
ELSEVIER
IJP
INTERNATIONAL JOURNAL FOR PARASITOLOGY
ISSN 0020-7519
VOLUME 40 ISSUE 13 NOVEMBER 2010

International Journal for Parasitology 40 (2010) 1525–1530

Contents lists available at ScienceDirect

International Journal for Parasitology

journal homepage: www.elsevier.com/locate/ijpara

Higher parasite richness, abundance and impact in native versus introduced cichlid fishes

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ARTICLE INFO

Article history:
Received 16 February 2010
Received in revised form 6 May 2010
Accepted 7 May 2010

Keywords:
Biological invasion
Enemy release
Nile tilapia
Metazoan parasites
Panama Canal
Oreochromis niloticus
Vieja maculicauda

ABSTRACT

Empirical studies suggest that most exotic species have fewer parasite species in their introduced range relative to their native range. However, it is less clear how, ecologically, the loss of parasite species translates into a measurable advantage for invaders relative to native species in the new community. We compared parasitism at three levels (species richness, abundance and impact) for a pair of native and introduced cichlid fishes which compete for resources in the Panama Canal watershed. The introduced Nile tilapia, *Oreochromis niloticus*, was infected by a single parasite species from its native range, but shared eight native parasite species with the native *Vieja maculicauda*. Despite acquiring new parasites in its introduced range, *O. niloticus* had both lower parasite species richness and lower parasite abundance compared with its native competitor. There was also a significant negative association between parasite load (abundance per individual fish) and host condition for the native fish, but no such association for the invader. The effects of parasites on the native fish varied across sites and types of parasites, suggesting that release from parasites may benefit the invader, but that the magnitude of release may depend upon interactions between the host, parasites and the environment.

1. Introduction

The enemy release hypothesis (ERH) posits that introduced species benefit from losing natural enemies such as parasites and pathogens (Williams, 1954; Elton, 1958). While plant and animal invaders generally escape their native enemies and are often less parasitized relative to conspecific populations in the native range (Mitchell and Power, 2003; Torchin et al., 2003), it remains unclear whether losing parasite species translates into a fitness advantage for invaders competing with native species in the introduced range (Torchin and Mitchell, 2004).

Studies testing predictions of the ERH often compare parasite species richness among native and introduced host populations as this approach is the simplest measure of release (Torchin and Lafferty, 2009). However, the extent to which 'escaping' parasite species results in a 'release' from the demographic constraints they impose on their hosts remains more difficult to evaluate (Keane and Crawley, 2002; Torchin and Mitchell, 2004), particularly in animal systems where adequate sample sizes are often difficult to obtain and analyse.

Numerous reasons exist for why there may be a disparity between parasite species loss and enemy release in an ecological context. While parasite species are expected to be lost from the native range, new species are generally acquired in the introduced habitat (Cornell and Hawkins, 1993; Poulin and Mouillot, 2003; Torchin et al., 2003). Yet, the consequences of this acquisition are difficult to predict, and can range from benign to severe disease, since new parasites do not share a co-evolutionary history with the introduced host (Shea and Chesson, 2002; Taraschewski, 2006; Dunn, 2009). Furthermore, compensatory effects may result from the loss of parasite species, whereby those parasites that remain may be released from inter-specific parasite competition and experience a higher abundance or fecundity within individual hosts (Fredensborg and Poulin, 2005; Lagrue and Poulin, 2008). Finally, if invaders truly benefit from escaping their native enemies in an ecological context, there should be some evidence that the loss of parasites has an effect on host fitness (Liu and Stiling, 2006). This is often assumed but not explicitly examined in studies of enemy release (Dunn, 2009).

