

Assessment of histological changes caused by the trematode *Tylodelphys* sp. in the central nervous system of *Galaxias maculatus*

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A recent experimental study has reported significant changes in the behaviour of the fish *Galaxias maculatus* due to the presence of the parasite trematode *Tylodelphys* sp. in its cranial cavity. The underlying mechanisms of these behavioural changes remain unknown. This study aims to elucidate potential histological alterations caused by the trematode *Tylodelphys* sp. in *G. maculatus* hosts. Specifically, cranial tissues from parasitized and non-parasitized fish were compared to assess possible structural changes or lesions associated with the presence of the parasites. It was found that *Tylodelphys* sp. does not induce visible changes in the brain, meningeal tissue, or cranial bones of the fish. *Tylodelphys* sp. primarily resides in the posterior region of the cranial cavity, within the cerebrospinal fluid surrounding the brain near the hypothalamus, basal nuclei, and other structures related to vision and locomotion. Therefore, *Tylodelphys* sp. appears to influence the behaviour of its fish host without causing direct damage to the brain tissue, possibly through increased cerebrospinal fluid pressure or chemical interactions with the host's brain, mechanisms that should be further investigated in future studies.

Keywords: Ecology, Fish, Histology, Parasitology.

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Un reciente estudio experimental ha reportado cambios significativos en el comportamiento del pez *Galaxias maculatus* debido a la presencia del trematodo parásito *Tylodelphys* sp., en su cavidad craneal. Los mecanismos subyacentes de estos cambios conductuales aún permanecen desconocidos. Este estudio se enfocó en elucidar posibles cambios histológicos causados por el trematodo *Tylodelphys* sp. en los hospederos *G. maculatus*. Específicamente, se compararon los tejidos de la cabeza de peces parasitados y no parasitados para evaluar posibles cambios estructurales o lesiones causadas por la presencia de los parásitos. Se encontró que *Tylodelphys* sp. no provoca cambios visibles en el cerebro, el tejido meníngeo ni el tejido óseo de los peces. *Tylodelphys* sp. se asienta principalmente en la zona posterior de la cavidad craneal, en el líquido cefalorraquídeo que rodea el cerebro cerca del hipotálamo, los núcleos basales y otras estructuras relacionadas con la visión y la locomoción de los peces. Por lo tanto, *Tylodelphys* sp. parece afectar el comportamiento de su pez hospedero sin causar lesiones directas en su tejido cerebral, posiblemente mediante un aumento de la presión del líquido cefalorraquídeo o a través de interacciones químicas con el cerebro del hospedero, aspectos que deberían ser esclarecidos en futuros estudios.

Palabras clave: Ecología, Histología, Parasitología, Peces.

INTRODUCTION

Many parasite species that use trophic transmission to infect their definitive host modify the behaviour or appearance of the intermediate hosts to increase their probability of being consumed by the definitive hosts (Combes, 2001; Moore, 2002; Poulin, 2010). Such alterations may include changes in stimuli response, modification of activity levels or changes in pigmentation (Poulin, 1998). The increase in the probability that the intermediate host will be ingested by the definitive host as a consequence of these modifications is referred to as parasite increased trophic transmission or PITT (Lafferty, 1992, 1999). For example, individuals of the Californian killifish (*Fundulus parypinnis*) infested by the trematode *Euaplorchis californiensis* exhibit up to a fourfold increase in activity compared to uninfected individuals, making them 10 to 30 times more prone to be predated upon by avian definitive hosts (Lafferty, Morris, 1996; Shaw *et al.*, 2009).

