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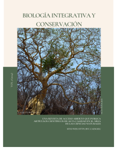

Foraging behavior of Mexican mojarra *Amphilophus istlanus* at potential risk from invasive fish predator *Amatitlania nigrofasciata*

Comportamiento de forrajeo de la mojarra mexicana Amphilophus istlanus en potencial riesgo por el depredador invasor Amatitlania nigrofasciata

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Abstract: Characterizing the behavioral traits of Mexican mojarra juveniles may help predict their survival when facing an introduced invasive predator species like the convict cichlid fish. We predicted that individuals in the presence of convict cichlids would reduce their swimming activity and food consumption. We hypothesized that the swimming activity and the food consumed by the Mexican mojarra in two contexts-with and without a potential predator threat-is related to its levels of aggressiveness. We tested this experimentally by evaluating the swimming activity and food consumption by juvenile mojarras in the presence of the invasive convict cichlid versus when they were not, and we related the consistency in the swimming activity of the Mexican mojarra juvenile with their aggressiveness. As we expected, the fish were less active when convict cichlids were present. Additionally, the swimming activity of the Mexican mojarra in the absence and presence of the invasive convict cichlid was related to aggressiveness; the individuals with the highest swimming activity and that consumed the most food was also the most aggressive. This suggests that the Mexican mojarra juvenile could suffer ecological consequences when faced with the invasive convict cichlid.

Keywords: *Amphilophus istlanus*, predation threat, swimming activity, food consumed, aggression.

Resumen: Caracterizar los rasgos conductuales de juveniles de la mojarra Mexicana puede ayudar a predecir su supervivencia ante la introducción de una especie depredadora invasora como el pez cíclido convicto. Nosotros predecimos que los individuos en presencia de cíclidos convictos podrían reducir su actividad de nado y su consumo de comida y nuestra hipótesis fue que la actividad de nado y la comida consumida por la mojarra mexicana en dos contextos -con y sin amenaza de depredación- está relacionada con sus niveles de agresividad. Probamos esto evaluando experimentalmente la actividad de nado y el alimento consumido cuando los juveniles estaban en presencia del pez invasor cíclido convicto y cuando no lo estaban y relacionamos la consistencia en la actividad de nado de los juveniles de la mojarra Mexicana con su agresividad individual. Como esperábamos, los peces fueron menos activos cuando los cíclidos convictos estuvieron presentes. Adicionalmente, la actividad de nado de la mojarra Mexicana en ausencia y presencia del cíclido convicto está relacionada con la agresividad; los individuos con mayor actividad de nado y que comieron más también fueron los más agresivos. Esto sugiere que los juveniles de la mojarra Mexicana podrían sufrir consecuencias ecológicas al enfrentarse al depredador invasor convicto.

Palabras clave: *Amphilophus istlanus, amenaza de depredación, actividad de nado, comida consumida, agresión.*

Introduction

The way that native potential prey species respond to the threat of predation has a critical effect on their fitness in environments altered by invasive predators (Blake & Gabor, 2014). Fundamental behavioral traits such as foraging activity, boldness, and aggressiveness vary among individuals (Martins & Bhat, 2014). Some behavioral traits can be advantageous in one situation but costly in another (Reale et al., 2000; Sinn et al., 2006). In fish, foraging behavior is often positively correlated with aggressiveness (Fabre et al., 2014) and growth (Winandy & Denoël, 2015) and negatively correlated with predation risk (Bell & Sih, 2007; Wilson et al., 2011; Reddon et al., 2013). An active individual will have a higher risk of predation compared to one that is less active (Jones & Godin, 2010). Individuals that have higher foraging activity have a higher chance of being seen if a predator is present, and they could be more likely to be captured and eaten (Biro & Dingemanse, 2009; Castanheira et al., 2013). The adaptive value of exploratory activity is determined by its costs and benefits in different contexts (Sih et al., 2004). Although this question has been frequently studied in various animals such as lizards (Cote & Clobert, 2007), birds (Groothuis & Carere, 2005), and fishes (Overli et al., 2005; Brown et al., 2014; Szopa-Comley et al., 2020), there is limited evidence linking the activity of native species and the effect of this behavioral trait when an invasive predator is present.