Studies which look beyond differences in parasite species richness often record the proportion of infected hosts in a population (parasite prevalence) (e.g., Torchin et al., 2003) or measure the abundance of a single parasite species (e.g., Pasternak et al., 2007; Han et al., 2008; but see Marr et al., 2008; Vignon et al., 2009). Yet, trends in these different measures of parasitism sometimes

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doi:10.1016/j.ijpara.2010.05.007

do not concur, and inferences on how they affect host fitness can therefore be limited. Some studies reporting invaders that exhibit patterns of decreased parasite species richness also report prevalences which are similar to or higher than those of host populations in the native range (Dunn, 2009). For example, in a study reporting lower parasite species richness in introduced versus native populations of the rabbit fish *Siganus rivulatus*, Pasternak et al. (2007) observed that the abundance of a pathogenic ectoparasitic flatworm was three times higher in the introduced hosts.

Some studies have evaluated differences in foliar, floral or seed damage by parasites to co-occurring native and introduced plants within invaded communities (e.g., Agrawal et al., 2005; Carpenter and Cappuccino, 2005; Cincotta et al., 2009) and others have evaluated how parasite loss mediates competition in animals (sensu Prenter et al., 2004). However, few studies have directly compared parasite impact among competitors, or explored how these differences relate to measures of parasite species richness and abundance. This comparison is important as many parasites have intensity-dependent effects (e.g., Szalai and Dick, 1991) and species richness alone may not accurately predict the impact of parasites on their hosts (Torchin and Mitchell, 2004). Indeed, while parasites are known to mediate competition among animals, often favoring invaders, this process is complex and the intermediate steps linking escape to release need to be evaluated (Prenter et al., 2004; Hatcher et al., 2006).

Here, we evaluate enemy release simultaneously across three metrics (parasite species richness, abundance and impact) in two species of con-familial fishes across five sites in the Panama Canal watershed. The black-belt cichlid (*Vieja maculicauda*) is native to Central America, and the Nile tilapia (*Oreochromis niloticus*) is introduced from Africa. *Oreochromis niloticus* and *V. maculicauda* overlap in habitat and have similar gut contents (González Gutiérrez, 2000; D. Roche, unpublished data), suggesting that they compete for resources in Panama. To assess whether parasite escape translates into a measurable advantage for the invader, we recorded all introduced and native species of metazoan parasites, estimated each of their abundances within and on the host body, and evaluated how parasites influence host condition.

2. Materials and methods

In March–April 2007, we used gill nets to collect 80 fish (40 *V. maculicauda* and 40 *O. niloticus*) across the five major regions of the Panama Canal watershed, including Lake Alajuela (9°15′21″N, 79°35′58″W), the Chagres River (9°12′23″N, 79°38′08″W), and the three arms of Lake Gatun near Barro Colorado Island (BCI; 9°10′03″N, 79°50′06″W), Río Gatun (9°15′21″N, 79°46′46″W) and Cuipo (9°04′12″N, 80°02′33″W). *Vieja maculicauda* is the only native cichlid fish commonly co-occurring with *O. niloticus* in this watershed and the two species do not co-occur elsewhere in Panama (González Gutiérrez, 2000; D. Roche, personal observation). Prior to the study, we dissected 18 fresh fish to identify metazoan parasite species and calibrate our methodology to dissect frozen fish ($n = 80$) for the remainder of the study. Fresh parasites were stained and mounted for identification following Vidal-Martínez et al. (2001). Identifications were informed by a 2006 survey of helminth parasites of freshwater fishes in Panama (Mendoza Franco et al., unpublished data; Mendoza Franco et al., 2007) and based on references by the same authors (Scholz et al., 1994; Aguirre-Macedo and Scholz, 2005; Violante-Gonzalez et al., 2007). Additionally, identifications were confirmed by taxonomic specialists of neo-tropical parasites via examination of photographs and fixed specimens. Trematodes were identified by M.L. Aguirre-Macedo at the CINVESTAV-IPN laboratory for parasitology in Mexico, nematodes by D. Gonzalez-Solis at ECOSUR, Unidad Chetumal, Mexico, and the single acanthocephalan recovered was examined by G. Salgado-Maldonado at the laboratory for helminthology, Universidad Nacional Autónoma de México, Mexico. We sub-sampled scales, muscle and intestine proportionally for each fish and quantified parasites using a stereomicroscope. Three subsets of the intestine (anterior, middle, posterior) were examined, representing 15% of the total length. One parasite species (*Oligogonotylus manteri)* was quantified using digital photographs with grids due to its very high abundance. We recorded parasite species richness and abundance (the number of parasites in a single host, see Bush et al., 1997), fish total length, and fish weight minus gonad weight (hereafter fish weight).

