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IMMUNOLOGY AND HOST-PARASITE INTERACTIONS - ORIGINAL PAPER

The return to land: association between hairworm infection and aquatic insect development

Jean-François Doherty[1] · **Robert Poulin**[1]

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Abstract

Host manipulation by parasites can shape host behaviour, community structure, and the flow of energy through food webs. A well-known example of host manipulation comes from hairworms (phylum Nematomorpha), which somehow cause their terrestrial insect definitive hosts to enter water, a phenomenon that has received lots of attention in recent years. However, little focus has been directed towards the interactions between hairworms and their aquatic insect hosts and the return of dormant hairworms from water to land. Here, we ask whether hairworm cyst infections impact, either directly or indirectly, the life history of their aquatic transport hosts. By observing the development of last-instar *Olinga jeanae* (Trichoptera: Conoesucidae) caddisfly larvae naturally infected with *Gordius*-type hairworm cysts under controlled conditions, we found that higher numbers of cysts per infected caddisfly correlated with a decrease in time to pupation. These new observations suggest that, apart from the striking host manipulation that brings the parasite from land to water, the presence of dormant hairworms is associated with changes in the development of their aquatic hosts, either through direct or indirect mechanisms, which may accelerate their transition from water to land.

Keywords Host-parasite interaction · Caddisfly · Pupation · Aquatic insect · Hairworm

Introduction

Host manipulation by parasites has received international recognition for the remarkable impacts it can have on hosts. From conspicuous changes in host appearance and behaviour (Andersen et al. 2009; Wesołowska and Wesołowski 2014) to broad effects on host community structure (Lefèvre et al. 2009; Thomas et al. 1998) and energy flow within food webs (Kuris et al. 2008; Preston et al. 2013), parasitic manipulators can alter their environment in profound ways. One of the most striking examples of parasite-mediated energy flow occurs in the riparian zone of Japanese streams (Sato et al. 2012; Sato et al. 2011), where orthopterans infected with gordiid hairworms (phylum Nematomorpha) are twenty times more likely to enter water, thus becoming an important food source for trout. Hairworms mature within terrestrial arthropods, mainly scavenger-type insects, and somehow cause their definitive hosts to enter water in order to complete their life cycle (Bolek et al. 2015). Due to the somewhat obvious behavioural changes observed in definitive hosts, most studies on hairworm manipulation have focused on their transition from land to water (Ponton et al. 2011; Sánchez et al. 2008; Thomas et al. 2002). Even though hairworms may only subtly alter host behaviour in ways that increase their likelihood of entering water, this phenomenon has been widely sensationalised in both the popular media and the scientific literature (Doherty 2020). However, far less attention has been given to the transition of hairworms from water to land. Here, we explore the relation between dormant hairworms and the life history of their aquatic hosts.

Most hairworm species enter water to reproduce (Bolek et al. 2015). After mating, females can lay several million eggs (Hanelt 2009), from which larvae hatch and are consumed by practically any aquatic animal present: insects, crustaceans, and even vertebrates (Hanelt and Janovy 2004; Torres et al. 2017). Upon consumption, larvae use specialised mouthparts to move through host tissues, where they eventually form a cyst (Hanelt and Janovy 2003). Aquatic macroinvertebrates

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✉ Jean-François Doherty
jeff-doherty@hotmail.com

[1] Department of Zoology, University of Otago, Dunedin, New Zealand

that exit water contribute to the hairworm life cycle, as they can be consumed by the definitive terrestrial hosts. These paratenic hosts comprise most known groups of aquatic insect larvae that mature into terrestrial adults, e.g. mayflies, midges, and caddisflies (Bolek et al. 2015). Measuring approximately 60–100 μm in length, hairworm larvae are small, dormant, and do not grow within their cyst (Bolek et al. 2013). Aquatic insects can mount defence reactions against hairworm larvae and cysts through melanotic encapsulation, a common form of insect immunity (Doherty et al. 2019; Poinar and Doelman 1974). However, apart from observations on host immunity, little is known of the impacts that hairworms have on their aquatic hosts.

