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INFORMATION ABOUT TRANSMISSION OPPORTUNITIES TRIGGERS A LIFE-HISTORY SWITCH IN A PARASITE

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Abstract.—Many microbial pathogens can switch to new hosts or adopt alternative transmission routes as environmental conditions change, displaying unexpected flexibility in their infection pathways and often causing emerging diseases. In contrast, parasitic worms that must develop through a fixed series of host species appear less likely to show phenotypic plasticity in their transmission pathways. Here, I demonstrate experimentally that a trematode parasite, *Coitocaecum parvum*, can accelerate its development and rapidly reach precocious maturity in its crustacean intermediate host in the absence of chemical cues emanating from its fish definitive host. Juvenile trematodes can also mature precociously when the mortality rate of their intermediate hosts is increased. Eggs produced by precocious adults hatch into viable larvae, capable of pursuing the parasite's life cycle. In the absence of chemical cues from fish hosts, the size of eggs released by precocious trematodes in their intermediate hosts becomes more variable, possibly indicating a bet-hedging strategy. These results illustrate that parasitic worms with complex life cycles have development and transmission strategies that are more plastic than commonly believed, allowing them to skip one host in their cycle when they perceive limited opportunities for transmission.

Key words.—Amphipods, *Coitocaecum parvum*, phenotypic plasticity, progenesis, transmission modes, trematode.

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The recent emergence of many wildlife diseases has highlighted how parasites can adjust to environmental changes that modify the conditions under which they are transmitted among hosts (Harvell et al. 1999, 2002; Daszak et al. 2000; Patz et al. 2000). Many directly transmitted microparasites display adaptive phenotypic plasticity in virulence or transmission route, responding quickly to factors influencing their opportunities for growth or transmission (Bull et al. 1991; Ebert and Mangin 1997; Kaltz and Koella 2003). In contrast, most taxa of parasitic worms possess complex life cycles involving two or more host species, and display transmission patterns that appear more rigid than those of microparasites (Bush et al. 2001; Combes 2001). In some groups, though, successful truncation of the life cycle is occasionally observed. Among trematodes, for instance, several species from numerous families appear capable of dropping one host from their life cycle (Poulin and Cribb 2002). Typically, the life cycle abbreviation is facultative, and thus only shown by some worms in the population. These worms achieve precocious sexual maturity in an intermediate host, via progenesis, rather than maturing following their transmission to the definitive host. What external cues modulate such flexible life cycles is presently unknown.

The present study addresses this important question using a model system amenable to experimental investigation. The trematode *Coitocaecum parvum* (Opecoelidae) is a common parasite of native New Zealand freshwater fishes (Macfarlane 1939; Holton 1984a). Its eggs, released in fish feces, hatch into free-swimming larvae that penetrate snails, in which they multiply asexually to produce cercariae, the next free-swimming infective stages. After being shed by snails, cercariae penetrate the amphipod *Paracalliope fluviatilis* (Eusiridae). The cercariae encyst as metacercariae in the amphipod's body cavity and await ingestion by a fish definitive host, where the worms will mature. However, some metacercariae grow larger than others and reach sexual maturity within the amphipod; they self-fertilise and produce eggs that are released in the amphipod's body cavity (Holton 1984b; Poulin 2001). Upon the amphipod's death, the eggs hatch into larvae that are infective to snails, thus bypassing the need for a fish host (Holton 1984b). A comparison of 16S mitochondrial DNA sequences (369 base pairs) from both ''normal'' adults from fish hosts and progenetic adults from amphipod hosts has revealed no differences at all (K. Donald and R. Poulin, unpubl. data). In contrast, divergences between related and sympatric species of opecoelid trematodes over the same 16S region are in the order of 1–3.5% (K. Donald, unpubl. data). Thus, the two developmental strategies are most likely an instance of intraspecific variability, and not a case of two related species living in sympatry. Phenotypic plasticity of this kind might be adaptive, reflecting state-dependent decisions made by parasites in response to local environmental variables (Thomas et al. 2002). Given that abbreviated life cycles have recently been reported in parasitic nematodes as well as trematodes (Jackson et al. 1997; Poulin and Cribb 2002; Levsen and Jakobsen 2002), it is important to elucidate what drives the adoption of these alternative transmission routes.