To reduce the number of explanatory variables in the analysis, we categorised parasite abundance within the following organ groups: vital organs (eyes, heart, brain, liver, spleen, kidney), gills, external organs (scales, fins), gut and other organs (mouth, opercula, muscle, mesentery, swim bladder, gall bladder, urinary bladder, gonads), as we expected that parasites occupying different organs may differentially impact their hosts. For consistency, we followed the same classification scheme for parasite species richness. Although parasites could also have been categorised by taxonomic group, we omitted this analysis from the study as the majority of the specimens recovered were trematodes.

Fish condition was measured as the residuals of a log(weight) to log(length) linear regression, separately for each species. Due to violations of multivariate normality for parasite richness (Kolmogorov–Smirnov (K–S) test; $P < 0.01$ for all parasite groups) and parasite abundance (K–S test; $P < 0.01$ for all but one parasite group) we used a multivariate analysis of variance (MANOVA) with randomizations (9999 permutations under the reduced model) to test for differences in parasite richness by group and parasite abundance by group between host species, controlling for site. Since fish condition was normally distributed for both *O. niloticus* (K–S test; $D = 0.094$, $P > 0.15$) and *V. maculicauda* (K–S test; $D = 0.074$, $P > 0.15$), we used a parametric analysis of covariance (ANCOVA) to test for the effects of parasite abundance by group on host condition, controlling for site. Randomization procedures were carried out with the program PERMANOVA (http://www.stat.auckland.ac.nz/~mja/Programs.htm); all other analyses were conducted in R v2.7.2 (http://www.R-project.org). We used $\alpha = 0.05$ for all tests.

3. Results

Across all sites, total parasite richness was more than twofold greater on native *V. maculicauda* (25 parasite species) compared with introduced *O. niloticus* (11 parasite species); we observed a similar ratio for average parasite richness on an individual host basis (7.6 versus 3.1 parasite species, respectively) (Table 1). We found 13 species of trematodes, eight nematodes, three monogeneans, one cestode, one mollusc, one acanthocephalan and one

Table 1
Parasite species richness by taxonomic group on host species *Vieja maculicauda* and *Oreochromis niloticus*, including the total number of species across all hosts and mean number of species per individual host.

Parasite group	*V. maculicauda* (native)	*O. niloticus* (introduced)
Trematoda	13	4
Nematoda	6	4
Monogenea	2	1
Copepoda	1	1
Mollusca	1	1
Acanthocephala	1	0
Pentastomida	1	0
Total no. species	25	11
Mean no. species	7.6	3.1

pentastomid (Table 2). Voucher specimens have been deposited in the G.B. Fairchild Museum of Invertebrates at the University of Panama, Panama City, Panama, and at the National Helminth Collection (CNHE 7225–CNHE 7268), Institute of Biology, Universidad Nacional Autónoma de México, Mexico City, Mexico.

Interestingly, all but one parasite species infecting *O. niloticus* were Neo-tropical in origin, and eight parasite species (73% of all parasites found on *O. niloticus*) were shared among both hosts (Table 2). Parasite richness separated by organ groups on individual hosts (see methods for categorisation) was significantly dependent upon host species ($F_{1,70} = 26.1$, $P = 0.0001$) and site ($F_{4,70} = 2.38$, $P < 0.05$) (interaction non-significant, $F_{4,70} = 1.25$, $P = 0.27$). Fig. 1 indicates that the number of parasite species was consistently higher in the native compared with the introduced fish species. Similarly, parasite abundance was significantly dependent upon host species ($F_{1,70} = 70.8$, $P = 0.0001$) and site ($F_{4,70} = 2.81$, $P = 0.0001$), and there was an interaction between these two factors ($F_{4,70} = 2.99$, $P = 0.0001$). However, the overall tendency was for parasite abundance to be greater in the native host (23 of the 25 possible combinations of parasite group and site, see Fig. 2).