Logically, the longer a hairworm spends as a cyst in its paratenic host, the likelier it is to die from host immunity, predation, or environmental perturbations, e.g. flooding or drought. Therefore, any change in host development time could affect the odds that a hairworm successfully completes its life cycle. Based on this rationale, we hypothesised that hairworm cysts, though apparently dormant, can accelerate the development of their aquatic insect host, either through direct or indirect mechanisms. This would expedite their return to land and improve their chances of completing their life cycle.

In this study, we tested whether hairworm cyst infections correlate with changes in the life history of aquatic hosts. To do so, we quantified the propensity to pupate in last-instar *Olinga jeanae* McFarlane (Trichoptera: Conoesucidae) caddisfly larvae under controlled conditions (caddisfly larvae must first pupate prior to emerging from water as flying adults). This is an abundant species in subalpine streams of New Zealand (Cowley 1978; Ward and McKenzie 1997) and is most likely one of the main paratenic hosts for *Gordius paranensis* found at the sampling site (Doherty et al. 2019; Schmidt-Rhaesa et al. 2000). Specifically, we tested whether the infection status or the intensity of hairworm cyst infection (the number of cysts per infected individual) correlated with an increase in the odds that caddisfly larvae pupated during a laboratory-controlled observational study. Since we measured the propensity to pupate in naturally infected hosts, we had to limit our study to a single life stage of individuals that most likely hatched around the same time in the stream. If detected, such impacts would suggest that even hosts infected with dormant hairworms are not entirely free from parasite-induced life history changes, whether these result from the side effects of infection or adaptive host manipulation.

Materials and methods

Sampling last-instar caddisfly larvae

Caddisfly larvae were collected on 23 March 2020 from Grasmere Stream (43°01′55"S 171°45′28"E) in the Canterbury region of New Zealand. In a 20-m section of the stream, larvae were collected by dragging fine mesh dip nets across the vegetation. Samples were then transported back to the laboratory in small containers of aerated river water, where they were kept until processing. Based on caddisfly case morphology (Cowley 1978), only *O. jeanae* larvae were collected from the sampling site. Live caddisfly pupae were removed from the samples and were used to measure pupal case width (the widest part of the case opening) and length using a microscope reticle (Fig. 1). Twelve pupal case widths were measured to estimate a lower 95% confidence limit of 1.8 mm. This estimate was used as a minimum threshold size for the inclusion of last-instar larval *O. jeanae* in this study. Although head capsule width is a better indicator of larval development, we could not measure this on live caddisfly larvae that hid within their case when disturbed. Moreover, when *O. jeanae* larvae close their case to pupate, the width and length of their case decrease slightly in size (Fig. 1). Therefore, any larva with a case width larger than 1.8 mm would have been in its last instar. In fact, these larvae were

Fig. 1 Lateral view of larval and pupal cases of the caddisfly *Olinga jeanae* (Trichoptera: Conoesucidae). Double-headed arrows indicate case width

visibly longer and larger than earlier instars and were consistent in size with previous descriptions (Cowley 1978; Ward and McKenzie 1997). Caddisfly case width can be a better predictor of larval biomass than case length (Martins et al. 2014) and infected *O. jeanae* larvae tend to harbour more cysts with age (Doherty et al. 2019). Therefore, hairworm cyst infections were likelier to be found in last-instar hosts. By only including caddisfly larvae from the same instar, we ensured that they most likely hatched around the same time in the stream, thus reducing the impact of any age-related confounding factors.