Digenetic trematodes constitute a large and diverse group of parasites characterized by complex life cycles involving more than one reproductive stage, and in some cases, utilizing multiple host species. In the case of the digenetic trematode *Tylodelphys* sp., a mollusk serves as the first intermediate host, and the second intermediate host can be either an invertebrate or a vertebrate (*e.g.*, crustacean, fish or amphibian). These are then preyed upon by the definitive host, which is typically a vertebrate predator, such as a bird. Many parasite species that use trophic transmission to infect their definitive hosts can influence the metabolism and behaviour of their intermediate hosts through direct alteration of tissue or organs of the host and/or chemical changes through primary and secondary metabolites (Lafferty, Morris, 1996; Poulin, 1998; Barber, Wright, 2005;

Barber, 2007; Macchi *et al.*, 2007; Vigliano *et al.*, 2009; Barriga *et al.*, 2012; Barber *et al.*, 2017; López-Rodríguez *et al.*, 2021). In general, digenetic trematodes get out of the first intermediate host, swim freely in the water and infect their second intermediate host penetrating its skin (Olsen, 1986). Some species migrate to the brain, probably via blood vessels or neural pathways (Hendrickson, 1979; Haas *et al.*, 2007). Localization of parasites in the brain may represent a strategy to escape from the host's immune system (Szidat, 1969; Barber, Crompton, 1997; Rosser *et al.*, 2016).

In Chile, puye *Galaxias maculatus* (Jenyns, 1842) is the second intermediate host of the trematode *Tylodelphys* sp. (Digenea: Diplostomidae) which settles unencysted in its cranial cavity at the metacercarial stage (Revenga, Schneinert, 1999). *Galaxias maculatus* is highly abundant in rivers of central Chile and Patagonia where it is an important resource for artisanal fishery (Górski *et al.*, 2018; Cussac *et al.*, 2020). *Tylodelphys* sp. has been reported to parasitize *G. maculatus* populations in multiple locations throughout its distribution range, often reaching high infection intensities (Viozzi *et al.*, 2009; George-Nascimento *et al.*, 2020).

A recent experimental study reported significant behaviour changes in *G. maculatus* due to the presence of the parasite *Tylodelphys* sp. in the cranial cavity. Infected fish were observed swimming more frequently near the water surface and exhibited delayed responses to predation risk (López-Rodríguez *et al.*, 2021). However, the underlying mechanisms driving these behavioural changes remain unknown. This study aims to elucidate potential histological alterations caused by the trematode *Tylodelphys* sp. in *G. maculatus* hosts. Specifically, cranial tissues from parasitized and non-parasitized fish were compared to assess possible structural changes or lesions associated with the presence of the parasites.

MATERIAL AND METHODS

Specimen collection and processing. *Galaxias maculatus* individuals were collected on the 24 August 2021 in two river basins: the Imperial River, 38°44'52.42"S 73°24'27.19"W, Araucanía Region, Chile, where high abundances of *Tylodelphys* sp. have been reported, and the Cruces River, 39°51'55.33"S 73°21'21.89"W, Los Ríos Region, Chile, where the absence of *Tylodelphys* sp. has been documented (George-Nascimento *et al.*, 2020). Fish were collected using a beach seine (6 m long, 1.2 m high, and 10 mm stretched mesh size). On each sampling occasion, collected fish were anaesthetised (benzocaine BZ-20®, Veterquímica, Santiago, Chile), identified to species level, measured and weighed. Subsequently, a maximum of 10 individuals of *G. maculatus* from each location were sacrificed with an overdose of the same anaesthetic and immediately preserved in Bouin's solution for further processing, in accordance with availability and following the guidelines of the Chilean Undersecretariat for Fisheries and Aquaculture.

In the laboratory, collected specimens were passed through a graded alcohol series (70%, 80%, 90%, 95% and 99%) to complete the dehydration process and proceed to the inclusion process through paraffin impregnate at 58°C. Subsequently, 7µm-thick sections were made using a manual rotation microtome. These sections were mounted on glass slides and rehydrated through a descending alcohol series (from

