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Testing the Enemy Release Hypothesis in the Invasive Fish *Amatitlania nigrofasciata* (Perciformes: Cichlidae) in Mexico

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Abstract—The enemy release hypothesis (ERH) posits that invasive species are released from their natural enemies in their invasive range, which promotes their successful invasion. In this study, we tested the ERH in a population of the convict cichlid *Amatitlania nigrofasciata*, an invasive species in Mexico. The ERH predicts that the convict cichlid: (a) is not infected by specialist helminth parasites in the invasive range; (b) has lower infection parameter values, as measured through richness, prevalence, abundance and diversity of helminths, than a native species—the redside cichlid *Cichlasoma istlanum*; and (c) is not affected in its condition factor by the abundance of helminths it carries. The convict cichlid was infected by two (33%) specialist helminths relative to the six specialist helminths that infect the cichlid in its native range. The convict cichlid had lower helminth richness and diversity than the redside cichlid. However, the prevalence and abundance of the parasite species varied between the host fish. While the prevalence and abundance of the nematode *Rhabdochona kidderi* was higher in the redside cichlid, the prevalence and abundance of the trematode *Uvulifer* sp. was higher in the convict cichlid. The condition factor in both host fish was not correlated with helminth abundance. Our results do not agree with the prediction that the convict cichlid is completely released from specialist parasites, nor with the prediction that this invasive species has lower infection parameter values than the native redside cichlid. However, our results agree with the prediction that the abundance of parasite helminths do not affect the cichlid's condition factor. More studies are necessary to determine the advantages that the convict cichlid could have in the invasive range when it is infected with a low richness and diversity of helminths.

Keywords: invasive species, convict cichlid, *Cichlasoma istlanum*, parasites, *Uvulifer*, *Rhabdochona kidderi*

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INTRODUCTION

Invasive fish species are a major threat to native ichthyofauna worldwide, but particularly to freshwater species (Dextrase and Mandrak, 2006; Dudgeon et al., 2006; Darwall et al., 2009). The convict cichlid *Amatitlania nigrofasciata* (Günther, 1867), is a native fish from Central America (Schmitter-Soto, 2007) that is cultivated and commercialized as an ornamental species in Mexico and other parts of the world (Martínez-Castro and Ramírez-Herrera, 2016). Due to accidental or deliberated release of individuals in fish farms, convict cichlid populations have been established in tropical and temperate regions out of its native geographic range (Piazzini et al., 2010; Duffy et al., 2013; Herrera-R et al., 2016).

In Mexico, at least 30 years ago, along the rivers of the Balsas and Panuco basin, *A. nigrofasciata* is known as an invasive species that can potentially threat the native fish species (Espinosa-Pérez and Ramírez, 2015; Mendoza et al., 2015). There is evidence that *A. nigrofasciata* may be displacing the redside cichlid *Cichlasoma istlanum* (Jordan and Snyder, 1899) through competition for breeding sites and/or alteration of its feeding behavior, swimming and use of shelters (Contreras-MacBeath et al., 2014; De la Torre-Zavala et al., 2018).

In invasion ecology, the enemy release hypothesis (ERH) states that the absence of coevolved enemies (predators, parasites and herbivores) for invasive species promotes the invasion success of the new range (Heger and Jeschke, 2018). However, most studies of the ERH have been tested on terrestrial ecosystems and in plants, but much less in both freshwater systems and vertebrates (Heger and Jeschke, 2014). Studies in freshwater systems have been performed in invasive cichlid fish and their metazoan parasites (Roche et al., 2010; Lacerda et al., 2013). In these studies, the richness and abundance of parasites in the host species was compared (i) between individuals from the native versus the invaded range; and (ii) with that of native species from the invaded range. The results showed mixed evidence, which could result from the fact that the comparisons in these studies did not distinguish between generalist and specialist parasites, albeit, according to the ERH, the focus of the studies should be the release of specialist parasites (Heger and Jeschke, 2018).

In this study, we tested the ERH on the convict cichlid and specialist helminth parasites, sampled from the Rio Ixtapan, Estado de Mexico, which is located within the range the convict cichlid has invaded in Mexico. If the convict cichlid is released from specialist parasites in the Rio Ixtapan, we expect the cichlid: (i) not to be infected by specialist helminths; (ii) to have lower infection parameter values—richness, prevalence, abundance and diversity of helminths—than the native redside cichlid *C. istlanum*; and (iii) to show a condition factor that is independent of helminth abundance. To test predictions (i) and (ii), we compared *A. nigrofasciata* and *C. istlanum* in terms of richness, prevalence, abundance and diversity of helminths found in each host species. To test prediction (iii), we related the condition factor of each host species with its own helminth abundance.