Here, I tested the general hypothesis that the trematode *C. parvum* can use information about its opportunities of transmission to a fish definitive host to adjust its life-history schedule. Specifically, I predicted that the trematode would alter its developmental schedule when it perceives its opportunities for transmission to fish to be limited, either because fish are locally absent or because the amphipod host has a limited life expectancy. In these conditions, the egg production strategies of the worms may also change; with transmission to fish unlikely, the worms may hedge their bets and invest more into each of the few eggs that can be produced.

METHODS

Naturally infected amphipods were collected from Lake Waihola (near Dunedin, New Zealand) and separated randomly into 16 groups of 40 individuals. Each group was placed in a plastic container (10-cm diameter) filled with 400 ml of aged lake water, and four containers were assigned to each of four treatments in a 2×2 factorial design. The treatments consisted of all possible combinations of two rearing temperatures, 15° and 22°C, and two regimes of water replacement, using either control water or fish-conditioned water.

Preliminary trials revealed that amphipod mortality is higher at 22° than at 15°C, whereas there are no differences in amphipod activity levels or reproductive output between the two temperatures (R. Poulin, unpubl. data). Both types of water were prepared daily by placing 1500 ml of aged lake water in two small, identical plastic tanks. Aged water consisted of water collected weeks prior to the experiment, to allow any chemical cues from fish to deteriorate. Four 5–6 cm long bullies *Gobiomorphus cotidianus* (Eleotridae), chosen randomly everyday from a pool of 15 fish, were added to one tank for 3 h to produce fish-conditioned water; nothing was added to the control water tank. Bullies are the only known fish definitive host of the trematode *C. parvum* in Lake Waihola, and by far the most abundant fish in the lake. The only other fish in the shallow lake areas where the amphipods occur is the introduced perch, *Perca fluviatilis*, and only the smallest size classes of perch feed on amphipods. Everyday, 150 ml of water was removed from each amphipod container and replaced with 150 ml of either control or fish-conditioned water, depending on treatment. In addition, a new 8-cm long strand of the macrophyte *Elodea canadensis*, covered with microalgae, was added to each container every two days, as food for the amphipods.

The experiment was terminated after 14 days, with all amphipods preserved in ethanol. Later, both amphipods and any worm they contained were measured under the microscope. If a worm had produced eggs, the latter were counted and a random sample of 10 per amphipod, or all eggs if there were fewer than 10, were measured (length and width) under 400× magnification. The volume of each egg was then computed using the formula for an ellipsoid, $(\pi L W^2)/6$, where L and W are the length and width of the egg, respectively.

To determine whether temperature per se, and not its influence on amphipod mortality, might be responsible for differences in worm length between the two rearing temperatures in the above experiment, the lengths of adult worms grown in fish at different temperatures were compared. Fourteen normal (nonprogenetic) adult worms were obtained from fish freshly caught in the lake in the spring (water temperature 12–15°C), and 18 adult worms were obtained from fish caught at the same time but kept in the laboratory (room temperature 20–22°C) for six weeks prior to dissection; the latter were used to produce fish-conditioned water for the previous experiment. Given the short life span of the trematodes in fish hosts (estimated to be 6–8 weeks; R. Poulin, pers. observ.), worms from the laboratory-held fish were probably new infections at the time of fish capture, and thus spent almost all their adult life at a high and constant temperature. Only fully developed, egg-bearing worms were used; these were measured under the microscope as for the worms dissected from amphipods.

