrated by its consumption on native fish and invertebrate prey (Abekura *et al*., 2004; Alexander *et al*., 2014), causing large shifts in the species composition and size structure of communities (Pereira, Vitule, 2019). This has led to the inclusion of the species in the list of 100 of the world's worst invasive alien species by International Union for Conservation of Nature and Natural Resources (IUCN) (ISSG, 2013).

In 1922, *M. salmoides* was introduced in Brazil for sport fishing, becoming widely distributed in artificial systems, such as reservoirs in South and South-east regions (Schulz, Leal, 2005). Having reproduced and grown rapidly in semi-natural systems, it is now considered a threat to the conservation of Brazilian ecosystems (Schulz, Leal, 2005; Garcia *et al*., 2014; Daga *et al*., 2016). A number of species have also been introduced as human food resources, including tilapia species *Oreochromis niloticus* (Linnaeus, 1758) and *Coptodon rendalli* (Boulenger, 1897) (Canonico *et al*., 2005).

Phylogenetically-related and ecologically similar to tilapiine species, an important native cichlid species in Brazilian freshwaters (including reservoirs) is *Geophagus iporangensis* Haseman, 1911, which is popularly known as cará. *Geophagus iporangensis* was previously known as *G. brasiliensis* (Quoy & Gaimard, 1824), which represents is a complex of species across Brazilian basins (*sensu* Argolo *et al*., 2020), from the coastal basins of the Northeast Brazil to coastal rivers in Eastern Uruguay. The evolutionary complexity (Argolo *et al*., 2020) and the fact that *G. iporangensis* is one of the most abundant groups of cichlids in Brazil makes it a typical species in southern Brazilian freshwaters. *G. iporangensis* along with the tilapiines constitute a diet resource for invasive predatory fish like *M. salmoides* in southern Brazilian reservoirs (Bezerra *et al*., 2019b), and are indeed the most abundant fish species in such environments where they co-occur (Frehse *et al*., 2021). However, the predation pressure of the largemouth bass toward others invasive species such as the tilapiines is still not fully described, as well as how it compares to the phylogenetically-related and ecologically similar native prey.

The scenario of non-native species interacting with natives at multiple trophic levels is common in man-made ecosystems. In these cases, the knowledge of interspecific interactions is crucial to understand the cumulative impact of multiple invaders (Simberloff, Von Holle, 1999; Hudina *et al*., 2011). Different outputs are possible when multiple non-native species coexist in an ecosystem (Frehse *et al*., 2021). These outputs can be co-existence, biotic resistance (Twardochleb *et al*., 2012; Skein *et al*., 2020) or invasional meltdown as a consequence of the facilitation amongst invasive species (Simberloff, Von Holle, 1999). Even so, studies focusing impacts of non-native preys are still limited (Cattau *et al*., 2016); and studies that investigate the interaction of introduced predators foraging on non-native preys are even more limited. Johnson *et al*. (2009) focused in the advantage of non-native prey in avoiding predation compared to its native counterparts and the resulting synergistic effects of the positive association of the non-natives.

For a predator like *M. salmoides,* an important factor in prey selectivity is the availability of the resources (Pinnegar *et al*., 2003). When a preferred prey is poorly available and considering the optimal foraging theory (Pyke, 1984), *M. salmoides* likely behaves in an opportunistic manner, assuming opportunism as the behavior of taking advantage of the circumstances. Thus, in newly colonized ecosystems, its diet may reflect local prey abundance and availability (Young, Cockcroft, 1994).

We aim to experimentally investigate the feeding selectivity of *M. salmoides* towards non-native tilapiine complex prey (*O. niloticus* and *C. rendalli*) compared to a phylogenetically-related native prey species (*G. iporangensis*) considering resources availability. We cannot anticipate the predator preference, but if there is preference towards one species, implications are important for the understanding of the impacts of multiple invaders towards native species. Even so, we do expect that food preference of *M. salmoides* may depend of availability of resources in the scenario of high availability, the predator may chose the better prey, thus showing clearer patterns of preference. To analyse this hypothesis, we use Manly-Chesson's index to determine the selective feeding between food items. This index may be the most meaningful indicator of prey type preference when preys are present in equal proportions (Confer, Moore, 1987) and is a useful measure for quantifying predator preference in selective predation, considering relative consumption and resource availability (Chesson, 1983).