Observational study design

On 1 April 2020, samples were screened for larvae with a minimum case width of 1.8 mm. A total of 84 larvae fitting this criterion were then equally and randomly distributed into two 10-L clear plastic tanks (42 larvae each) filled with aerated river water, to avoid overcrowding. Air stones circulated the water, thus creating a current, which is preferable for caddisfly larvae. Tanks were kept at room temperature and water temperature was monitored in each tank with HOBO TidbiT v2 data loggers (Onset, USA). Three small ceramic tiles were placed in each tank to allow larvae to move around and eventually use as a substrate on which to attach their pupal cases. Larvae were fed *ad libitum* with frozen watercress (*Nasturtium* sp.) collected from the sampling site. This plant species was abundant in the stream and all the caddisflies used here were collected from that site. On a weekly basis, roughly two-thirds of the water were replaced and food was added. At that time, the tanks were inspected for pupae, which are easily distinguished from larvae by their darker colour (Fig. 1). These observations were stopped when approximately half of the larvae had pupated, which was on 2 September 2020. On that date, larvae and pupae were killed and stored in 75% ethanol until processed in the laboratory. Then, the intensity of hairworm cyst infection (total number of cysts per individual caddisfly) was determined by flattening individual host tissues between a microscope slide and cover glass. All cysts were counted, including partially and fully melanised ones (Doherty et al. 2019). Since hairworm cysts are resistant and are not known to dissolve within host tissues, the number counted in the laboratory was considered as the total number of hairworm larvae that had successfully infected their host prior to collection.

Statistical analyses

All statistical analyses were performed in R version 4.0.3 (R Core Team 2021). Firstly, to test the prediction that infection status impacts the likelihood that caddisfly larvae pupate during the observation period, we used a generalised linear model (GLM) with the "glm" core function. Since the response variable can only assume one of two outcomes (larva or pupa), a logistic regression with a binomial distribution was implemented into the model. Fixed effects were the infection status (infected or uninfected), the width of the larval or pupal case, and the tank in which the caddisfly was placed. A second binomial regression was used to test the prediction that the intensity of hairworm cyst infection impacts the odds that caddisfly larvae pupate before the study ended. Uninfected individuals were not included in this second model, as it focused on infected individuals only. Here, fixed effects were the total number of cysts per infected individual (intensity of infection), case width, and the rearing tank. The tank could be considered a random effect in both models, but since two tanks fall below the recommended minimum of five levels for a mixed-effects model to calculate a robust estimate of variance, we included it as a fixed effect in the GLM (Harrison et al. 2018). In both models, none of the data was transformed. To assess model fit, residuals were verified with a binned residual plot, as recommended for logistic regressions (Gelman and Hill 2006).

Results

Hairworm cyst infection in *Olinga jeanae*

The study lasted a total of 154 days. In tanks 1 and 2, 38 (90.5%) and 34 (80.9%) caddisflies survived and were either active larvae or pupae. The water temperature in both tanks varied within 0.5 °C from each other. The numbers of pupated larvae in these tanks were 20 (52.6%) and 17 (50.0%). A total of 52 (72.2%) caddisflies harboured at least one hairworm cyst and were thus included in the model testing for the intensity of infection. From these infected individuals, 26 (50.0%) pupated during the study. Larval case width varied between 1.8 and 2.0 mm. All hairworm cysts closely resembled each other in size and shape. Due to the possibility of a hairworm species complex (Hanelt et al. 2015; Tobias et al. 2017), cysts were identified as *Gordius*-type cysts based on their morphology (Szmygiel et al. 2014). The distribution of hairworm cyst intensity is presented in Fig. 2a.

Host development and the intensity of hairworm cysts

All regression estimates from both models are presented in Table 1. In the first model testing the impact of infection on the propensity to pupate in larval caddisflies, none of the predictors had any effect. For the second model that included only infected individuals, the intensity of hairworm cyst infection positively correlated with the likelihood that