RESULTS

Overall, 94 worms were recovered from the 336 surviving amphipods. The percentage of male amphipods varied among containers from 51% to 97%, but did not differ significantly among treatments (two-way ANOVA on arcsine-transformed data, both main effects and interaction, all $P > 0.28$). Except for four amphipods each harboring two worms, all other infected amphipods had a single worm; excluding the eight worms from the doubly infected amphipods had no effect on any of the subsequent results. However, there were differences among treatments in the percentage of amphipods harboring trematodes (effect of water type: $F_{1,12} = 8.3$, $P = 0.014$; effect of temperature: $F_{1,12} = 3.53$, $P = 0.085$; interaction, $P > 0.21$); this resulted in unequal numbers of worms per treatment, the outcome of chance events during the grouping of the amphipods at the onset of the experiment. As expected, amphipod survival was significantly lower at 22°C than at 15°C (Fig. 1A). Therefore, the trematodes harbored by amphipods at 22°C have a narrower window of transmission to their fish host because of their intermediate host's reduced life expectancy.

The growth achieved by the trematodes during the experiment also differed among treatments: worms were significantly longer when exposed to control water than when exposed to fish-conditioned water and were longer at the higher temperature than at the lower one (Fig. 1B). In other words, the worms accelerated their development either when there were no chemical signals that the fish definitive hosts were present in the surrounding water or when the mortality rate of the amphipod intermediate host was increased. Amphipod length did not differ among treatments (main effects and interaction, all $P > 0.16$); in any event, worm length was not related to amphipod length ($r = 0.093$, $n = 94$, $P = 0.373$).

Adult worms obtained from fish hosts reared either in the cold waters of the lake (mean ± 1 SEM, 0.761 ± 0.025 mm, $n = 14$) or the warmer laboratory temperature (0.767 ± 0.020 mm, $n = 18$) had body lengths that were slightly longer than those of progenetic worms, as expected from the greater availability of nutrients in the gut of fish compared to the body cavity of amphipods. However, there was no difference in the mean length of these two groups of adult worms from fish ($t_{30} = 0.19$, $P = 0.85$), suggesting that the difference observed in progenetic worms from amphipods reared at different temperatures is due to the indirect effect of host mortality rather than a direct effect of temperature.

Only worms at least 0.5 mm long, but not all of them, produced eggs. Thus, there was a significant difference ($t_{92} = 7.51$, $P = 0.0001$) in length between worms that produced eggs (mean ± 1 SEM, 0.645 ± 0.017 mm, $n = 20$) and those that did not (0.432 ± 0.014 mm, $n = 74$). Worm length correlated weakly with both the log-transformed number of eggs per worm ($r = 0.427$, $n = 20$, $P = 0.06$) and the log-transformed mean egg volume ($r = -0.419$, $n = 20$, $P = 0.068$). There was evidence of a trade-off between the number of eggs produced and their average volume (Fig. 2). In other