99% to 70%), followed by a treatment with Xylol to remove paraffin. Mounted tissue sections were then stained with Hematoxylin-Eosin (H-E). Stained histological sections were examined under an Olympus U-CDMA3 microscope (Olympus, Tokio, Japan) and photographed using a coupled JENOPTIK camera (Jena, Germany) and ProResCapture 2.10 software. The number of *Tylodelphys* sp. specimens in the cranial cavity of each fish was quantified through visual inspection of sequential histological sections using optical microscope. This method enabled the identification of individual parasites in each cranial cavity. The precise location of parasite settlement within the cranial cavity was also evaluated. Tissues in each histological section were categorized as anterior, medial, and posterior based on general anatomical boundaries of the teleost brain: anterior (olfactory bulbs and telencephalon), medial (optic lobes), and posterior (cerebellum and myelencephalon) (Ullmann *et al.*, 2010; Wulliman *et al.*, 2012; Kenney *et al.*, 2021). Finally, tissues from parasitized (P) and non-parasitized (NP) fish were compared to identify possible differences, such as presence of rodlet cells (indicative of inflammatory response), inflammation, colour alterations (Reite, 2005; Reite, Evensen, 2006; Dezfuli *et al.*, 2007).

Data analysis. Meningeal brain tissues from parasitized *G. maculatus* were visually compared to those from non-parasitized individuals. This analysis was performed on groups of fish of similar size, ensuring that parasitized specimens used in the comparisons had at least 10 parasites inside their cranial cavity. To assess the location of *Tylodelphys* sp., its numerical abundance was compared among three cranial regions (anterior, medial, and posterior) using a Kruskal-Wallis test followed by a *post-hoc* test.

RESULTS

A total of 99 specimens of *Galaxias maculatus* were collected (31 from sites with previous records of *Tylodelphys* sp. and 68 from sites without known records) (Tab. S1). We observed a 100% prevalence and a mean abundance of 25.6 (range: 1 to 54) of *Tylodelphys* sp. in individuals collected from the Imperial River and absence of this trematode was detected in individuals from the Cruces River. The number of parasites in the posterior region of the cranial region (mean = 8) was significantly higher compared to the anterior and medial regions ($H = 37.23$, $P < 0.0001$; Fig. 1).

Histological sections stained with Hematoxylin-Eosin revealed distinct cranial cavity tissues, including muscle, bone, meningeal, and brain tissues (Fig. 2). Parasites were readily distinguishable from surrounding tissues, unencysted, and located externally to the brain within the meningeal cavity (Fig. 2A).

No histological changes in the colour or structure of the brain were found, meningeal, or bone tissues were observed in parasitized specimens (Fig. 3). Some parasites were located in close proximity to brain tissue (Figs. 3A, C, E, G). Brain tissue from parasitized and non-parasitized fish showed similar staining characteristics, with an intense pink colour in areas associated to ocular motion, head and neck control, and interhemispheric communication (Fig. 3). The meningeal cavity appeared white and exhibited no apparent difference between parasitized and non-parasitized fish (Fig. 3). No evidence of inflammation, necrosis, tissue regeneration, or abnormal structures was detected in the brain, meningeal, or cranial tissues of parasitized individuals (Figs. 3A, C, E, G).

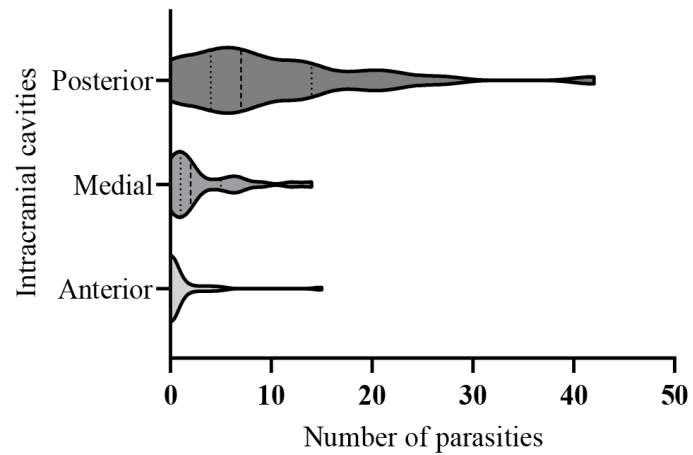


FIGURE 1 | Violin graph (first quartile, median, third quartile) depicting the number of *Tyloodelphys* sp. metacercariae in three regions within the cranial cavity of *Galaxias maculatus*, based on dorsal view histological sections at 4x magnification.