Parasite abundance by group ($F_{5,14} = 1.05$, $P = 0.43$) and site ($F_{4,14} = 1.63$, $P = 0.22$) had no significant effect on host condition in *O. niloticus* (interaction non-significant, $F_{16,14} = 0.59$, $P = 0.85$). Conversely, the effect of parasite abundance on host condition for the native *V. maculicauda* approaches significance ($F_{5,10} = 3.17$, $P = 0.057$), and varied across parasite groups and sites (interaction $F_{20,10} = 6.62$, $P = 0.002$). A breakdown of correlations by site and parasite group indicated that five of 25 possible relationships (five parasite groups at five sites) were statistically significant and negative (one-tailed tests for inverse relationships), even after omitting significant results due to co-linearity (Table 3). The probability of obtaining this number of significant negative relationships by chance was extremely low ($P = 0.007$, binomial test).

4. Discussion

Our results suggest that enemy release can be an important mechanism favoring biological invasions into new communities, but that this process is complex. With the exception of the African monogenean parasite *Cichlidogyrus dossoui*, all parasites found on *O. niloticus* were acquired from the introduced range, the majority of which were also present on the native host, *V. maculicauda.* At the simplest level, this finding is consistent with the main predictions of the ERH: *O. niloticus*, which is heavily parasitized in its native range in Uganda and elsewhere in Africa (D. Roche, unpublished data; Pariselle et al., 2003; Kaddumukasa et al., 2006), experiences an escape from its native parasites.

However, our results illustrate that studies testing the ERH would also benefit from considering the ecological component of enemy release in the context of the introduced community

Table 2
List of parasite species indicating parasite taxonomic group, origin as native (N) or introduced (I), host species (*Vieja Maculicauda*, *Oreochromis niloticus*), prevalence (percentage of individuals infected out of 40) and mean abundance (average number of parasites of a given species among all members of the host population) across all sites.

Parasite species	Origin	*V. maculicauda*		*O. niloticus*	
		Prevalence	Mean abundance	Prevalence	Mean abundance
Trematoda					
Oligogonotylus manteri	N	1.00	25564.85	–	–
Culuwiya cichlidorum	N	0.63	47.13	0.10	0.13
Ascocotyle sp.	N	0.78	7.60	–	–
Atrophacaecum astorquii	N	1.00	149.18	0.20	1.00
Cladocystis trifolium	N	0.20	2.00	–	–
Clinostomum complanatum	N	0.15	0.20	–	–
Diplostomum compactum	N	0.45	3.80	0.08	0.10
Posthodiplostomum sp.	N	0.50	2.20	–	–
Proterodiplostomidae sp. 1	N	0.05	0.08	–	–
Proterodiplostomidae sp. 2	N	0.03	0.03	–	–
Stunkardiella minima	N	0.20	3.45	–	–
Pelaezia loosi	N	0.53	1.93	0.08	0.05
Genarchella sp.	N	0.03	0.03	–	–
Nematoda					
Brevimulticaecum sp.	N	0.03	0.13	0.05	0.08
Spiroxys sp.	N	–	–	0.73	92.58
Contracaecum sp. type 2	N	0.03	0.10	–	–
Falcaustra sp.	N	0.28	32.40	0.08	37.55
Hysterothylacium sp.	N	0.10	0.15	–	–
Raphidascaris sp.	N[a]	0.10	0.25	–	–
Eustrongylides sp.	N	0.03	0.03	–	–
UnID	N	–	–	0.03	0.03
Monogenea					
Cichlidogyrus dossoui	I	–	–	0.75	6.50
Cichlidogyrus sp. 1	I	0.03	0.03	–	–
Cichlidogyrus sp. 2	I	0.03	0.03	–	–
Copepoda					
Ergasilus sp.	N	1.00	32.40	0.60	3.60
Mollusca					
Unionid glochidia	N	0.35	1.25	0.38	18.40
Acantocephala					
Oncicola sp.	N	0.03	0.08	–	–
Pentastomida					
Unidentified	N	0.03	0.05	–	–
Total no. species		**25**		**11**	

[a] Neo-tropical: native to South America but unreported from Central America.