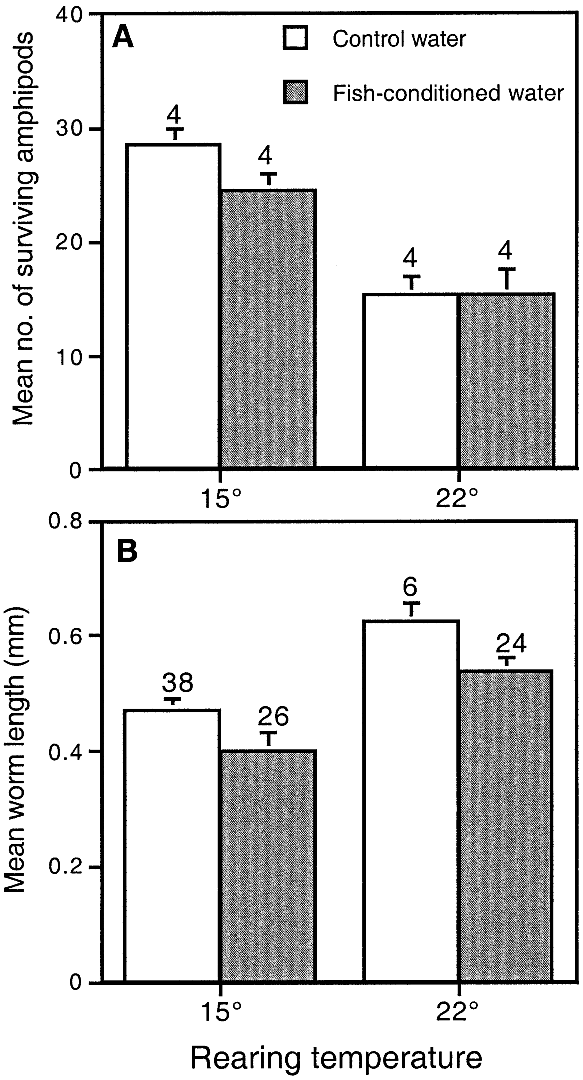

FIG. 1. (A) Effects of rearing temperature and the presence of fish odors in the water on the mean (± 1 SEM) number of amphipods surviving per container and (B) on the mean (± 1 SEM) length achieved by the worm *Coitocaecum parvum* in those amphipods. Only temperature influenced amphipod survival (two-way ANOVA: $F_{1,12} = 43.34$, $P = 0.0001$; effect of water type and interaction, both $P > 0.25$). In contrast, both treatments affected worm length (effect of temperature: $F_{1,90} = 19.17$, $P = 0.0001$; effect of water type: $F_{1,90} = 5.423$, $P = 0.022$; interaction, $P > 0.8$). Numbers above bars are sample sizes.

words, worms that produced many eggs tended to produce small eggs, and vice versa.

Using measures of egg numbers and egg size corrected for worm length, I found no effect of either water type or rearing temperature on egg output or average egg size (main effects and interactions, all $P > 0.11$). In contrast, variability in egg volumes among eggs produced by single worms, measured as the coefficient of variation, was significantly higher in the treatments using control water than in those with fish-conditioned water (Fig. 3). Thus, worms reared in the absence of chemical cues from their fish definitive host produced a wider range of egg sizes than those reared in conditions associated with higher rates of transmission to fish.

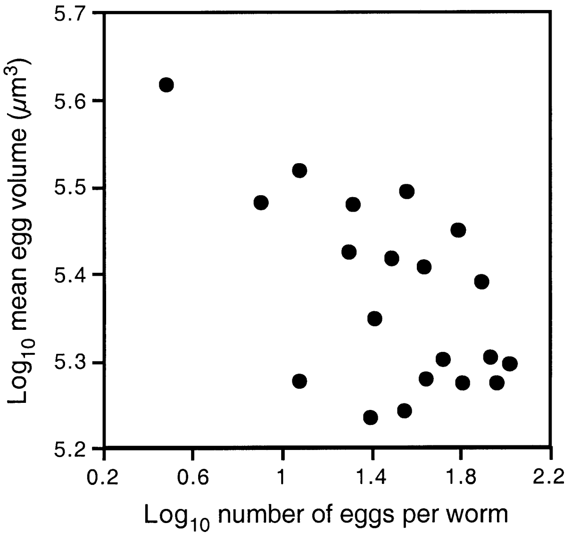

FIG. 2. Relationship between the mean volume and the numbers of eggs produced by the worm *Coitocaecum parvum* in amphipod intermediate hosts ($r = -0.558$, $n = 20$, $P = 0.0106$). Using residuals from the linear regressions of these two variables against worm length (mean egg volume: $F_{1,18} = 3.75$, $R^2 = 0.172$, $P = 0.068$; egg numbers: $F_{1,18} = 4.02$, $R^2 = 0.183$, $P = 0.06$), to control for the influence of worm size, the apparent trade-off between egg numbers and egg volume remains significant ($r = -0.463$, $n = 20$, $P = 0.04$).

