

Cost of exposure to trematode cercariae and learned recognition and avoidance of parasitism risk by fathead minnows *Pimephales promelas*

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Fathead minnows *Pimephales promelas* exposed to cercariae of the trematode *Ornithodiplostomum* sp. incurred a significant mass loss 17 days after exposure to 20 or 120 cercariae. Parasite-naïve *P. promelas* showed no evidence of innate recognition or avoidance of cercariae. After a single exposure to cercariae, however, fish responded to chemical and visual cues of dead (thawed) cercariae with a reduction in activity. Encounter rate with cercariae, and hence infection rate, increased with fish activity. The data indicated that experienced *P. promelas* associated parasitism risk with novel chemical and visual cues that later triggered avoidance behaviour. Parallels and interactions between antiparasite behaviour and antipredator behaviour open new avenues for behavioural ecological research in risk-sensitive decision-making.

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Key words: behavioural avoidance; cost of parasitism; host activity; learning; *Ornithodiplostomum*.

INTRODUCTION

Parasites influence host physiology, behaviour and fitness (Hart, 1994; Moore, 2002). The ways in which they affect individual hosts are as varied as the parasites themselves. At a minimum, parasites redirect somatic resources of their host towards their own growth and development and thus, exact a metabolic cost (Barber *et al.*, 2000). In response, natural selection should promote mechanisms for hosts to detect and avoid parasites and indicators of the risk of parasitism (Goater & Holmes, 1997; Wisenden *et al.*, in press).

The evolutionary origin of antiparasite behaviours may be difficult to distinguish from the evolutionary origin of antipredator behaviours (Poulin *et al.*, 1999). Indeed, generic behavioural reactions to risk may serve to reduce exposure to both parasites and predators. For example, predators often locate their host or prey by detecting motion (Lima & Dill, 1990). Similarly, the infective stages of many ecto- and endo-parasites detect their host *via* visual, chemical

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and tactile cues that indicate host motility (Haas, 1994; Poulin *et al.*, 1999). Not surprisingly, reduced activity is a common counter-strategy used by hosts and prey to reduce risk of detection by parasites and predators (Lawrence & Smith, 1989; Lima & Dill, 1990; Poulin *et al.*, 1991; Chivers & Smith, 1998; Thiemann & Wassersug, 2000).

As with predator avoidance, parasite avoidance begins with detection of the parasite or indicators of the risk of parasitism (Lima & Dill, 1990; Smith, 1992; Hart, 1994; Kiesecker *et al.*, 1999; Kiesecker & Skelly, 2000; Wisenden *et al.*, in press). In aquatic ecosystems, chemical cues represent reliable public information about predation risk (Dodson *et al.*, 1994; Kats & Dill, 1998; Wisenden, 2003; Wisenden & Chivers, 2006). These chemical cues elicit evasive responses innately or evasive responses can be acquired by associating novel neutral stimuli with stimuli known to be correlated with risk (Brown, 2003). Injury-released chemical cues reliably provide public information about the presence of an actively foraging predator, that in turn afford nearby prey the opportunity to associate the appearance and chemical signature of a novel predator with predation risk (Chivers & Smith, 1998). A remarkable property of this type of learning is that one event is sufficient for near-permanent recognition of a novel predator with risk (Suboski, 1990; Chivers & Smith, 1994; Brown, 2003). In future encounters with the predator, indirect indicators of risk are sufficient to elicit an evasive behavioural response.

Given that sophisticated behavioural learning paradigms exist to counter predation risk, it is plausible that the same learning mechanism may be used for the detection and avoidance of parasitism risk. Here, parasite-naïve fathead minnows *Pimephales promelas* Rafinesque were tested for innate recognition and avoidance of cercariae of the trematode *Ornithodiplostomum* sp., or if not, can they do so after being given the opportunity to associate parasitism risk with olfactory and visual indicators of parasites? This flexible learning would allow *P. promelas* to adapt and respond to risk that changes form throughout host ontogeny, and ecological time and space. *Pimephales promelas* present an ideal test organism for acquired recognition of parasitism risk because they have been used for many studies in learned associations of predation risk (Chivers & Smith, 1998). Moreover, natural populations of *P. promelas* typically harbour many different types and life cycle stages of parasites, one of which is the trematode *Ornithodiplostomum* sp. (Diplostomatidae) that is amenable to experimental manipulation. Cercariae of *Ornithodiplostomum* sp. use *P. promelas* as a second intermediate host (unpubl. obs.), typically encysting within the body cavity. The aims of this study were (1) to measure metabolic cost of infection by cercariae of *Ornithodiplostomum* sp., (2) to determine if *P. promelas* have innate recognition and avoidance of these costs and (3) to determine if behavioural avoidance responses are acquired after experience of exposure to cercariae.