MATERIALS AND METHODS

Study Area

We sampled fish individuals in seven sites along the main stream of Rio Ixtapan in Central of neotropical Mexico: (1) San Miguel Ixtapan (18°47′ N, 100°9′ W), (2) El Sitio (18°45′ N, 100°18′ W), (3) San Lucas (18°47′ N, 100°18′ W), (4) Bejucos (18°46′ N, 100°25′ W), (5) Betarrón (18°45′ N, 100°28′ W), (6) Pochote (18°44′ N, 100°30′ W) and (7) Balderrama (18°43′ N, 100°32′ W). Individuals were sampled with a fishnet of 3 m of diameter and 0.9 cm mesh, from February to November of 2016. The species were identified with the taxonomic keys of Miller (2005) and treated according to the Mexican Official Norm 033-SAG/ZOO-2014 (SAGARPA, 2015). We collected a total of 88 individuals of the invasive species *A. nigrofasciata* and 74 individuals of the native species *C. istlanum*.

Host and Helminth Parasites Processing

For each fish sampled, we measured the standard length (cm), total length (cm), height (cm) and weight (g). Each specimen was then revised for ecto and endoparasites under the microscope following standard procedures (Vidal-Martínez et al., 2001).

For each helminth species, we determined the following infection parameters: prevalence, mean intensity and mean abundance, with their corresponding confidence intervals according to Bush et al. (1997) and Reiczigel et al. (2019). Then, for each host species, we distinguished the helminth assemblages as component communities and infracommunities. Component communities were described in terms of diversity, equity and dominance, through the indices of Shannon–Wiener (H'), the effective number of species, Pielou (J') and Berger–Parker (B) (Moreno, 2001; Magurran, 2004). Infracommunities were described in terms of mean species richness and mean Brillouin diversity. Helminths host specificity was determined by following the criteria from Poulin and Mouillot (2005).

To estimate the species richness expected in each host fish, we contrasted the observed helminth richness against a species accumulation curve adjusted to the Clench model (Jiménez-Valverde and Hortal, 2003). We estimated the proportion of observed richness in a given host as the ratio between the total observed richness in the host and the richness estimated with the Clench model.

For each fish sampled, we estimated the fish condition (Kn) following Le Cren (1951):

$$\mathrm{Kn} = W/aLb,$$

where W is the body weight (g), L is the total length (cm), and a and b are parameters of the linear regression between the logarithms of weight and total length of the fish in the sample.

Statistical Analysis

To compare the different infection parameters and the parasite community metrics between the two host fish species, we proceeded as follows. Prevalence and abundance of helminths between the two host species was compared by applying a Chi-squared test and a bootstrapping T-test, respectively (Reiczigel et al., 2019). Shannon–Wiener diversity of parasites between the two host was compared with a Hutchenson t-test (Hutchenson, 1970), whereas species richness and Brillouin diversity between host fish were compared with a Mann–Whithney U test. Finally, the relationship between the condition factor and helminth abundance in each host was evaluated with a rank Sperman correlation. All the analyses were carried out in the software Quantitative Parasitology Web (Reiczigel et al., 2019) and PAST v3.14 (Hammer et al., 2001).

RESULTS

The convict cichlid *A. nigrofasciata*, sampled in the Rio Ixtapan, was found to be infected by three different helminth species: two trematodes and one nematode; two of them are specialist parasites and one is a generalist. In its native range, the convict cichlid is infected by six specialist helminth parasites (Table 1). In contrast, the redside cichlid *C. istlanum* was found

Table 1. Cichlid specialist helminths of *Amatitlania nigrofasciata* in Rio Ixtapan and in its native distribution range (Central America)

Helminth	Rio Ixtapan (present study)	Central America (Kohn et al., 2006; López-Jiménez et al., 2018; Sandlund et al., 2010)
Crassicutis cichlasomae	Absent	Present
Uvulifer sp.	Present	Present
Sciadicleithrum bicuense	Absent	Present
Sciadicleithrum meeki	Absent	Present
Rhabdochona kidderi	Present	Present
Procamallanus rebeccae	Absent	Present

Table 2. Infection parameters: prevalence (P), mean intensity (MI) and mean abundance (MA) of helminths of *Amatitlania nigrofasciata* and *Cichlasoma istlanum* from Rio Ixtapan basin. CI = confidence interval at 95%; * Specialist, § Generalist, nc = not calculated; dash (–), helminth is not found