The introduction of a new species to the environment causes behavioral changes in native species (Castaldelli et al., 2013; De la Torre et al., 2018). The Mexican mojarra, *Amphilophus istlanus* (Jordan & Snyder, 1899), is a cichlid native to the Balsas basin and has been affected by the introduction of invasive species such as the convict cichlid, *Amatitlania nigrofasciata* (Günther,1867) by reducing swimming activity, spending more time hiding (De la Torre et al., 2018), and is subject to interference competition (Archundia & Arce, 2019; Molina et al., 2021). The convict cichlid is an invasive predator that consumes spawn (eggs) and juveniles of the Mexican mojarra (EA, 2023 unpublished data). However, it is unknown whether Mexican mojarra juveniles respond behaviorally to the presence of the invasive fish or perceive it as a potential predator.

Here, we predicted that Mexican mojarra individuals in the presence of convict cichlids would reduce their swimming activity and food consumption. We hypothesized that the swimming activity and food consumption by the Mexican mojarra in two contexts-with and without a potential predator threat-is related to its levels of aggressiveness. We experimentally evaluated the individual consistency of the Mexican mojarra's swimming activity with and without the presence of an adult convict cichlid (a potential predator) and evaluated whether individuals' swimming activity is positively related to their aggressiveness. Understanding these dynamics could provide information relevant to the conservation of the native Mexican mojarra.

Materials and methods

Fishes and maintenance conditions

Fifth-generation juveniles of Mexican mojarras were obtained from different parents reared in captivity at the "El Rosario" fish farm in Morelos, México (18°33'35.5"N; 99°15'55.2" W). We used 14 two-month-old juvenile Mexican mojarra that weighed 0.64 g ± 0.11 g (mean ± standard deviation throughout) and had a total length of 2.39 cm ± 0.38. We ensured that the juveniles had never been in contact with convict cichlids. Fourteen invasive convict cichlids weighing 16.31 ± 2.34 g and measuring (TL) 10.02 ± 0.76 cm were captured from the Apatlaco River, Zacatepec Morelos, Mexico (18º39′46.2″ N; 99º11′ 56.5″W) and transported to the Laboratorio de Acuicultura, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos. Convict fish were maintained individually in 20 L tanks for two weeks prior to the experimental period with another conspecific visible to avoid social deprivation (Raymond et al., 2015). The Mexican mojarra juveniles were kept in a single 40 L tank for two weeks prior to the experimental period. All tanks had constant oxygenation at 27.5 ± 1.0 ºC and a pH of 7. The tank had a polyvinyl chloride (PVC) pipe measuring 20 mm in diameter by 70 mm long as a shelter (De la Torre et al., 2018). Juveniles of Mexican mojarra were fed once a day *ad libitum* with mosquito (*Culex quinquefasciatus*) larvae (Say, 1926). Convict cichlids were fed once a day with live juveniles of Mexican mojarra for three days prior to start of the experiments. Similar procedures have been used by Gelowitz et al. (1993) and Mathiron et al. (2015) with success; we thus think it is likely that juveniles of Mexican mojarra perceive the convict cichlid as a potential threat, despite having no previous experience encountering it. For both species, the fecal contents and uneaten food were removed daily from the maintenance tanks using a siphon, and 15% of the water from each tank was changed daily (De la Torre et al., 2018).

Consistency of swimming activity

We quantified the behavior of Mexican mojarra individuals while foraging in two contexts: in the presence of a convict cichlid (potential predator) and without the convict cichlid. For both contexts, we used a 40 L (30 cm x 50 cm x 27 cm) tank divided into two parts (a stimulus zone and an experimental zone) using a transparent 0.5 cm mesh and a solid opaque barrier that did not allow chemical, physical or visual exchange between the fish. For the potential predation threat test, a convict cichlid that had been previously fed with Mexican mojarra juveniles was placed in the stimulus zone and a juvenile of Mexican mojarra was placed in the experimental zone (fig. 1). The convict cichlid and the Mexican mojarra were left to acclimatize to the tank for 10 min with both the mesh and opaque barriers in place. For the Mexican mojarra, the feeding was suspended 24 hours before starting the experiments to standardize hunger levels. To begin the experimental period, the opaque barrier was removed, such that the compartments were divided only by the mesh, and mosquito larvae were added to the experimental zone as food for the mojarras. The experimental trial started at 10:00 h and the tank was recorded for 10 min using a Panasonic DMC-GH4 video camera. From the video recordings, we quantified swimming activity, which was the time in seconds that the Mexican mojarra was moving from one point to another in the water column (Brown & Dreier, 2002). The amount of food consumed was quantified as the number of mosquito larvae consumed. At the end of each trial, the Mexican mojarra juvenile was placed in an individual tank until the next trial. The experimental tank was emptied and rinsed thoroughly with tap water. After 24 hours, the same individual was tested under similar conditions and procedures without the presence of the convict cichlid. At the end of this test, the Mexican mojarra juvenile was placed in your tank and tested aggressive behavior after 24 hours. All tests (with a potential predator threat, without convict cichlid presence, and aggressiveness test) were made in random order (Eaton et al., 2016).