MATERIAL AND METHODS

We carried out a series of food preference experiments with fish that naturally coexist in reservoirs in southern Brazil. The introduced tilapiine species were chosen due to their high abundance and reproductive rate in these reservoirs, and their categorization as invasive species; while the native *G. iporangensis* prey was chosen because it is a typical and abundant species in the region.

The fishes used in the experiments were captured in March 2018 in the Passaúna reservoir located within Curitiba's metropolitan area (between parallels 25° 15'– 25° 35' S and meridians 49° 25' – 49° 20' W, see Sotiri *et al*. (2021) for an environmental description of the reservoir), Paraná State, Brazil. In this reservoir, the preys and the predator are the most abundant fish species (Frehse *et al*., 2021). Vouchers of species are all available at Museu de História Natural do Capão da Imbúia (MHNCI), Curitiba, Brazil. We collected small-sized predatory *M. salmoides* (15–20 cm total length, MHNCI 12484) and small sized prey (2–5 cm total length) consisting of non-native tilapias *O. niloticus* (MHNCI 12689) and *C. rendalli* (MHNCI 12130) and native prey *G. iporangensis* (MHNCI 12602). Although fish were not weighted, we argue that the standardization of size and the number of replicates minimized weight differences between experimental treatments (see below).

Fish collections were made under a permanent license for collection of zoological material SISBIO N° 24779. Prey were collected by casting a net trawl (mesh diameter 10 mm) near to the reservoir bank, and the predator *M. salmoides* was caught on rod and line. Upon collection, fishes were immediately transported to the laboratory where they were placed in 310 L water boxes for acclimation for at least two months where temperatures were maintained at 23 °C. Prey fishes were fed with commercial fish food, while predator was fed with beetle larvae, *Tenebrio molitor* Linnaeus, 1758 (Subhadra *et al*., 2006). During acclimation, both prey and predator were treated with Aqualife and Ictio (Labcon®; www.alconpet.com.br) to prevent disease.

The two non-native prey species were used together because they both belong to the same tribe, tilapiine within the family Cichlidae, with similar ecology and behavior (Canonico *et al*., 2005). Besides that, they are also representative of invasive species complexes found in the region (Cassemiro *et al*., 2018; Frehse *et al*., 2021). Experimental trials were conducted from May to December 2018 in 35 L black plastic boxes (experimental arenas) containing chlorine-free drinking and aerated water. The temperature was equally maintained at 23°C and experiments were conducted with natural light conditions. Individual predators were placed in an arena and then left without food for 72 h. After this time, native and non-native preys with similar body sizes were added simultaneously in equal amounts across a range of densities: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 13, 15, 16 fish per species origin (N = 5–7 arenas per density; a total of 76 experimental arenas). That is, for a density '1', one native and one non-native prey were added. Predatory *M. salmoides* were left to interact with the prey fish for 48 h before they were removed and the amount of remaining prey counted. The experimental time and densities were determined after pilot experiments showing that, in this time interval the predator had enough time to consume at least half of the prey offered. It was also possible to reach the asymptote of available vs. consumed prey graph with the used densities – *i.e.*, from this point on, consumption may remain constant. To eliminate possible noise from competition between preys, experimental arenas did not have shelters (Champneys *et al*., 2021). For logistical and ethical reasons, predatory *M. salmoides* (n = 20) were reused between treatments; however, they were only used once per fish density. After use in one trial, predators were placed in a tank for three days and fed a diet of *T. molitor* before 72 h without food and reused in a new trial. At the end of experiments, predators and remaining preys were euthanized using Benzocaine 80 mg/L or Eugenol 70–90%.