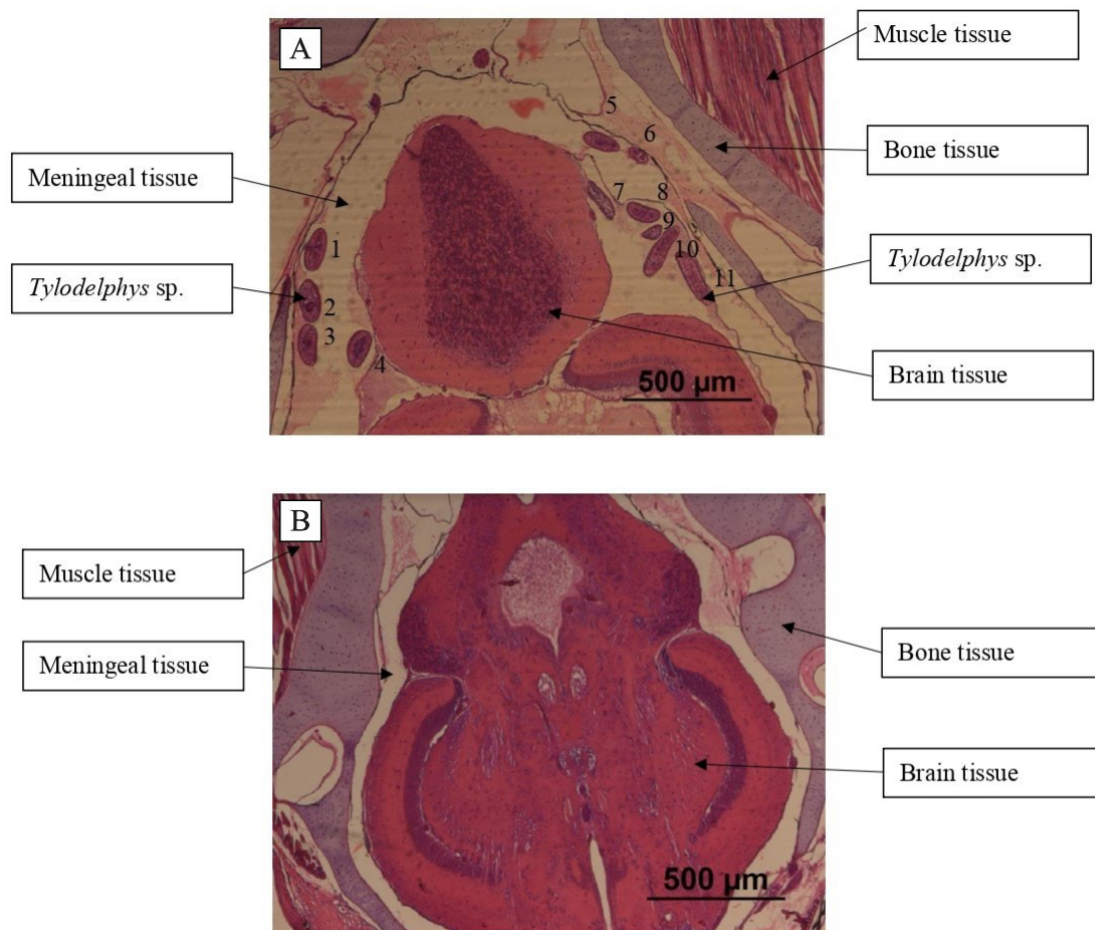


FIGURE 2 | Dorsal views of the histological section of *Galaxias maculatus* heads parasitized by *Tyloodelphys* sp. (A) and non-parasitized (B). Eleven visible metacercariae of *Tyloodelphys* sp. are numbered. Hematoxylin-Eosin staining (H-E); 4x magnification.