Aggressive behaviors

Tests of aggression were performed in a tank identical to the one used for the swimming activity trials; however, the stimulus zone was left empty and a mirror was placed behind the opaque divider between the experimental and stimulus zones (Desjardins & Fernald, 2010). The opaque barrier was removed at the beginning of the aggression test (Fig. 1). Like the swimming activity tests, the juvenile Mexican mojarra was allowed to acclimate to the tank for 10 min, and the experiment began at 10:00 h. The tests were video recorded for 10 min and the videos were analyzed to evaluate aggressive behaviors in the Mexican mojarra by counting the number of ramming and frontal swimming events it performed against the mirror (Balzarini et al., 2014). A ramming event was counted when the Mexican mojarra approached the mirror quickly and made physical contact with the mirror; frontal swimming was the time in seconds that the mojarra spent swimming repeatedly back and forth parallel to the mirror (Schürch & Heg, 2010). Each individual was tested in random order in each trial, with potential predation threat, without convict cichlid presence and aggressive behavior with a 24 h break between each test (Belgrad & Griffen, 2016). The water conditions during all tests were the same as in the maintenance tank.

Statistical analysis

Experimental fish were not physically marked, but their identities were known because they were always kept in and returned to the same individually numbered tank. Examination of histograms, quartile-quartile plots, and boxplots showed a symmetrical distribution consistent with a normal distribution, and the result of the Shapiro-Wilk test of normality was non-significant for foraging activity and food consumed. To determine whether individuals behaved differently when the convict cichlid was present versus absent, we, therefore, used a paired t-test to compare the swimming activity and food consumed by each individual between the two treatments. To determine whether individuals were consistent in each behavior in the two contexts or whether there was an association in individuals' rankings across different behaviors, we first ordered the individuals consecutively, assigning the smallest number to the individual with the highest value for the given behavior and the largest number to the individual with the lowest value for each variable. Thus, number 1 was assigned to the fish that had the highest swimming activity, ate the most mosquito larvae, or had the most aggressive behaviors (the sum of ramming and frontal swimming), and number 14 was given to the individual with the lowest activity, that ate the fewest mosquito larvae, or had the least aggressive behaviors. This ranking was performed separately for each variable and treatment, resulting in a total of six ranks for each individual. We then performed six Kendall Rank tests to test the consistency of individuals' ranks in each behavior between the two treatments (two tests), between behaviors within each treatment (two tests), and between aggressive behaviors and foraging behaviors (two tests) (Kolok, 1999; Arce & Alcaraz, 2013). All statistical analyses were conducted using Statistica ® v.10 (alpha = 0.05).

Ethics approval

We used the minimum number of fish necessary to yield clear results and accomplish the experimental goals. The fish used in this study are not an endangered or protected species and did not suffer any injury.