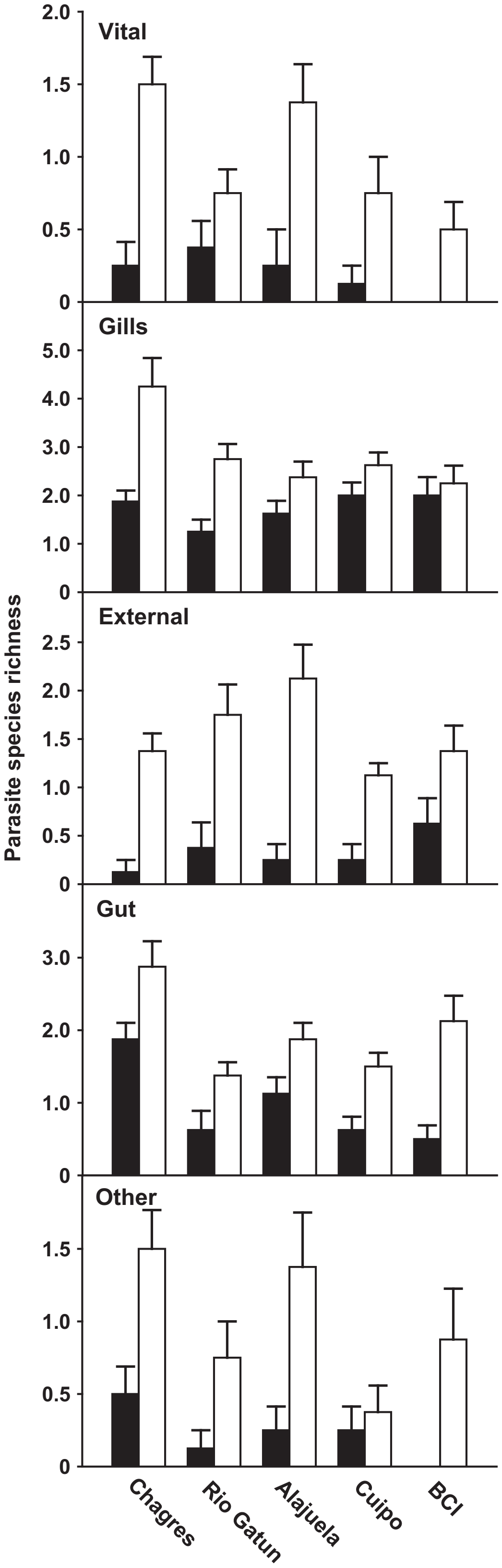

Fig. 1. Mean parasite species richness within groups at each sampling site in the Panama Canal watershed for *Vieja maculicauda* (white shading) and *Oreochromis niloticus* (black shading). Error bars are standard errors. BCI, Barro Colorado Island.