Helminth	Host species					
	Cichlasoma istlanum			*Amatitlania nigrofasciata*		
	P (CI)	MI (CI)	MA (CI)	P (CI)	MI (CI)	MA (CI)
Trematoda						
§*Centrocestus formosanus* Nishigori, 1924	16.2 (9.3–26.3)	2 (1.42–2.5)	0.32 (0.15–0.54)	5.68 (2.3–12.9)	2.4 (1.2–3.8)	0.13 (0.03–0.36)
§*Clinostomum* sp.	6.7 (2.7–15.3)	1.2 (1–1.4)	0.08 (0.01–0.16)	–	–	–
§*Diplostomum compactum* Lutz, 1928	1.3 (0.1–7.2)	3 (nc)	0.04 (0–0.12)	–	–	–
§*Petasiger* sp.	1.3 (0.1–7.2)	1 (nc)	0.01 (0–0.04)	–	–	–
§*Posthodiplostomum mínimum* MacCallum, 1921	39.1 (28.2–50.7)	2.5 (1.93–3.41)	1.01 (0.6–1.49)	–	–	–
**Uvulifer* sp.	32.4 (22.5–43.9)	5.0 (3.3–7.7)	1.6 (1–2.8)	62.5 (51.7–72.3)	10.7 (7.67–15.6)	6.7 (4.77–9.93)
Monogenea						
*Dactylogyridae gen. sp.	9.4 (4.5–18.7)	4.7 (2.5–8.2)	0.44 (0.16–1.13)	–	–	–
Nematoda						
**Rhabdochona kidderi* Pearse, 1936	82.4 (71.8–89.9)	7.6 (5.85–10.5)	6.2 (4.74–8.81)	56.8 (46–67.1)	4.6 (3.48–6.09)	2.6 (1.85–3.61)
§*Contracaecum* sp.	1.3 (0.1–7.2)	1 (nc)	0.01 (0–0.04)	–	–	–
§*Spiroxys* sp.	2.7 (0.5–9.3)	3.5 (1–3.5)	0.09 (0–0.41)	–	–	–

to be infected by ten different helminth species: six trematodes, three nematodes and one monogenea (Table 2). Based on the species accumulation curve, the estimated helminth richness was 3.06 for *A. nigrofasciata* and 10.5 for *C. istlanum*. In both cases, the proportion of observed helminth richness was above 90%.

At the infracommunity level, *C. istlanum* showed higher mean helminth richness than *A. nigrofasciata*

Table 3. Helminth community descriptors of *Amatitlania nigrofasciata* and *Cichlasoma istlanum* from Rio Ixtapan basin

Descriptor	Host species	
	Amatitlania nigrofasciata	*Cichlasoma istlanum*
Component community		
Richness of helminths	3	10
Specialist helminths	2	3
Generalist helminths	1	7
Shannon diversity index (H')	0.66	1.19
Effective number species	1.9	3.28
Pielou's eveness index (J')	0.60	0.51
Berger–Parker index (B)	0.70	0.63
Infracommunity		
Mean richness of helminths	1.25 +/– 0.71	1.91 +/– 1.11
Mean Brillouin diversity index	0.43 +/– 0.11	0.53 +/– 0.23

Table 4. Spearman correlation coefficient (rs) between helminth abundance and Le Cren's condition factor of *Cichlasoma istlanum* and *Amatitlania nigrofasciata* from Rio Ixtapan basin

Host species	Helminth	Spearman correlation coefficient, rs	*p*-value
Cichlasoma istlanum	*Rhabdochona kidderi*	0.2	0.07
	Posthodiplostomum minimum	0.03	0.70
	Uvulifer sp.	–0.05	0.65
	Centrocestus formosanus	0.13	0.24
	Dactylogyridae gen. sp.	0.12	0.30
Amatitlania nigrofasciata	*Rhabdochona kidderi*	0.08	0.45
	Uvulifer sp.	0.04	0.64
	Centrocestus formosanus	0.0003	0.99

($U = 4371$, $p < 0.001$; Table 3). Helminth diversity, as estimated with the Shannon and Brillouin indices, was lower in the convict cichlid than in the redside cichlid (Table 3); this was observed in both the component community (t-Hutchenson = 11.6, $p < 0.001$) and the infracommunity ($U = 2275$, $p < 0.001$) levels. The trematode *Uvulifer* sp. was the most abundant parasite in the convict cichlid while the nematode *Rhabdochona kidderi* was the most abundant in the redside cichlid (Table 2).

Both host fish shared three helminths species: the nematode *R. kidderi* and the trematodes *Uvulifer* sp. and *Centrocestus formosanus*. The comparison between the two host species, regarding the prevalence and abundance of each helminth parasites, showed no statistical differences for *C. formosanus*, but statistical differences were observed for *Uvulifer* sp. and *R. kidderi*. The trematode *Uvulifer* sp. was two times more prevalent and four times more abundant in the convict cichlid *A. nigrofasciata* ($\chi^2 = 14.5$, $p < 0.001$; t-bootstrap, $p < 0.01$), whereas the nematode *R. kidderi* was 1.5 times more prevalent and two times more abundant in the native host *C. istlanum* ($\chi^2 = 9.3$, $p < 0.001$; t-bootstrap, $p < 0.01$) (Table 2).