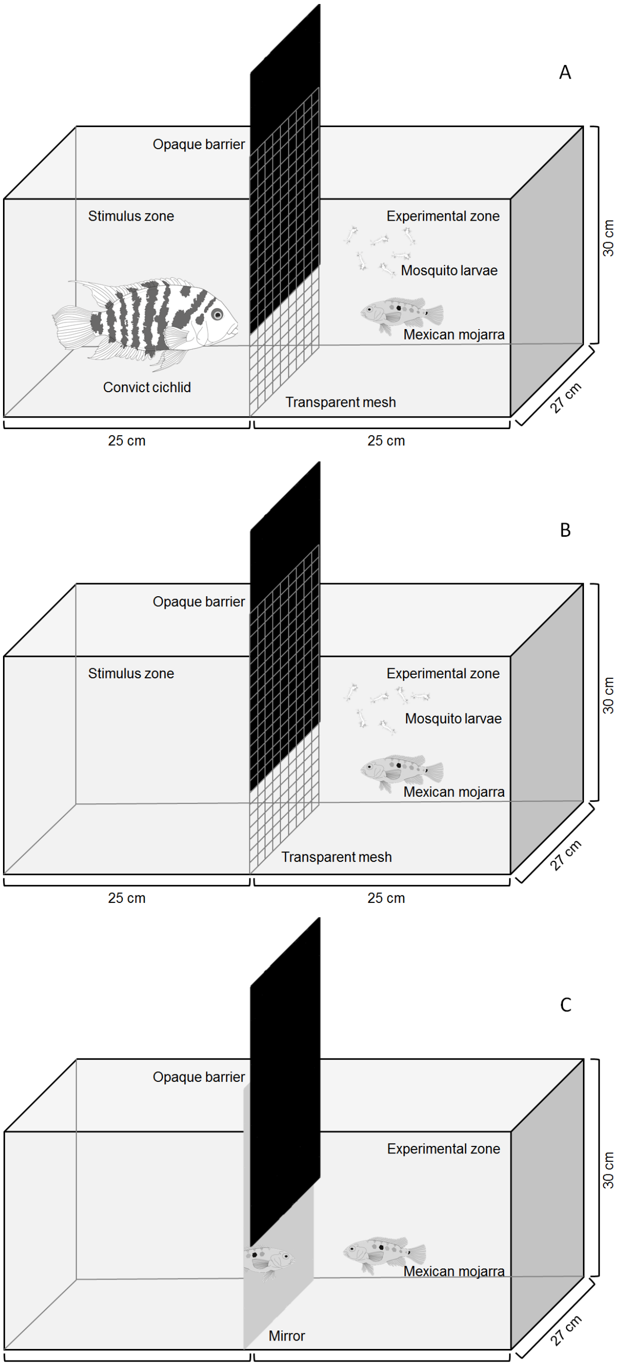

Figure 1. Schematic diagram of the experimental tests of the Mexican mojarra juvenile. A) with a potential predator threat, B) without convict cichlid presence, C) in an aggressiveness test.

Results

Overall, the Mexican mojarras had higher swimming activity when the convict cichlid was absent (498.71 ± 17.03 s) than when the convict cichlid was present (336.29 ± 32.25 s; t= 4.83, n= 14, P = 0.0003; Fig. 2A). Similarly, they consumed more mosquito larvae when the convict was absent (4.14 ± 1.24 items) than when it was present (1.50 ± 0.50 items; t= 2.74, n= 14, P = 0.016; Fig. 2B).

The ranking of swimming activity was consistent between the two treatments (convict cichlid present

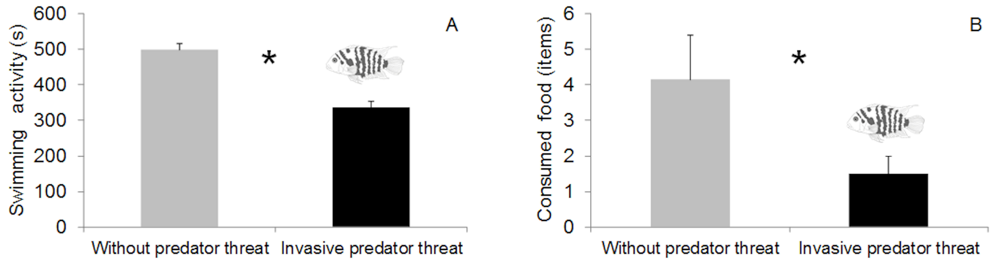

Figure 2. A) Swimming activity, and B) food consumption for Mexican mojarra juveniles when the convict cichlid (a potential predator) was absent versus present. The bar height represents the mean and the error bars are the standard error of the mean. Asterisks indicate significant differences ($P < 0.05$).