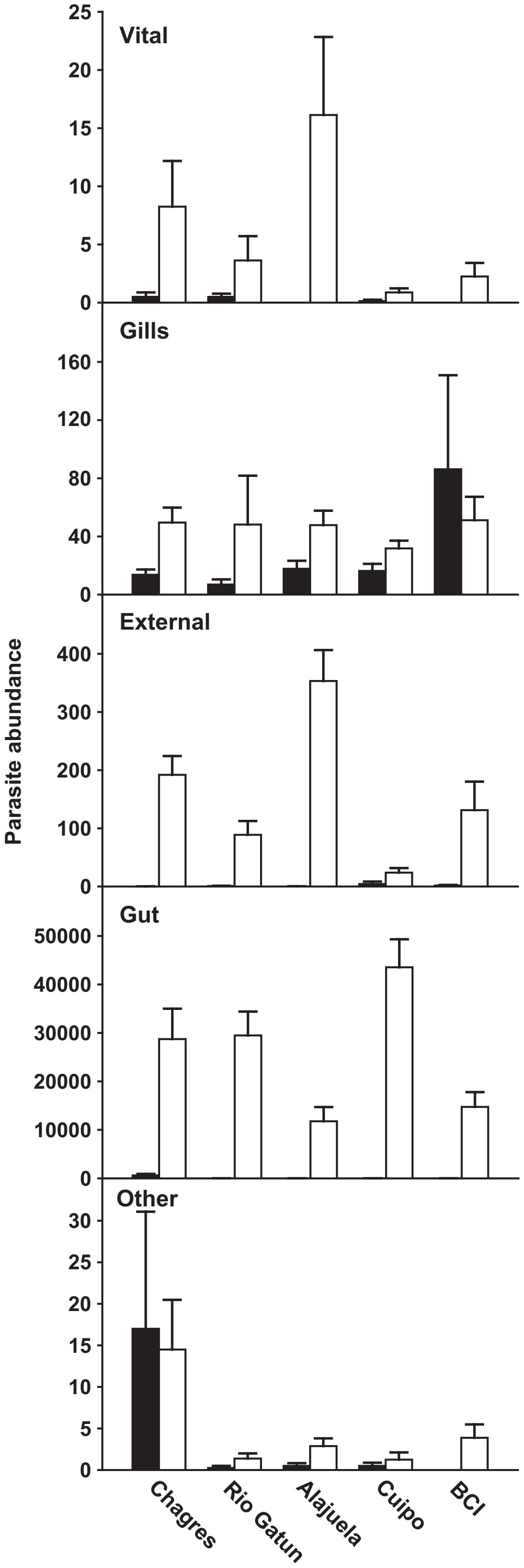

Fig. 2. Mean parasite abundance within groups at each sampling site in the Panama Canal watershed for *Vieja maculicauda* (white shading) and *Oreochromis niloticus* (black shading). Error bars are standard errors. BCI, Barro Colorado Island.

(Torchin and Mitchell, 2004). Since the majority of the parasites infecting *O. niloticus* were acquired from the introduced range, the potential benefits from escaping its natural enemies could be reduced. Indeed, these novel parasite-host associations may create unexpected effects of the parasites on the introduced host, which can either be stronger or weaker than for co-evolved

Table 3
Correlation coefficients between parasite abundance and host condition in *Vieja maculicauda*. Rows are interaction terms between parasite groups and sites; rows in bold are significant negative relationships.

Pgroup*Site	Pearson (*r*)	*P*
Vital*chagres	0.75	<0.05
Vital*Rio_Gatun	**−0.64**	**<0.05**[a]
Vital*Alajuela	**−0.71**	**<0.05**
Vital*Cuipo	0.38	ns
Vital*BCI	**−0.64**	**<0.05**
Gills*chagres	−0.16	ns
Gills*Rio_Gatun	**−0.65**	**<0.05**[a]
Gills*Alajuela	0.34	ns
Gills*Cuipo	−0.46	ns
Gills*BCI	0.11	ns
Ext*Chagres	0.52	ns
Ext*Rio_Gatun	0.29	ns
Ext*Alajuela	**−0.82**	**<0.01**
Ext*Cuipo	0.62	ns
Ext*BCI	−0.39	ns
Gut*Chagres	0.41	ns
Gut*Rio_Gatun	0.20	ns
Gut*Alajuela	−0.10	ns
Gut*Cuipo	0.08	ns
Gut*BCI	**−0.73**	**<0.05**
Other*Chagres	0.29	ns
Other*Rio_Gatun	0.32	ns
Other*Alajuela	−0.19	ns
Other*Cuipo	−0.42	ns
Other*BCI	−0.28	ns

[a] Indicates co-linearity; ns, non-significant; BCI, Barro Colorado Island.

species (Dunn, 2009). These possible consequences need to be explored.