The choice of our experimental design was to compare feeding preference in a scenario of prey coexistence. We analyzed if there is a preference of *M. salmoides* by a type of prey (native or non-native) using the Manly-Chesson's index with the following equation.

$$(1)\ \propto_i = \frac{r_{i/}p_i}{\sum_{i=l}^{m} r_{i/}p_i}$$

Where m is the total number of prey types consumed and compares the relative availability of a prey Pi with their relative consumption ri. Manly-Chesson's index ranges from zero to one. If α = 1 / m, the predator feeds randomly and preys are consumed proportionally to their abundance in the environment. If α > 1 / m, the index indicates preference; and α < 1 / m indicates avoidance (Cochran-Biederman, Vondracek, 2017). Manly-Chesson's index is a function of forage ratio (forage proportion) (ri / Pi), therefore the sum of all α for a predator is normalized to 1. Therefore, a higher median Manly-Chesson's value would indicate a more specialist feeding strategy, with consumers feeding heavily on a few species, rather than feeding weakly on many types (Confer, Moore, 1987). In ours experimental, given that the types of prey were offered in equal proportions, Pi is always 0.5, and the Manly-Chesson index, for a non-native or native prey, is equal to the relative consumption of that prey (ri):

$$(2)\ \propto_i = ri$$

We performed the Manly-Chesson index with the *dietr* package (Borstein, 2020), function Electivity in R (R Development Core Team, 2018). Once the index values were obtained, they were related with the prey availability using a simple linear regression. In this case, the index was calculated for non-native prey type and represents the relative consumption of non-native prey, for that the higher the index, the higher was the consumption towards the non-native prey. Therefore, Manly-Chesson's index was considered a response variable that indicate the effect size of prey selectivity, and the pattern of the regression against prey density would demonstrate the relationship between food preference and availability, accounting for the fact that preys were simultaneously offered in the same experimental unit. Additionally, we carried out a functional response analysis to reach the maximum consumption rate of the predator (S1).

RESULTS

We found that the relative consumption of non-native prey type is higher when prey availability increases compared to native prey (Fig. 1). Indeed, the simple linear regression show that Manly-Chesson index was related to prey availability, increasing towards the non-native prey as availability increases (Manly-Chesson for non-native prey = 0.5 + 0.007 Prey Availability, $R^2 = 0.031$, $F_{1, 74}$, $p = 0.012$) (Fig. 2). Even so, it was

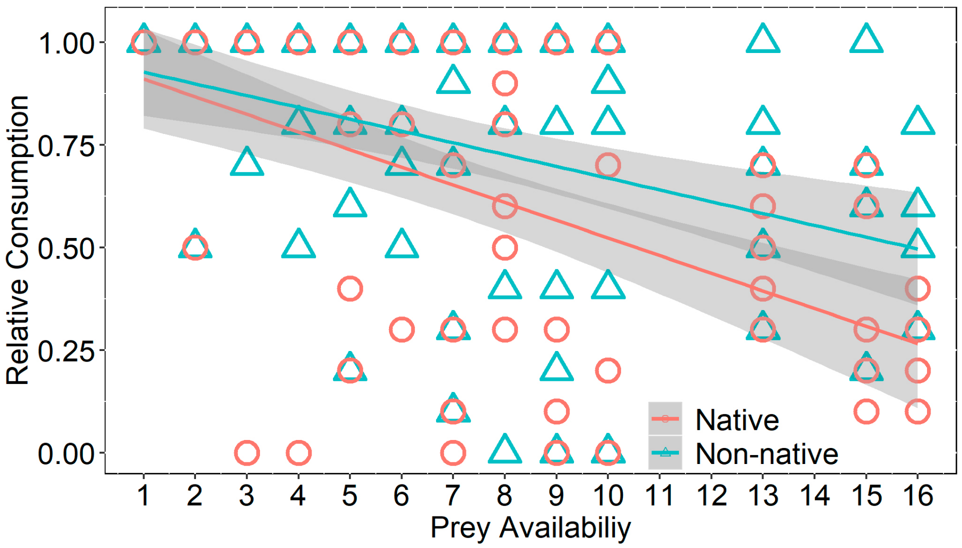

FIGURE 1 | Relative consumption of non-native (*Oreochromis niloticus* and *Coptodon rendalli*) and native (*Geophagus iporangensis*) prey, considering different prey availability for *Micropterus salmoides*.

