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# Host preference of an introduced 'generalist' parasite for a non-native host

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#### ABSTRACT

Parasites can invade new ecosystems if they are introduced with their native hosts or if they successfully infect and colonise new hosts upon arrival. Here, we ask to what extent an introduced parasite demonstrates specialisation among novel host species. Infection surveys across three field sites in Gatun Lake, Panama, revealed that the invasive peacock bass, *Cichla monoculus*, was more commonly infected by the introduced trematode parasite *Centrocestus formosanus* than were three other common cichlid fishes. Laboratory infection experiments were conducted to determine whether parasitism might be driven by differential encounter/exposure to parasites or by differential infection susceptibility/preference across different host species. These experiments were performed by controlling for parasite exposure in single host (compatibility) experiments and in mixed host (preference) experiments. In all cases, the peacock bass exhibited higher infection rates with viable metacercariae relative to the other potential fish hosts. Our experiments thus support that an introduced generalist parasite shows apparent specialisation on a specific novel host. Further studies are needed to determine whether these patterns of specialisation are the result of local adaptation following invasion by the parasite.

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#### 1. Introduction

The widespread introduction of non-native species is responsible for major environmental and economic impacts worldwide (Vitousek et al., 1997). Of particular concern are introduced parasites and pathogens, which can lead to emerging diseases of humans (Daszak et al., 2000), commercially valuable species (Cleaveland et al., 2001) and wildlife (Dobson and Foufopoulos, 2001). When parasites and pathogens are introduced into regions where their original "native" hosts are already established, a ready-made biotic environment exists for the parasite/pathogen to persist and spread (Woolhouse and Gowtage-Sequeria, 2005). However, some introduced parasites/pathogens establish and spread in new communities lacking hosts from their native range, which they accomplish by infecting novel hosts (Woolhouse et al., 2001). Yet to establish, persist and spread without their native hosts, introduced parasites must either be generalist species that can infect a broad variety of new hosts with some degree of success or they must specialise on new hosts in a novel community (Combes, 1981; Font, 2003). Here we ask to what extent does an

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introduced generalist parasite specialise on specific novel hosts in a new environment?

The relative contribution of host species to parasite reproduction and transmission, R<sub>0</sub>, (Anderson and May, 1981), will depend on their encounter rates and infection compatibility with different hosts, and can also be affected by host preference exhibited by the parasite (Combes, 1991). These properties (e.g., encounter, compatibility and preference), jointly determine a parasite's host range, also expressed as the extent to which a parasite specialises on a given set of potential host species. Parasite-host range is invariably shaped by the biogeographical and evolutionary history of both parasites and hosts, and is an important determinant of the extent to which introduced parasites can infect host species in novel ecological communities and persist in new ranges. Yet while host range is a central feature of the ecology and evolutionary history of host-parasite interactions (Combes, 2001; Poulin and Keeney, 2008), little is known about the factors underpinning a parasite's host range in nature (Perlman and Jaenike, 2003). This is because it is typically impossible to discern the relative contributions of differences in encounter rates and compatibility across different potential host species under natural conditions (Kuris et al., 2007). Thus, in order to investigate drivers of host specialisation, laboratory experiments that manipulate host-parasite encounter rates are needed to disentangle the likely drivers of parasite-host

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specificity (Bush and Clayton 2006; Kuris et al. 2007). Here, we evaluate the extent to which generalist species can demonstrate increased specialisation across potential host species, and attempt to discern the proximate causes (e.g., encounter, compatibility or preference), eliciting natural patterns of infection with laboratory experiments.

To this end, our study is unique in two ways. First, tests that attempt to elucidate ecological and evolutionary drivers of host specificity typically focus on native species and long-established host-parasite associations (Little et al., 2006; Simková et al., 2006; Sears et al., 2012). By contrast, our use of non-native parasites and novel hosts is more informative for inferring interactions during the early stages of host-parasite community assembly. Second, laboratory experiments testing for patterns of host specificity typically focus on parasites thought to be highly host-specific, and often document infection compatibility with an unexpectedly broad range of novel host species typically not encountered in nature (Perlman and Jaenike, 2003; King and Cable, 2007; Poulin and Keeney, 2008). Conversely, our experiments consider whether a parasite putatively considered a generalist (from its native range) shows unexpectedly high host-specificity in its introduced range among a set of host species with which the parasite does not share a common evolutionary history. Overall, our combined survey-experimental approach for introduced parasites on novel hosts should provide theoretical and practical insights concerning the ecological and evolutionary processes underpinning host-parasite associations in expanded geographical ranges.