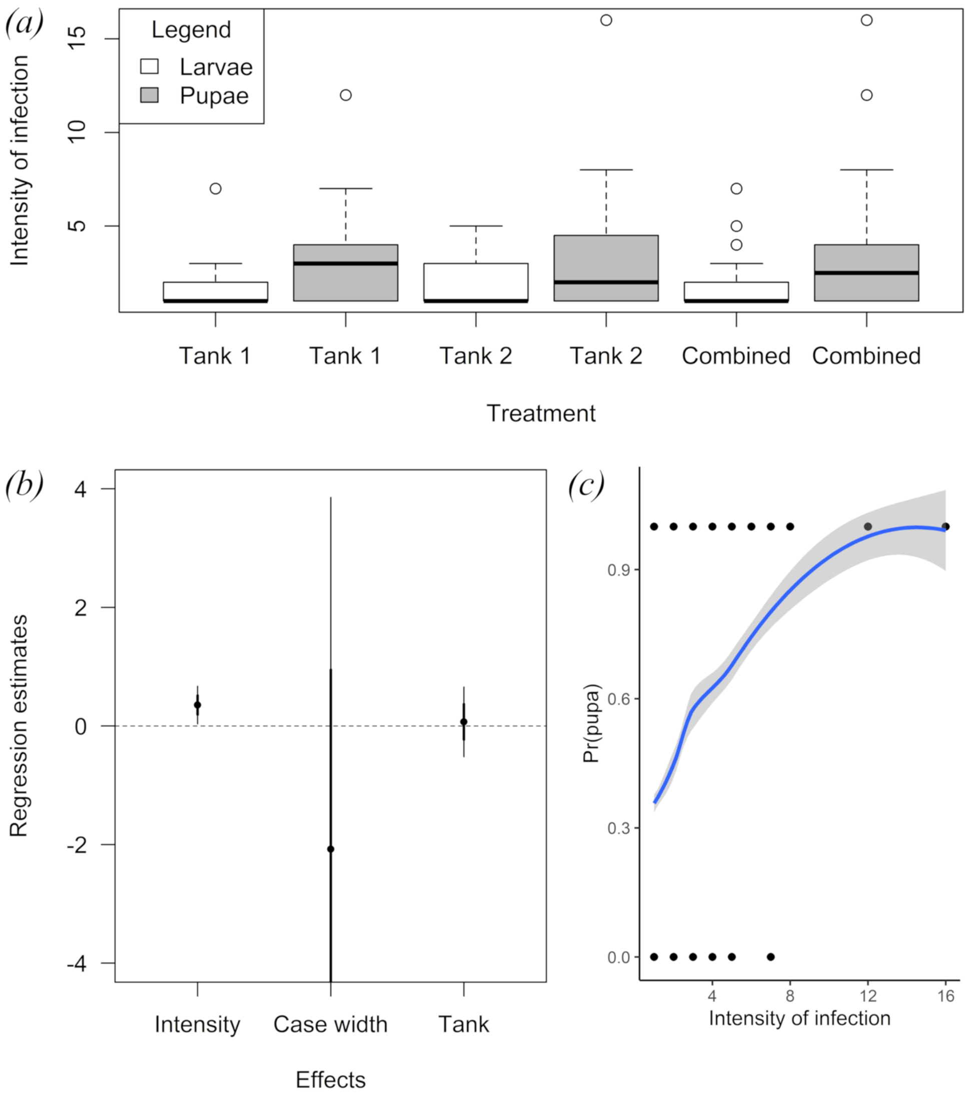

Fig. 2 **A** Boxplot of the intensity of *Gordius*-type hairworm (Nematomorpha) cyst infection (number of cysts per infected individual) in larval and pupal stages of the caddisfly *Olinga jeanae* (Trichoptera: Conoesucidae). **B** Logistic regression estimates for the fixed effects of the model testing for intensity of infection, with 95% error bars. A regression estimate that is different from 0 (including error bars) indicates that the corresponding effect has an impact on the likelihood that a caddisfly will pupate before the end of the study. **C** Loess curve of the predicted effect of intensity of hairworm cyst infection on the probability that a caddisfly will pupate before the study ended (blue line). The grey area represents the 95% confidence band of the fitted logistic regression model

O. jeanae larvae would pupate before the end of the study (Fig. 2b); each additional hairworm cyst was associated with 43% higher odds of pupating (Fig. 2c). In this model, the tank in which a caddisfly larva was placed and the width of its case did not correlate with the likelihood of it pupating before observations stopped (Fig. 2b).