DISCUSSION

This study finds that information on perceived opportunities for transmission to a fish definitive host spark life-history changes in a parasitic trematode still in its interme-

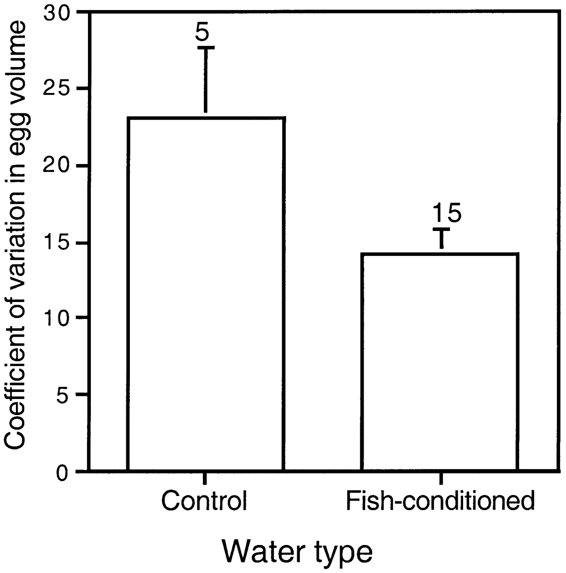

FIG. 3. Effects of the presence of fish odors in the water on the mean (± 1 SEM) coefficient of variation in the volume of eggs produced by the worm *Coitocaecum parvum*. The variability in egg volumes, measured for each worm as the coefficient of variation (standard deviation × 100/mean), was significantly influenced by water type ($F_{1,16} = 6.707$, $P = 0.0197$) but not by rearing temperature (temperature effect and interaction with water type, both $P > 0.2$). Numbers on bars are sample sizes.

diate host. The results show that growth decisions and developmental strategies in this parasite are plastic, and conditional upon opportunities for transmission. When predation by fish on amphipod intermediate hosts is perceived as unlikely, the metacercariae in amphipods quickly achieve sizes comparable to those of ''normal'' adult worms in fish definitive hosts. This is one of the first experimental demonstrations that parasitic worms are capable of sophisticated state-dependent adjustments to their life cycles (Thomas et al. 2002). Previous examples are very few. For instance, the monogenean *Pseudodiplorchis americanus*, parasitic in amphibians, uses physiological cues from its host to adjust the onset of its own reproduction and to synchronise the release of infective stages with the rare periods of host availability (Tinsley 1990). Similarly, larvae of the nematode *Strongyloides ratti*, parasitic in rats, are more likely to develop into sexual adults when issued from immune rats than from immuno-suppressed hosts (Gemmill et al. 1997); presumably, facultative sexual reproduction and the genetic variability it promotes are adaptive when the parasite perceives that genetic resistance is spreading in the host population. The present example shows that a parasite can also use external cues to modify its development schedule and skip what would otherwise be a normal step in its life cycle.

Trematodes in the experiment also produced eggs of more variable sizes when reared in the absence of chemical cues from potential fish hosts, perhaps reflecting a bet-hedging strategy. The few eggs released by a progenetic worm inside an amphipod may be the only ones it ever produces. Because egg number in progenetic worms is limited to approximately 200 (Macfarlane 1939; Poulin 2001), it may be advantageous to increase variability in offspring size to ensure that some survive. Environmental unpredictability can select for greater offspring variability (Crump 1981; McGinley et al. 1987). Indeed, egg sizes vary considerably within trematode species that release their eggs in unstable environments (Poulin and Hamilton 2000). Lake Waihola is under tidal influences and the physicochemical conditions in the shallow water where amphipods live are extremely variable. The trade-off between egg numbers and egg size may favor the simultaneous production of some well-provisioned eggs and several smaller ones. In normal adult *C. parvum* inside fish, this trade-off may be relaxed as the worms produce thousands of eggs over their life span. The assumption here is that larger eggs lead to offspring of higher quality. However, Xu and Dresden (1989) found that among mature eggs of the trematode *Schistosoma mansoni*, larger size classes often failed to hatch. The situation for *C. parvum* may be different, and at this stage the fitness consequences of variability in the size of its eggs remains unclear.