The global spread of the trematode, Centrocestus formosanus is of concern due to its ability to infect and cause disease in wild and endangered fishes (Mitchell et al., 2000), and commercially valuable species (Vélez-Hernández et al., 1998). This parasite has spread to freshwater habitats around the world following the invasion of its first intermediate snail host (Salgado-Maldonado et al., 1995), the Asian red-rimmed melania, Melanoides (Thiara) tuberculata, which was first reported in Panama in 2003 (Garcés and Garcia, 2004). *Centrocestus formosanus* has a complex life cycle: free-swimming larval cercariae emerge from snail hosts and encyst as metacercariae in the gills of second intermediate fish hosts (Scholz and Salgado-Maldonado, 2000). The parasite is then trophically transmitted to a piscivorous avian or mammalian definitive host (where the parasite sexually reproduces) when the infected fish is eaten, thereby completing its life cycle (Chen, 1942). The parasite, while it is highly specialised to its first intermediate snail host, has been reported to infect dozens of fish species across different families throughout its broad geographic range (Scholz and Salgado-Maldonado, 2000).

While this parasite is reported to have a broad host range throughout its global distribution, its potential to specialise on particular fish host species in its native or introduced ranges has not been examined. In order to measure specialisation in nature, a robust comparison of parasite prevalences and abundances across multiple co-occurring host species is necessary (Poulin, 2011). In order to gain some insight into the possibility of C. formosanus to specialise on a particular host species in a novel habitat, we evaluated natural patterns of parasitism across four potential cichlid fishes common in Gatun Lake, Panama, the native cichlid "vieja" (Vieja maculicauda) and three introduced cichlids, peacock bass (Cichla monoculus), oscar (Astronotus ocellatus), and Nile tilapia (Oreochromis niloticus). These four species are the most common cichlids in the Gatun Lake (Gonzalez-Gutierrez, 2000) and, importantly, none of these species shares an evolutionary/biogeographical history with C. formosanus, which is native to southeastern Asia (Scholz and Salgado-Maldonado, 2000).

We first compared prevalences and abundances of *C. for*mosanus infection across the four fish species to evaluate natural

patterns of parasitism of this introduced parasite. This is the first known report of C. formosanus in Panama and unlike reports from elsewhere, our field comparison suggests that the parasite is not broadly distributed across the fish hosts but rather appears to be specialised on the peacock bass, a novel fish host with which the parasite does not a share a long-term co-evolutionary history. We hypothesise that the patterns of infection in the field could be driven by differences in encounter/exposure rates, susceptibility of the fishes to the parasite or the host preference of *C. formosanus*. To distinguish these hypotheses, we used laboratory experiments that (i) held encounter rates constant to test for differences in infection compatibility in single-species trials and (ii) tested host preference in mixed-species experiments. Our laboratory experiments corroborate field comparisons, suggesting that higher infection rates in the peacock bass are due to both greater host preference for peacock bass by C. formosanus and increased compatibility with that host compared with the other fishes. The potential specialisation by this introduced parasite on a common introduced host could provide further insight into how introduced parasites establish, integrate and potentially evolve in novel assemblages of hosts in recently expanded geographic ranges. However, additional research is needed to discern whether this potential specialisation is the result of local adaptation of the parasite to a common introduced host.

#### 2. Materials and methods

#### 2.1. Field comparisons

Gatun Lake, part of the Panama Canal, was formed when the Chagres River was dammed early in the 20th century. The lake now has a biotic community of native and introduced species with broad biogeographic origins at all trophic levels, including aquatic plants, invertebrates such as snails and clams, and vertebrates such as fishes and reptiles (Zaret and Paine, 1973; Gonzalez-Gutierrez, 2000). The Asian red-rimmed melania snail, *M. tuberculata*, was first reported in Panama in 2003 as one of the two most abundant introduced mollusks in Gatun Lake (Garcés and Garcia, 2004), yet the pathway and chronology of the introduction and invasion (and that of its trematode parasite, *C. formosanus*) in Panama is unknown.

In February and March of 2010, we guantified prevalences, abundances and intensities (Bush et al., 1997) of C. formosanus in four common and co-occurring cichlid fish species (C. monoculus, A. ocellatus, O. niloticus and V. maculicauda) across four sites within Gatun Lake: Gamboa (09°09'22" N, 79°51'22" W), Barro Colorado Island (09°10'02" N, 79°50'07" W), Rio Gatun (09°15'21" N, 79°46'46" W) and Rio Chagres (09°12'23" N, 79°38'07" W). All of the fish were sampled near the shore where they were likely exposed to C. formosanus cercariae shed from M. tuberculata in the littoral zone. Fish were caught using a 30 m monofilament gill net (divided into three panels with 1.5 cm, 3 cm and 4.5 cm wide filaments). The net was set three to four times each morning at each site over a 60 day period to reach a comparable sample size (n = 15) for each species at each site. Approximately 1 h after the nets were set, live fish were removed and transported in oxygenated 189.27 L coolers to the Smithsonian Tropical Research Institute (STRI) Naos Marine Laboratory in Panama City where they were euthanised by spinal incision and dissected for parasites. We removed and examined gill arches immediately after the fish were euthanised using stereomicroscopes. Encysted C. formosanus metacercariae were identified using a compound microscope that allowed visual inspection of diagnostic features of this parasite (Yanohara and Kagei, 1983).

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