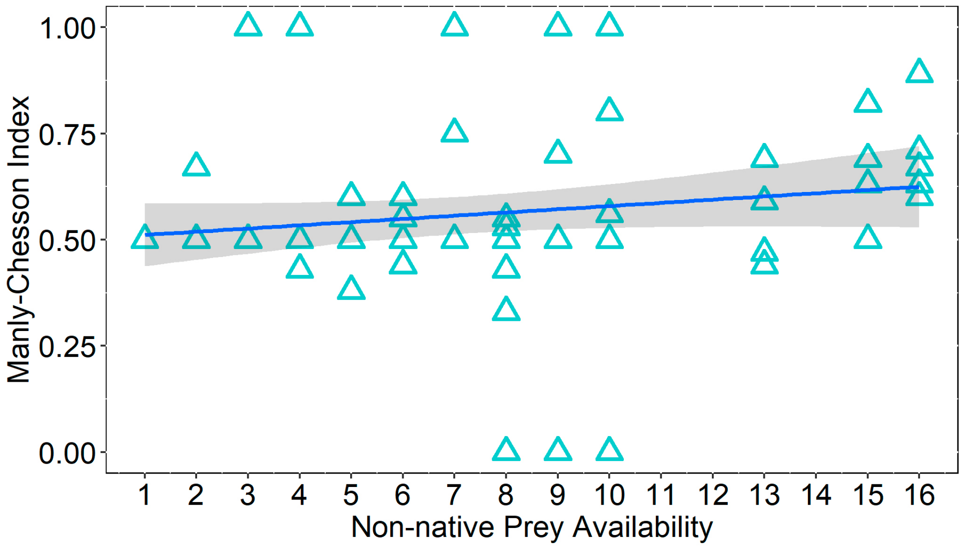

FIGURE 2 | Relationship between the Manly-Chesson selectivity and prey availability for *Micropterus salmoides*. Higher values indicate preference for non-native species. Shading represents 95% confidence intervals. Note that because the index fluctuates between 0 and 1, with 2 types of prey and equal availability of prey for both types, the result of the index for one prey is exactly the opposite of the other. For this reason, the graph only shows the results of the index for the non-native species. The graph for the other type of prey would be the spectral image of this one.

clear that *M. salmoides* showed higher consumption of non-native prey compared to native particularly at high prey densities.

DISCUSSION

We generated evidence that the invasive *M. salmoides* consumes a higher number of non-native prey cichlids compared to natives, when offered simultaneously at equal densities, especially at high prey densities. It was indeed expected that an opportunistic and generalist behavior of *M. salmoides* occur particularly when prey densities were low. Opportunistic behavior at low densities could increase the predation effect on native prey. We emphasize that this refers only to a generalist behavior regarding these two types of prey and it is not possible to generalize this behavior to the entire range of the diet, given the experiment was limited to only three typical preys of the predator. It was clear in our experimental essay that both prey types were vulnerable to active hunting by *M. salmoides*, also an expected scenario given the absence of shelters and the ecomorphological traits of this predator (Luger *et al*., 2020). Considering prey size, the results obtained were in line with those obtained by Cuthbert *et al*. (2020) suggesting that even small and intermediate *M. salmoides* exhibit higher attack rates in small and intermediate preys. We expected that our results also reflected behavioural differences between the two prey types. The native prey was observed to be less active compared to the non-native prey. Thus, the natives can benefit from an anti-predator behaviour of taking cover, “freezing” or reducing activity during certain times of day to avoid being detected by a chasing predator. This could indicate an important role in trade-off between risk of predation and foraging and other fitness-enhancing activities (Clark, 1994).