Table 1 Regression estimates for the generalised linear models testing the impact of the infection status or the intensity of *Gordius*-type hairworm (Nematomorpha) cyst infection on the propensity to pupate in larval caddisfly *Olinga jeanae* (Trichoptera: Conoesucidae). Significant effects in bold have a regression estimate whose standard error range does not overlap 0 and a *z*-score greater than 2

Model	Effect variables	Regression estimate	Standard error	*z*-score
Infection status	Infection status	−0.1766	0.5416	0.744
	Case width	−0.1760	0.4909	0.720
	Tank	−0.1181	0.4760	0.804
Intensity[a] of infection	**Intensity of infection**	**0.3542**	**0.1619**	**2.187**
	Case width	−2.0785	3.0281	−0.686
	Tank	0.0701	0.2997	0.234

[a] Denotes the mean number of cysts per infected individual

Discussion

This study, to our knowledge, is the first to report noticeable changes in the natural life history of paratenic hosts infected with dormant hairworm cysts. We show that, within a laboratory-controlled observational study lasting several months, last-instar caddisfly larvae harbouring more cysts were likelier to pupate earlier than ones harbouring less. Interestingly, in only a few cases have caddisfly larvae been reported harbouring cysts (Doherty et al., 2019; Poinar, 1991; Table 3 in Schmidt-Rhaesa, 2013); most reported cases consist of caddisfly larvae infected with juvenile or adult hairworms (Schmidt-Rhaesa & Kristensen, 2006; Table 10 in Schmidt-Rhaesa, 2013). Although controlling for the age of naturally collected caddisfly larvae is difficult, the data suggest that larval caddisfly case width did not affect pupation rates. However, since we included only larvae of the same instar, hosts had most likely hatched around the same period in the stream and were probably very close in age. In both tanks, the prevalence of cysts in caddisfly larvae (74.3%) was near that of pupae (70.3%). Also, infection status alone did not appear to correlate with the odds of caddisflies pupating during the study, which suggests that the presence of at least one hairworm cyst was not enough to precipitate their transformation into pupae. More likely, what mattered was the intensity of infection, e.g. only pupae were observed harbouring eight or more cysts. In other words, although only half of the infected caddisflies pupated during the study, those that did generally harbour more cysts.

Collecting naturally infected hosts and placing them in controlled conditions obviously have its limitations. It is unknown whether all the caddisfly larvae from the collection site had equal access to the same food sources prior to collection, or whether larvae fed at similar rates. In a closely related species, *Olinga feredayi* (McLachlan) (Trichoptera: Conoesucidae), it was shown that larvae need to consume more when exposed to a lower-quality food source (Burrell and Ledger 2003). This can lead to a state of starvation, which could decrease the time to pupation (Truman and Riddiford 2002). However, the caddisfly larvae used in this study were collected from the same abundant patch of watercress, suggesting that individuals had access to the same food source and developed under similar conditions. Moreover, larval case width varied within a very narrow range (1.8–2.0 mm), indicating that individuals were closer in age to each other than to other instars, even though practically nothing is known of the development times of *O. jeanae* instars. In addition, individuals of all life stages (excluding adults during winter) from overlapping generations can be found year-round in the same area (Cowley 1978; Doherty et al. 2019). These uncontrolled variables make it challenging to quantify the real effects of hairworm cyst load on aquatic host development. For instance, the time of infection for each hairworm is unknown. Perhaps certain caddisfly larvae had longer hairworm infection times prior to collection. Ideally, to properly test the correlation found here, caddisfly larvae would need to be reared in the laboratory and exposed to variable numbers of hairworm larvae at fixed times. Unfortunately, it has not been possible to obtain enough mature hairworms from the sampling region to effectively rear them in the laboratory, obtain eggs, and expose caddisfly larvae to infective hairworm larvae.