The Le Cren's condition factor showed no correlation with the helminth abundance in both host fish (Table 4).

DISCUSSION

The ERH, applied to host fish and helminth parasites, predicts that invasive species are released from specialist parasites in the invasive range. In this study, we observed that helminth richness in the invasive cichlid *A. nigrofasciata* was three species; two species, *R. kidderi* y *Uvulifer* sp. are specialist parasites of cichlids natives to Mexico or Central America (Salgado-Maldonado, 2006, 2008; López-Jiménez et al., 2018). In contrast, six species of parasites: *R. kidderi*, *Uvulifer* sp., *Sciadicleithrum bicuense*, *Sciadicleithrum meeki*, *Crassicutis cichlasomae* and *Procamallanus rebeccae* (Kohn et al., 2006; Sandlund et al., 2010; López-Jiménez et al., 2018), infect *A. nigrofasciata* in its native range. In consequence, our results suggest that individuals of

A. nigrofasciata, in the Rio Ixtapan, are released from nearly 70% of the known specialist species that infect the cichlid. A similar pattern has been observed in other populations of *A. nigrofasciata* established in Mexico; one in River Amacuzac (Salgado-Maldonado et al., 2001) and other in River Atlapexco (Salgado-Maldonado et al., 2004). Yet, in the Gillbach River, Germany (Emde et al., 2016) and in a freshwater channel in California, USA (Matey et al., 2015), *A. nigrofasciata* was completely released from specialist parasites.

The convict cichlid and the redside cichlid shared the specialist helminths *R. kidderi* and *Uvulifer* sp. However, while the redside cichlid showed a higher prevalence and parasite load of *R. kidderi*, the convict cichlid showed a higher prevalence and parasite load of *Uvulifer* sp. The higher parasite prevalence or load that each host fish species presented might be related to their diets. On the one hand, both fish species feed on aquatic insects (Ephemeroptera and Trichopteran) that are intermediary hosts (Moravec, 2007); yet, the redside cichlid is an entomophagous species that feeds mainly on Ephemeroptera and Trichopteran, whereas the convict cichlid is an omnivorous species with a lower rate of insect predation (Trujillo-Jiménez, 1998). A higher insect predation by the redside cichlid is likely to increase its infection by *R. kidderi*. On the other hand, the trematode *Uvulifer* sp. uses fish species as a second intermediary host; infection occurs when the host planorbid snails *Helisoma* releases cercariae (free-swimming larval stage) of *Uvulifer* sp., which come into contact with the host fish (Hoffman and Putz, 1965). The convict cichlid is known to feed on plant remains and detritus in a proportion higher than the redside cichlid does (Trujillo-Jiménez, 1998). These food resources are mainly located in sites with a higher presence of planorbid snalis (Dillon, 2000). Therefore, it is likely that the convict cichlid gets infected in these sites during foraging activity.

The ERH also predicts that invasive host fish show lower helminth richness and diversity than native host fish. We observed that the convict cichlid showed lower helminth richness and diversity than the redside cichlid. However, in a different region in Mexico, both the redside cichlid and the convict cichlid showed the same richness (10 species) of helminths (Salgado-Maldonado et al., 2001).

Finally, the ERH predicts that the condition factor of the invasive convict cichlid is independent of helminth abundance. Our results agree with this prediction; there was no relationship between the convict cichlid's condition factor and the abundance of the parasites *C. formosanus*, *Uvulifer* sp. and *R. kidderi*. A similar pattern was observed in populations of the invasive cichlids *Oreochromis niloticus* in Costa Rica (Roche et al., 2010) and *Cichla piquiti* in Brazil (Lacerda et al., 2013). The lack of relationship between the convict cichlid's condition factor and the abundance of the trematode *Uvulifer* sp. can be associated to the low infection that this trematode showed in the convict cichlid. While we observed an average of 6.7 cysts of *Uvulifer* sp. in the convic ciclid, in temperate fish species the condition factor is negatively affected when the parasite abundance overpasses 50 cysts per individual host (Lemly and Esch, 1984).

CONCLUSIONS

In the present study, we observed that the invasive convict cichlid *A. nigrofasciata*, in the Rio Ixtapan basin, is not completely released from specialist parasites. However, in contrast to the native redside cichlid *C. istlanum*, the convict cichlid hosts a lower richness and diversity of parasites. Furthermore, the abundance of parasites observed in the convict cichlid has no effect on the host's condition factor. Together, lower values of richness and diversity of parasites in the convict cichlid, and the lack of relationship between the cichlid's condition factor and its parasites abundance, can potentially increase the invasive success of this fish species in the study region.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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