It is important to note that heightened consumption on non-native prey may have little impact on the exotic tilapiine populations in Passaúna reservoir as their abundance is far higher than the native prey *G. iporangensis* (estimated as 4.96 ton*km^{-2}*year^{-1} compared to 1 ton*km^{-2}*year^{-1}, respectively) as well as their reproductive rates (see Bezerra *et al*., 2019b). The higher consumption of individuals from the successful populations of *O. niloticus* and *C. rendalli* in the reservoirs of the Metropolitan Region of Curitiba may thus indicate a positive effect of the invasive preys in sustaining *M. salmoides* populations without being affected by top-down control (see Bezerra *et al*., 2019b). Thus, changes in the biomass of *O. niloticus* and *C. rendalli* and its hybrids can result in significant changes in the biomass of *M. salmoides* (Bezerra *et al*., 2019b). Our results add evidence for a positive effect between interacting non-native species, which can result in the ‘Invasional Meltdown’ phenomenon (Simberloff, Von Holle, 1999; Kuebbing *et al*., 2013; Braga *et al*., 2018). Interestingly, such facilitation scenario was generated by a ‘negative’ predator-prey ecological interaction, which at a first glance seems counterintuitive, but well explained by the biology of the tilapiine species. Given the high reproduction rate and successful colonization in the urban reservoirs (Starling *et al*., 2002; Sánchez-Botero *et al*., 2014), we argue that tilapias are not negatively affected by a voracious invasive predator, but instead facilitate the establishment of the invasive predator (see Bezerra *et al*., 2019b). Such impact of tilapias is still underestimated, particularly in Brazil where there is a strong movement of denial against tilapias impacts (Charvet *et al*., 2021). Finally, it is important to note that results became even more relevant given the preys and the predator studied here are the most abundant fish species in the Passaúna reservoir (Frehse *et al*., 2021).

Indeed, the present study has contributed to our understanding of trophic relationships between native and non-native species. Taken together, patterns were in accordance with others that highlight the opportunistic behaviour of *M. salmoides* at low densities (Hodgson, Kitchell, 1987) and depending of prey characteristics (morphology, behaviour, abundance, availability), which consequently dictate its feeding strategy at high densities (Taylor *et al*., 2019; Luger *et al*., 2020). Further, invaders such as *M. salmoides* have a great phenotypic plasticity, even acting at different trophic levels (Almeida *et al*., 2012). The trophic level at which opportunistic invasive species establish can be determined by the ecological characteristics of invaded communities. For example, Costantini *et al*. (2018) showed that *M. salmoides* can change their feeding habits and their trophic level depending on the availability of prey. Additionally, this predator played an important role within trophic networks, as changes in their populations could generate cascading effects (Schindler *et al*., 1997).

As a result of the current dynamics of globalization, most ecosystems have suffered from simultaneous introduction of several invasive species, adding complexity in the understanding of species interactions (Simberloff, Von Holle, 1999). Most research, however, remains on the study of single-species invasions (Magalhães, Ratton, 2005; Hudina *et al*., 2011; Costa-Novaes, Carvalho, 2012; Kuebbing *et al*., 2013). Quantifying and predicting the negative impacts of multiple non-native invasive species are highly important for conservation in diverse regions such as Neotropics; particularly in human altered environments. Here we have shown how the presence of multiple invasive fish with high reproductive rates may result in synergistic effects, with greater potential damage to natural ecosystems. We also provided an approach of experimentation and analysis to address the scenario of multiple invasions, especially in Neotropical water bodies. We highlighted the probability of increased impact when invasive species coexist in the same ecosystem, even when the predominant interaction between invasive species is a 'negative' ecological interaction, such as predator-prey.

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AUTHORS' CONTRIBUTION

Liliana Paola Cárdenas-Mahecha: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing-original draft, Writing-review and editing.

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Andre Andrian Padial: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENT

The experiment was carried out following the protocols of Conselho Nacional de Controle de Experimentação Animal (CEUA) and the American Veterinary Medical Association (AVMA, 2013); and all animals used were euthanized according to the procedures of Divisão de Gestão Ambiental da Universidade Federal do Paraná (UFPR). The use of animals in the experiments and the procedures performed were authorized by the certificates N° 1027 and 1199 of CEUA from UFPR.

COMPETING INTERESTS

The authors declare no competing interests.

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