and absent; $W = 0.95$, $df = 1$, $P = 0.03$, Fig. 3A), as was the number of food items consumed ($W = 0.87$, $df = 1$, $P = 0.04$, Fig. 3B). The Mexican mojarra juveniles with the highest swimming activity were consistently those that consumed the most food without predation threat ($W = 0.94$, $df = 1$, $P = 0.03$, Fig. 3C) and with potential predation threat ($W = 0.99$, $df = 1$, $P = 0.01$, fig. 3D). The Mexican mojarra juveniles with the highest swimming activity were consistently the most aggressive ($W = 0.96$, $df = 1$, $P = 0.02$, fig. 3E). The Mexican mojarra juveniles that consumed the most mosquito larvae were consistently the most aggressive ($W = 0.89$, $df = 1$, $P = 0.04$, Fig. 3F).

Discussion

The ability to recognize a predation threat is essential for animals' survival (Arvigo et al., 2019). Predators are a selection pressure on prey, and native fish may not recognize invasive predators as a threat (Davis, 2018). In our work, the fact that the Mexican mojarra in general spent less time feeding and consumed fewer prey items when convict cichlid was present suggests that they identified it as a potential predator and adjusted their behavior accordingly. Similar effects have been observed in the fish *Esox lucius* and *Gasterosteus aculeatus*, which decrease their mobility when a predator is present (Lehtiniemi, 2005). This strategy allows prey to avoid being perceived by predators and therefore increases their survival (Gerritsen & Strickler, 1977; Grand & Dill, 1997). However, moving less has energetic implications (Cooke et al., 2003). Prey species must balance the need to avoid predation with the need to forage (Brown et al., 2006). With an invasive predator, this trade-off is particularly important because this risk is novel and selection has not yet had a chance to shape the optimal response to the novel predator (Arce & Córdoba-Aguilar, 2018). The juvenile stage is critical in the development of fish since they do not have reserve energy and need to feed constantly (Hamre et al., 2013) and it is also the time when the fish are most vulnerable (Paradis et al., 1996).

Knowledge about behavioral traits provides a framework in which to understand individual animals' behavioral responses to biotic and abiotic environmental conditions that vary throughout their lifetime (Reale & Festa-Banchet, 2003). Predation is an important factor in the evolution of animal behavior and is considered one of the major causes of mortality for the most active individuals (Biro & Booth, 2009). In our work, the consistency of swimming activity in individual Mexican mojarra juveniles is repeatable with and without predation risk. Furthermore, the most active Mexican mojarra juveniles were consistently the ones that consumed the most food. This is similar to results in *Negaprion brevirostris* (Poey, 1868), where more explorative individuals have higher rates of encounter with food, eat more, and have faster growth than less explorative conspecifics (Dhellemmes et al., 2021).

Cichlids that depend on parental care for their reproductive success are more aggressive and face more risks during the search for resources than species that do not perform parental care (Rangeley & Godin, 1992; Smith & Wootton, 1999; Clement et al., 2005; Fulmer et al., 2017). Even during the juvenile stage, territorial species carry out aggressions during competition for resources (Thresher, 1985). In environments with predation risk, individuals who consistently maintain aggressive behavioral strategies are those who most frequently face risk (Harris et al., 2010). In this work, the Mexican mojarra juveniles with the most swimming activity were also the most aggressive. The positive correlation between activity and aggressiveness has been tested in *Gasterosteus aculeatus* (Bell & Sih, 2007). Aggressiveness in the Mexican mojarra has been observed during competition for territories (Archundia & Arce, 2019; Molina et al., 2021) and sexual partners (Castillo & Arce, 2021). In the Mexican mojarra, the most aggressive juveniles could also be those who are most