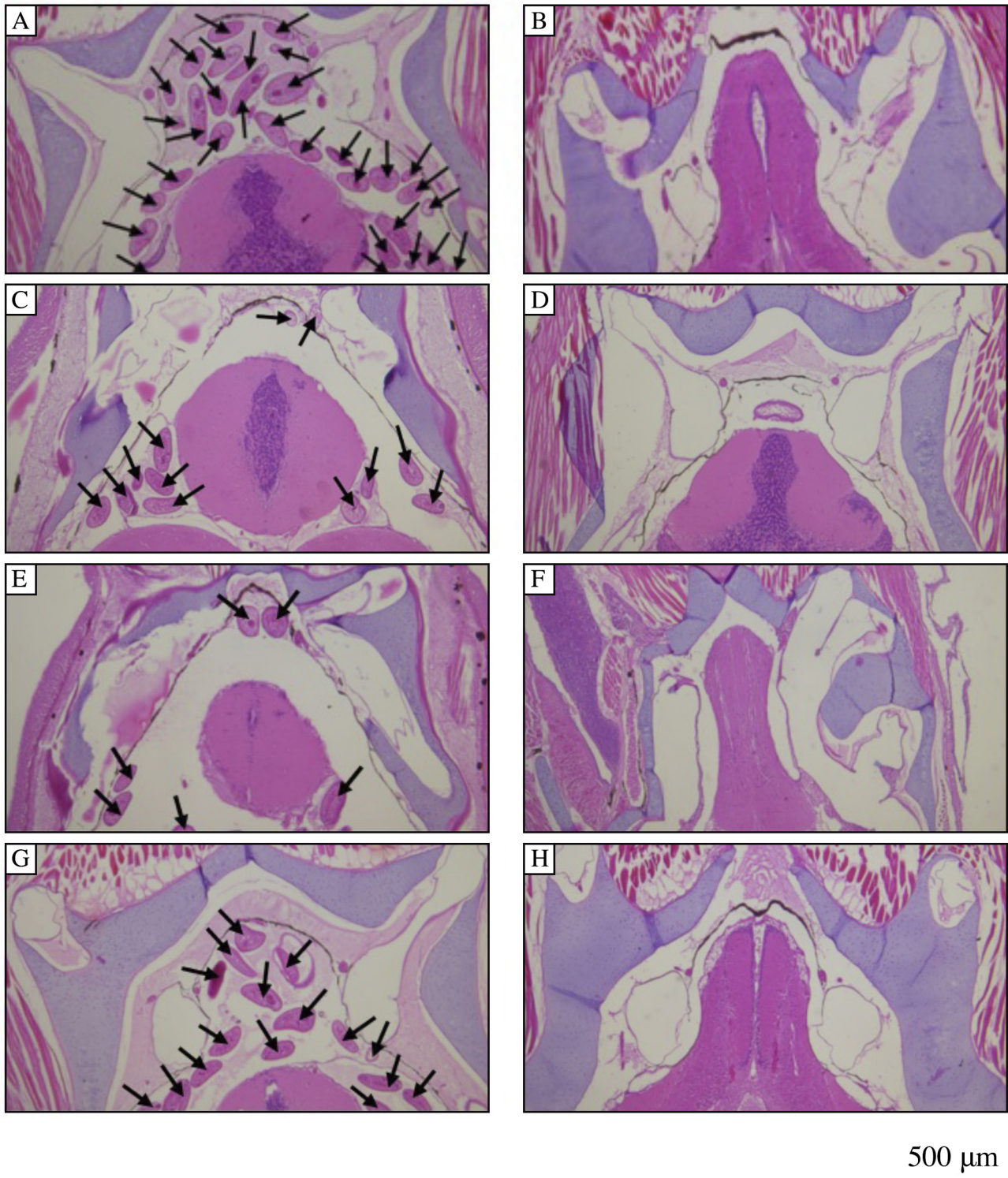


FIGURE 3 | Dorsal view of eight histological sections of the heads of *Galaxias maculatus* parasitized by *Tylodelphys* sp. (A, C, E, G) and non-parasitized (B, D, F, H). Arrows indicate *Tylodelphys* sp. metacercariae. Hematoxylin-Eosin staining (H-E); 4x magnification.