At one level we found that, despite the transfer of native parasites to the introduced host (see also Jiménez-García et al., 2001), the native *V. maculicauda* harboured more than twice the number of parasite species compared with the introduced *O. niloticus*, both in the overall sampled population and at the scale of individual hosts. Thus, the introduced host still experienced a net benefit in terms of lower parasite species richness compared with the native host.

This escape from parasite species, however, might still not translate into enemy release. Theoretically, a reduction in the number of parasite species could decrease inter-specific competition between parasite species within individual hosts, which in turn could result in higher abundances of the remaining parasite species. In such a case, total parasite abundances might not differ between native and introduced hosts, and enemy release may not occur. However, our results suggested otherwise. We found that parasite abundance was lower on the introduced host, *O. niloticus*, compared with the native host, *V. maculicauda*, at all but two of the 25 possible combinations of parasite groups and sites (Fig. 2).

At a third level, we found no evidence that parasites had negative effects on host condition for the introduced *O. niloticus*, whereas there was a negative relationship between parasite load and host condition for the native *V. maculicauda*. This pattern is also consistent with the ERH. The parasite advantage gained by *O. niloticus* in the introduced range should be relative to the impact of parasites on the native competitor, *V. maculicauda*, minus the impact of parasites on itself (Torchin and Mitchell, 2004). Therefore, the differential impact of parasitism on these two competing hosts most likely favours *O. niloticus*. However, determining the exact advantage gained by this species is difficult as it will depend on the strength of the competitive interactions between the two species, a variable which was not explicitly measured in this study.

As a final point illustrating the subtle issues associated with enemy release, we consider the heterogeneity in the response of host condition to parasite abundance. While overall there was a negative association between the abundance of parasites and the condition of native hosts, these impacts were not consistent across parasite groups and sites. This heterogeneity suggests a potential variation in other factors such as resource availability or environmental variables which may interact with the effects of parasitism (e.g., Marcogliese et al., 2005; Hansen et al., 2006). Further studies might elucidate the potential interactions between enemy release and the environment as suggested by the resource-ERH (R-ERH) in plants (Shea and Chesson, 2002; Blumenthal, 2006; Blumenthal et al., 2009).

In conclusion, despite the acquisition of new parasite species in the introduced range, most of which were shared with *V. maculicauda, O. niloticus* had fewer parasite species, was infected less per individual host, and experienced less impact from parasites on host condition relative to the native fish. Since the effects of parasites on the native host were heterogeneous across parasite groups and sites, our results also agree with recent experiments on plants suggesting that enemy release is a variable process which creates "opportunity windows", or instances when invaders progress in native communities (Agrawal et al., 2005). We demonstrate how enemy escape could translate into a measurable advantage for an animal invader over its native competitor in the introduced range. However, further studies are needed which examine the effect of parasites on other fitness parameters such as host survivorship and fecundity, and which explore the extent to which higher parasitism and reduced body condition influences competitive interactions among native and introduced hosts.

Acknowledgements

We thank the Natural Sciences and Engineering Research Council of Canada (NSERC, Canada), le Fonds québécois de la recherche sur la nature et les technologies (FQRNT, Canada), l'Office Québec-Amériques pour la jeunesse (OQAJ, Canada), the Smithsonian Tropical Research Institute (STRI, Panama) and the National Science Foundation (NSF, USA, DEB 0541673) for funding. We thank C. Schloeder, Y. Kam, A. Terrero, S. Binning and the personnel of the Ministerio de Desarollo Agropecuario de Panamá for help with collections and dissections, and M.L. Aguirre-Macedo, V.M. Vidal-Martínez, D. González-Solis and G. Salgado-Maldonado for help with parasitological identification.

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