



Intra-host competition between co-infecting digeneans within a bivalve second intermediate host: Dominance by priority-effect or taking advantage of others?

Tommy L.F. Leung^{a,b,*}, Robert Poulin^b

^aZoology, School of Environmental and Rural Science, University of New England, NSW 2351, Australia

^bDepartment of Zoology, University of Otago, 340 Great King Street, P.O. Box 56, Dunedin 9054, New Zealand

ARTICLE INFO

Article history:

Received 27 September 2010

Received in revised form 18 November 2010

Accepted 19 November 2010

Available online 16 December 2010

Keywords:

Interspecific interactions

Co-infections

Priority effect

Competition

Trematoda

Echinostomatidae

ABSTRACT

We experimentally investigated the interactions between two parasites known to manipulate their host's phenotype, the trematodes *Acanthoparyphium* sp. and *Curtuteria australis*, which infect the cockle *Austrovenus stutchburyi*. The larval stages of both species encyst within the tissue of the bivalve's muscular foot, with a preference for the tip of the foot. As more individuals accumulate at that site, they impair the burrowing behaviour of cockles and increase the probability of the parasites' transmission to a bird definitive host. However, individuals at the foot tip are also vulnerable to non-host predators in the form of foot-cropping fish which selectively bite off the foot tip of exposed cockles. Parasites encysted at the foot base are safe from such predators although they do not contribute to altering host behaviour, but nevertheless benefit from host manipulation as all parasites within the cockle are transmitted if it is ingested by a bird. Experimental infection revealed that *Acanthoparyphium* sp. and *C. australis* have different encystment patterns within the host, with proportionally fewer *Acanthoparyphium* metacercariae encysting at the foot tip than *C. australis*. This indicates that *Acanthoparyphium* may benefit indirectly from *C. australis* and incur a lower risk of non-host predation. However, in co-infections, not only did *C. australis* have higher infectivity than *Acanthoparyphium*, it also severely affected the latter's infection success. The asymmetrical strategies and interactions between the two species suggest that the advantages obtained from exploiting the host manipulation efforts of another parasite might be offset by traits such as reduced competitiveness in co-infections.

© 2010 Australian Society for Parasitology Inc. Published by Elsevier Ltd. All rights reserved.

1. Introduction

For a parasite with a simple, direct life-cycle, a host may simply be a habitat and source of nutrient that it can exploit to produce offspring. However, for those with multi-host life-cycles, the role of a host is dependent on the particular developmental stage of the parasite. Such parasites often utilise intermediate hosts as vehicles to reach a definitive host to complete their life-cycle; this is usually accomplished when the definitive host ingests an infected intermediate host via trophic transmission (Lafferty, 1999). Because the likelihood of the parasitised individual being ingested by the definitive host is very low considering the number of alternative prey available, some parasites can alter the phenotype of the intermediate host to improve transmission success by making the host more susceptible to predation (reviewed by Poulin, 1995; Moore, 2002). For these host-manipulating parasites,

the altered host phenotype can be seen as a manifestation of their host exploitation strategy (Poulin, 2007).

If a host-manipulating parasite finds itself sharing an intermediate host with another manipulator that utilises the same definitive host (and thus transmission route), cooperation between the two species may occur, leading to a situation known as “co-piloting” (Lafferty et al., 2000). However, host manipulation can also be costly (Poulin, 1994; Poulin et al., 2005) and if manipulation itself is a phenotypically plastic trait that is context-dependent, one might expect that in the presence of another manipulator, a manipulative parasite may adopt a strategy more akin to “hitchhiking”: taking advantage of the other's manipulative effort without contributing to actual host manipulation (Thomas et al., 1998). Thus the outcome of co-infection between manipulators with similar life-cycles sharing the same intermediate host is not always predictable. The dynamics of interspecific associations between parasites have rarely been addressed experimentally (see Karvonen et al., 2009 for exceptions). Here we use a bivalve-trematode system, which involves two species of host-manipulating trematodes sharing a common bivalve intermediate host, to investigate the outcome of co-infection between different species of host-manipulating parasites.

* Corresponding author at: Zoology, School of Environmental and Rural Science, University of New England, NSW 2351, Australia. Tel.: +612 6773 4083; fax: +612 6773 3814.

E-mail address: tommylfeung@gmail.com (T.L.F. Leung).

The New Zealand cockle *Austrovenus stutchburyi* is commonly infected by the encysted stage of two species of trematodes: *Curtuteria australis* and *Acanthoparyphium* sp. A (hereafter referred to as *Acanthoparyphium*) (Echinostomatidae). The cockle becomes infected when free-living larval stages of the parasites, known as cercariae, enter the cockle through its inhalant siphon. The cercariae then penetrate the cockle's foot where they form encysted stages called metacercariae – when metacercariae accumulate at the tip of the cockle's foot they impair its function (Mouritsen, 2002). Field data indicates that while the relative abundance and infection intensity of both parasites varies between different host populations, the prevalence of each species is close to 100% (Babirac et al., 2004). Thus, both trematodes almost always co-occur in the same individual host.

Both of these species alter the bivalve's behaviour by inhibiting its ability to bury itself into the sediment and forcing the cockle to remain exposed on the sediment surface (Thomas and Poulin, 1998). By doing so, they increase the probability of the cockle being eaten by a bird definitive host (Thomas and Poulin, 1998). The two species are considered ecological equivalents not only because they induce the same behavioural modification in their common intermediate host, but they also coexist on multiple levels – field samples indicate that at a population level, not only are they present in the same localities, they also encyst within the same part of the cockle's body, specifically within the foot muscle, with both species sharing an apparent preference for the tip (Babirac et al., 2004).