DISCUSSION

This study demonstrates that the presence of *Tylodelphys* sp. metacercariae in the cranial cavity of the puye *Galaxias maculatus* does not induce histological alterations in brain, meningeal and cranial tissues. Prior research has shown that parasites in the central nervous system can alter host behaviour (Lafferty, Morris, 1996; Pulkkinen *et al.*, 2000; López-Rodríguez *et al.*, 2021), including increase surface swimming (Lafferty, Morris, 1996; López-Rodríguez *et al.*, 2021). Our findings suggest these behaviour shifts may stem from chemical interactions at the molecular level rather than direct physical damage caused by parasite.

Metacercariae of *Tylodelphys* sp. preferentially settle in the posterior region of the cranial cavity (Fig. 1), placing them in proximity to critical neural structures such as the hippocampus, hypothalamus, basal nuclei and cerebellum. These brain regions are implicated in locomotion, memory, hormonal regulation, and voluntary motor control (Siegmund *et al.*, 1997; Barber *et al.*, 2000; Shaw *et al.*, 2009; Grobbelaar *et al.*, 2015; Gopko *et al.*, 2017; Kenney *et al.*, 2021; López-Rodríguez *et al.*, 2021). Thus, behavioural alterations may result from functional disruptions in these areas due to the presence of parasites. In contrast to reports of morphological changes, such as skull enlargement in *Pimephales promelas* infected by the trematode *Ornithodiplostomum ptychocheilus* (Sandland, Goater, 2001), no such changes were observed in *G. maculatus*.

Similar to *Tylodelphys* sp., *Euhaplorchis californiensis* localizes in the posterior region of the brain of host fish *Fundulus parvipinnis* and affects host behaviour by modulating serotonergic activity (Shaw *et al.*, 2009). However, unlike *E. californiensis*, *Tylodelphys* sp. does not encyst but remains in free form in the cranial cavity of *G. maculatus* and no evidence of cyst walls or encapsulation was observed in histological sections. Although this limits direct comparisons, the higher metabolic activity of unencysted parasites may result in secretion of bioactive compounds capable of influencing host neural activity. Furthermore, we cannot rule out the possibility that unencysted metacercariae possess some degree of motility within brain tissues, as has been documented in other host-parasite systems (Lafferty, Morris, 1996). Such motility, even if limited, could facilitate strategic positioning near critical neural structures to potentially affect host behaviour enhancing transmission through trophic interactions. While histological damage was absent, *Tylodelphys* sp. inhabits cerebrospinal fluid spaces (Shaw *et al.*, 2009). Obstruction of cerebrospinal fluid flow can increase intracranial pressure, potentially resulting in hydrocephalus, altered meningeal morphology, impaired balance or vision loss due to swelling of the optic discs (Kenney *et al.*, 2021). Thus, the parasite may influence host behaviour via fluid pressure changes or chemical interactions with the brain and surrounding tissues. In conclusion, *Tylodelphys* sp. primarily localizes in the posterior cranial cavity of *G. maculatus*, adjacent to key neural structures. Although no histological alterations were detected, future studies should investigate potential neurochemical pathways through which parasite-derived metabolites might alter host behaviour.

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AUTHORS' CONTRIBUTION

Paulina Rivera: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft.

Ruby López-Rodríguez: Conceptualization, Data curation, Investigation, Validation, Writing—review and editing.

Daniela Mardones: Data curation, Visualization.

Nicole Colin: Investigation, Validation, Writing—review and editing.

Konrad Górski: Conceptualization, Funding acquisition, Resources, Supervision, Validation, Writing—review and editing.

ETHICAL STATEMENT

Capture methods and animal handling procedures followed institutional guidelines and regulations and were approved by the Ethics and Bioethics Committee of the Universidad Austral de Chile (373/2019).

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

COMPETING INTERESTS

The authors declare no competing interests.

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