The accelerated growth of the trematodes at 22°C may be due in part to the direct influence of temperature itself, and not to its indirect effect on amphipod survival. Discriminating between these possibilities would require raising the worms in vitro at different temperatures, something that has proven difficult for trematodes in general (Irwin 1997) and impossible for *C. parvum* (R. Poulin, pers. obs.). However, two lines of evidence argue against a direct effect of temperature on trematode growth. First, 91 of the 109 studies reviewed by Atkinson (1994) that have quantified the influence of rearing temperature on the growth and final size of ectotherms have reported that higher temperatures reduce growth (see also Atkinson 1995). In comparisons among trematode species, the relative growth from the metacercarial stage to the adult stage did not differ between species using endothermic definitive hosts and those using ectothermic hosts (Poulin and Latham 2003); this suggests that the thermal regime experienced by growing trematodes does not influence their final size. The best-documented effect of temperature on metacercarial growth is the fact that metacercarial development stops below some critical temperature (Chubb 1979). The lowest temperature used in my experiment (15°C) falls within the range of summer water temperatures in Lake Waihola, and the trematode can develop at this temperature. Therefore, the 15°C treatment did not prevent the normal growth of the worms.

The second, and perhaps more convincing, line of evidence comes from the observation that adult *C. parvum* reared in fish at different temperatures did not differ in length. Worms from the laboratory-held fish were most likely new infections at the time of fish capture, and subsequently attained their final size at room temperature. Still, they did not grow larger than worms developing in lake fish at colder temperatures. The temperature-induced reduction in amphipod survival may therefore have been the key factor in the enhanced growth of worms at 22°C.

In contrast, the effect of water type has no explanation other than a direct influence of fish odors. Several crustaceans respond promptly to chemical cues from their predators by altering their behavior or life-history schedules, or by producing offspring with defensive morphological structures (Dodson 1989; Neill 1990; Larsson and Dodson 1993; Kats and Dill 1998; Tollrian and Dodson 1999). The trematode *C. parvum* must detect physiological changes in its amphipod host that are associated with predator-induced responses; in turn, the parasite responds by slowing down its own growth in anticipation of its impending transmission to a fish, where it will pursue its development. In contrast, situations where ingestion by a fish definitive host appears unlikely promote precocious development, and ultimately the abbreviation of the normal three-host cycle to a two-host cycle.

These results demonstrate that a parasite can use available information on its opportunities for transmission in order to adjust its developmental schedule. Previous studies have suggested that the size achieved by a larval worm in its intermediate host may be dependent on whether it shares the intermediate host with other parasites (Dezfuli et al. 2001; Parker et al. 2003). This flexibility in development, however, was expected merely from resource constraints faced by several parasites co-occurring in the same host. In the present system, resource limitation was not an issue: the parasites occur singly inside amphipods, they are orders of magnitudes smaller than the host, and their size is independent of host size. In addition, it was not only the size, but also the sexual development of the worms that was variable in this experiment.

Adaptive scenarios have been proposed for the evolution of complex, multihost life cycles in parasitic worms (Morand et al. 1995; Brown et al. 2001; Choisy et al. 2003), but it is the few species showing a facultative simplification of the cycle that offer the best chances of elucidating what drives the evolution of transmission routes. Alternative transmission strategies have been reported, mostly as anecdotal observations, from over 30 different trematode families (Poulin and Cribb 2002). Their widespread occurrence in the phylogenetic tree of trematodes suggests multiple, independent origins (Poulin and Cribb 2002). My results show that these alternative life cycles may be cases of adaptive phenotypic plasticity, and they suggest that the transmission pathways of parasitic helminths may be much more flexible than previously thought.

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