While the metacercariae can encyst anywhere within the cockle's foot and all parasites are transmitted if the cockle is eaten by a bird, only those that encyst at the foot tip are responsible for altering host behaviour (Mouritsen, 2002). However, this manipulation comes at a cost. Those at the tip are vulnerable to foot-cropping fish which are unsuitable hosts for the parasites, whereas those at the base of the foot are safe from foot-croppers (Mouritsen and Poulin, 2003b). Thus, metacercariae at the base of the foot can benefit from enhanced transmission without incurring the associated risk. Do *Acanthoparyphium* and *C. australis* display similar or distinct selection of encystment sites in the cockle's foot? And if so, do they alter their site selection (and thus contribution to host manipulation) in the presence of metacercariae of the other species?

The coexistence of *Acanthoparyphium* and *C. australis* metacercariae within cockles indicates that competitive displacement does not occur (at least at an ecosystem-scale) and that they may act in synergy to modify host behaviour (Babirac et al., 2004). However, nothing is known about the dynamics of their co-infection within the cockle. It is unknown how interactions between these two host-manipulators are mediated by factors such as differential infectivity, if competitive exclusion or facilitation between the two species occurs within individual hosts, or whether temporal factors such as order of arrival can influence the pattern of infections. Here, we use laboratory infections to investigate the dynamics of these interactions, and shed light upon the evolutionary ecology of multi-parasite infection. Our specific aims are: (i) to experimentally determine and compare the encystment pattern of both *Acanthoparyphium* and *C. australis* within the cockle foot when they infect alone or together, and (ii) to determine if co-infection influences the infection success of both species.

2. Material and methods

2.1. Study organisms

Approximately 100 cockles, *A. stutchburyi*, were collected from a sand flat at Otakou, Otago Harbour, New Zealand's South Island. The

infection intensity by trematodes is known to be relatively low at that site (Mouritsen, 2002). Prior to experimental infection, the cockles were held in plastic containers (300 mm long × 130 mm wide × 150 mm high) filled with seawater and approximately 60 mm of fine sand, and aerated with an airstone.

The free-living cercarial stages of *C. australis* and *Acanthoparyphium* are shed from their gastropod first intermediate hosts, the mud whelk *Cominella glandiformis* and the mud snail *Zeacumantus subcarinatus*, respectively. The cercariae are continuously produced through asexual multiplication by the clonal stages of the trematodes which reside within the gastropod host. Infected gastropods are induced to shed cercariae by placing them individually into a clear plastic cylindrical container (60 mm high × 40 mm wide) filled with seawater and incubated at 25 °C under constant illumination.

The collection, screening procedure and husbandry of the whelks infected with *C. australis* are detailed in Leung and Poulin (2010) and Leung et al. (2010). Approximately 800 mud snails, *Z. subcarinatus*, were collected from Lower Portobello Bay, Otago Harbour. They were screened to find individuals infected by *Acanthoparyphium* in the same manner as the whelks and kept in the same type of container under the same environmental conditions, and were provided with strips of sea lettuce (*Ulva lactuca*) ad libitum for food.

While the *Acanthoparyphium* infecting *Z. subcarinatus* has been found to consist of a species complex (Leung et al., 2009), the same study also indicated that the overwhelming majority of *Acanthoparyphium* collected from Lower Portobello Bay are sp. A, which is the species known to infect cockles. For this study, a few cercariae from each of the snails used for experimental infections were individually sequenced at the 16S region, which allows discrimination among different species of *Acanthoparyphium* (Leung et al., 2009). All resulting sequences corresponded with known sequences of *Acanthoparyphium* sp. A.

2.2. Infection treatments

There was a total of five infection combinations and the number of cockles assigned to each infection varied depending on cercarial availability – *C. australis* only ($n = 24$), *Acanthoparyphium* only ($n = 20$), *C. australis* and *Acanthoparyphium* simultaneously ($n = 18$), *C. australis* followed by *Acanthoparyphium* ($n = 20$), and *Acanthoparyphium* followed by *C. australis* ($n = 17$). Each cockle was exposed to a total of 60 cercariae. In mixed-species infections, each cockle was exposed to 30 cercariae from each species. In non-simultaneous infections, a period of 1 week separated infection by the first species and the second species. The five combinations resulted in a total of three treatments for each species; (1) infecting alone or arriving first, (2) infecting after the other species, (3) infecting simultaneously with the other species.

The cercariae of both *Acanthoparyphium* and *C. australis* were obtained from their respective gastropod hosts. Snails or whelks were induced to shed in the same manner as described for screening infected individuals. A group of 20 snails and 20 whelks were selected to provide a pool of mixed genotype cercariae. The same group of snails and whelks was used throughout the entire duration of the experiment across the different treatments. For details regarding the protocol of handling and labelling the cercariae with fluorescent dye, see Leung et al. (2010). Cercariae of both species were treated identically, although the shedding period and availability of *Acanthoparyphium* cercariae from the mud snail *Z. subcarinatus* was more erratic than for *C. australis*. For infection treatments that involved both species, the cercariae of each species were labelled with a different coloured dye, alternating between a green and a red fluorescent dye to differentiate the metacercariae of the two species. The dyes used have been found not to affect

Download English Version:

<https://daneshyari.com/en/article/8500288>

Download Persian Version:

<https://daneshyari.com/article/8500288>

[Daneshyari.com](https://daneshyari.com)