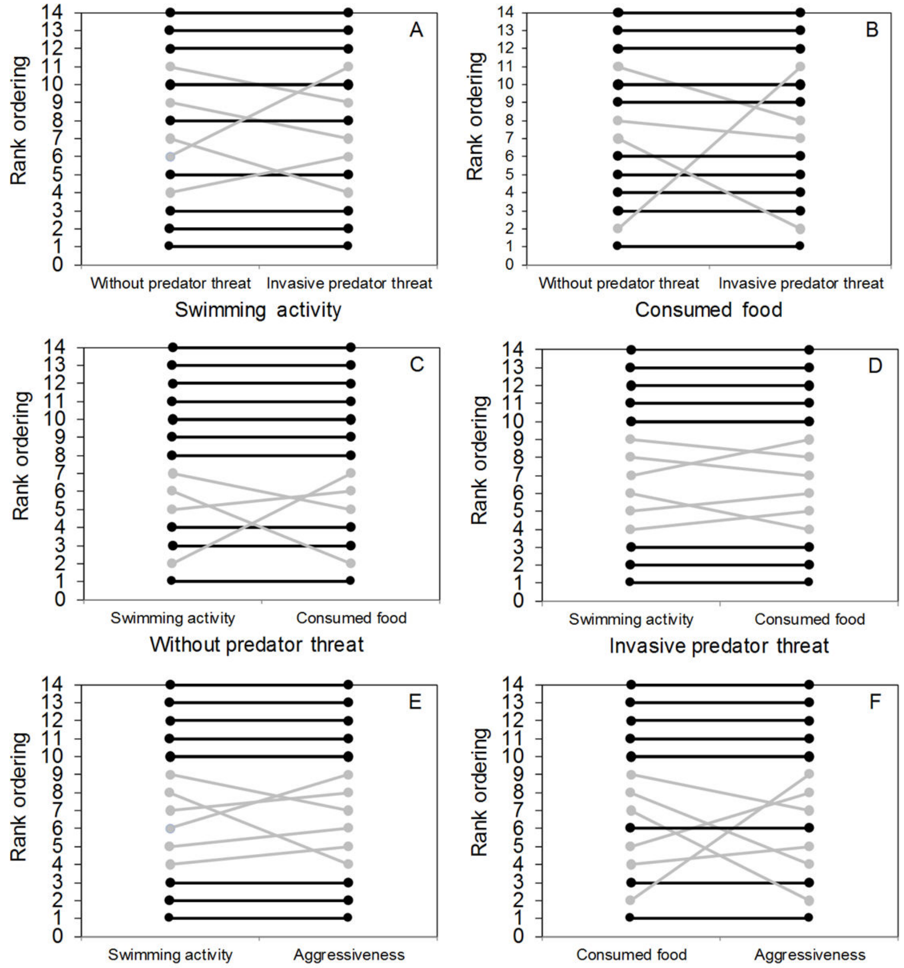

Figure 3. Rank ordering and consistency of behavior of the Mexican mojarra juvenile in A) swimming activity; B) food consumed; C) swimming activity and consumed food without convict cichlid (a potential predator); D) swimming activity and food consumed food with convict cichlid present; E) swimming activity and aggressiveness; F) food consumed and aggressiveness. Black lines denote the same rank and gray lines denote a change in rank between the two conditions or behaviors.

at risk from predation (Hess et al., 2016). Aggression plays a role in determining individual survival and reproductive success (Nicieza & Metcalfe, 1999). Aggression is strongly correlated with growth; more aggressive fish grow faster, while less aggressive fish are more vulnerable to being attacked by conspecifics and having reduced access to food (Metcalfe, 1986). It is essential to conduct further research to assess both the benefits and consts of aggressive behavior.

Feeding and constant movement during the juvenile stage is essential for physiological development (Schütz & Barlow, 1997). In fish, the response to risk depends on various factors including phenotypic plasticity and previous experience (Balasch & Tort, 2019). Interindividual variation in behavior contributes to variation in fitness (Smith & Blumstein, 2008; Boyer et al., 2010; Mutzel et al., 2013). Studying behavioral traits in native fish species can help to understand the ecological consequences of invasive predator species, especially in an environment with a high level of competition like the Balsas River basin (Franco & Arce, 2022). Our results did not allow us to determine whether the behavior of the Mexican mojarra was due to conspecifics dying from the attack of the invasive fish (conspecific odor) or whether they responded to the convict cichlid as a predator specifically. More studies are required to understand the population stability of the native Mexican mojarra after the arrival of the invasive predator convict cichlid, and understanding the responses of the native cichlid to the potential threats of this invasive fish could help to inform conservation strategies.

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Ethical approval

All applicable guidelines of the Ley General del Equilibrio Ecológico y la Protección al Ambiente were followed. Fish in this experiment did not suffer any injury, and the study did not use endangered or protected species.

Data availability statement

The data generated during the current study are available from the corresponding author upon reasonable request.

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