Our observations of natural hairworm infections suggest that the more cysts a caddisfly larva harbours, the more likely it is to pupate earlier. Within this context, it is impossible to determine if the rate of pupal development or the emergence of adult caddisflies could also be associated with hairworm infection. Adult caddisflies need to emerge from the stream in order for the hairworms they carry to be consumed by their final host. This is a critical component in the transition from aquatic host to terrestrial one. Although little is known of the life history of *O. jaenea*, adults have been observed at the height of austral summer in January (Cowley 1978). Whether adults with more hairworm cysts emerge earlier in the season is unknown. However, caddisflies that spend less time as larvae or pupae are less likely to die from predation. Fish and other predators, like the New Zealand dobsonfly *Archichauliodes diversus* collected from the same sampling site (Doherty et al. 2019), decrease the odds of successful hairworm transmission. Although this study provides a narrow scope on the life cycles of both host and parasite, it suggests that selection may have favoured a decrease in host development time, which would maximise the successful transition of hairworms from water to land. In order to make a direct connection between the emergence of adult caddisflies and the successful transmission of hairworms, future investigations would have to successfuly rear and infect caddisflies, and have them eventually emerge as adults to associate the time of emergence with hairworm cyst load. However, keeping individuals under experimental conditions for many months can also come with its own string of complications.

Apart from predation, multiple abiotic stressors such as water temperature and pesticides can affect the development and survival of caddisfly larvae (Mochizuki et al. 2006; Schulz and Liess 1995). However, practically nothing is known of the impact that parasites can have. Aside from the study limitations discussed above, we present two possible mechanistic explanations as to why the intensity of hairworm cysts was positively correlated with the odds of caddisfly larvae pupating. Firstly, the accumulation of hairworm cysts over time may trigger a host response that accelerates the development process toward pupation. As stated above, hosts may have evolved to develop faster in response to repeated exposure to hairworm larvae, to avoid future infections. For instance, larvae of the cat flea *Ctenocephalides felis* experience accelerated development rates and emerge from pupae earlier when experimentally infected with the gregarine protist *Steinina ctenocephali* (Alarcon et al. 2017). Arguably, caddisfly larvae that pupate more rapidly are less likely to acquire additional hairworm larvae. The second possible scenario that could explain the effects observed in this study relates to the potential manipulation of aquatic host development by hairworms. Even though hairworms are dormant (after a brief active period) within aquatic hosts, they may have evolved to alter host development through unknown mechanisms. For example, microphallid trematodes that encyst as metacercariae (dormant stage of trematodes) within the heads of the amphipod *Gammarus insensibilis* can alter host behaviour and even reproductive output (Arnal et al. 2015; Gates et al. 2018). If hairworms were adapted to manipulate the development of aquatic insect larvae, they would likely have evolved mechanisms targeting important regulatory functions such as the juvenile hormone signalling pathway, a vital system that controls insect growth (Jindra et al. 2013). For instance, microsporidians of the genus *Nosema* cause excessive amounts of juvenile hormone that disrupt normal growth patterns in multiple insect hosts (Fisher and Sanborn 1962). Still, more research is needed to explore the hidden interactions between hairworms and their paratenic hosts.

To conclude, we have shown that the presence of hairworms in naturally infected caddisfly larvae correlates with a decrease in time to pupation. Ideally, this study should be replicated with experimentally infected hosts to determine if dormant hairworm cysts truly impact paratenic host development through direct or indirect mechanisms. Nonetheless, these observations provide novel insight into the infection dynamics between hairworms and their aquatic hosts. Interestingly, the intensity of hairworm cyst infections in aquatic macroinvertebrates fluctuates throughout the year (Chiu et al. 2016; Doherty et al. 2019). Higher intensities have been observed from our sampling site (unpublished results), so that the association found here may be even stronger in other seasons. This study has further elucidated the complex yet hidden interactions between hairworms and their paratenic hosts. It also reveals that the dramatic host manipulation that brings the parasite from land to water may be matched by a more subtle one that brings the parasite back from water to land.

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Author contribution JFD and RP conceived and designed the study. JFD conducted the experiment, collected the data, performed the statistical analyses, and wrote the paper. RP provided critical feedback throughout.

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Data availability Data will be made available by the authors upon reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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