MATERIALS AND METHODS

HOST-PARASITE SYSTEM

Ornithodiplostomum sp. is an as yet undescribed species of trematode parasite. Its close congener *Ornithodiplostomum ptychocheilus* Faust, is a well known trematode

of *P. promelas* (Radabaugh, 1980; Sandland & Goater, 2000, 2001). In lakes and ponds in Alberta, *Ornithodiplostomum* sp. typically co-occurs with *O. ptychocheilus* in the same individual fish (Sandland, 1999). *Ornithodiplostomum ptychocheilus* encysts within the optic lobes of *P. promelas* (Sandland & Goater, 2001), whereas *Ornithodiplostomum* sp. encysts in the body cavity (unpubl. data). Their life-cycles are very similar, both involving physid snails as first intermediate host, *P. promelas* as second intermediate host and fish-eating birds as definitive hosts. Infection of fish occurs via penetration through the skin. There are three phases of metacercarial development in the close congener *O. ptychocheilus* (Sandland & Goater, 2000): (1) 0–4 weeks post-infection (PI) is a period of maximal growth where metacercariae approximately double in size, (2) 6–8 weeks is when encystment occurs and (3) post-encystment reduction in size when metacercariae reduce body length by c. 50% and become quiescent to await ingestion by the definitive host. Peak pathology in *O. ptychocheilus* infected fish occurs between 2 and 4 weeks based on impaired optomotor response, which coincides with the time of maximal metacercaria growth (Shirakashi & Goater, 2005). Assuming similar life histories for *O. ptychocheilus* and *Ornithodiplostomum* sp., 17 days, was chosen as a time when maximal metabolic demand on *P. promelas* should be most detectable.

Fish were obtained from the Environmental Protection Agency facility in Duluth, MN, U.S.A. These fish were laboratory reared and thus parasite-naïve. They were purchased as 30 days-old juveniles, and they were c. 50 days old when used in the experiments. Fish were housed in a 185 l tank at 18° C, with a 12L:12D photoperiod. Fish were fed daily with commercial flake food.

For experimental infections involving cercariae of *Ornithodiplostomum* sp., the methods used by Sandland & Goater (2000) for *O. ptychocheilus* were followed. Eight, 1-day-old chickens were fed metacercariae collected in May 2007 from the infected viscera of wild *P. promelas* obtained from Gold Spring Lake, southern Alberta, Canada (49°05'50" N; 111°59'49" W). Trematode eggs were collected from chicken faeces 5 days PI, and F1 pond snails (*Physa gyrina*), laboratory reared from parents collected in June 2007, were exposed to the miracidia produced from incubated eggs. The *P. gyrina* were housed in 2 l plastic containers at 18° C, with a 12L:12D photoperiod and were fed romaine lettuce daily.

COST OF PARASITISM EXPERIMENT

Infected *P. gyrina* were isolated in small glass vials of dechlorinated water for 2 h under artificial light to facilitate release of cercariae. Cercarial density was determined by counts of 1 ml of cercariae suspension added to 15 ml of dechlorinated water and 2 ml of 70% ethanol to kill (immobilize) cercariae. Three different infection exposures were used after Sandland & Goater (2000): 0 cercariae (control), 20 cercariae (low) and 120 cercariae (high) per fish. Counts of the three dishes were averaged to estimate the volume of cercarial suspension required to produce the three treatment groups: control = 0, low = 0.23 ml and high = 1.4 ml.

Fish (mean \pm s.e., L_T , total length, 21.5 ± 0.2 mm, $n = 60$) were selected arbitrarily and placed individually into plastic containers (300 \times 180 mm, 5.7 l) containing 3.0 l of dechlorinated water that was changed weekly. Fish were measured and weighed (M , g) at the beginning of the experiment and again at 17 days PI. Each minnow was anaesthetized in a solution of one drop of 99% phenoloxxyethanol in 40 ml of dechlorinated water and photographed through a dissection microscope. Measurements of L_T were made from digital images using ImageJ software. Exposure to cercaria infection was conducted in 118 ml containers holding 30 ml of dechlorinated water. Each fish was exposed to one cercarial suspension (0, 0.23 ml or 1.4 ml for each treatment group) for 2 h (Sandland & Goater, 2000) and then returned to its container. At 5 weeks PI, 10 *P. promelas* from each treatment were dissected to determine metacercariae intensity.

Regression residuals of $\ln M$ and $\ln L_T$ represent M corrected for L_T and served as a measure of physical condition. To detect cost of parasitism on physical condition, residuals among treatment groups were compared using one-way ANOVA at the start of the experiment and again at 17 days PI.

RECOGNITION AND AVOIDANCE OF PARASITISM RISK EXPERIMENT

Nine infected *P. gyryna* were isolated in small vials with dechlorinated tap water for 2 h under direct artificial light to collect cercariae. Cercaria counts in three 1 ml aliquots were averaged to estimate the volume of water needed to obtain a dose of 50 and 150 cercariae using the methods described above for cost of parasitism experiment.

Fish (mean \pm s.e., L_T , 28.7 ± 0.1 mm, $n = 24$) were placed individually in 118 ml plastic cups with 30 ml of dechlorinated water. Three conditioning treatment groups ($n = 8$ fish per group) were used to test for acquired recognition and avoidance: (1) water control, (2) parasite-naïve fish and (3) parasite-experienced fish. Fish in the water control and naïve treatment groups each received 10 ml of plain dechlorinated water. Fish in the experienced treatment group received 10 ml of dechlorinated water each containing 50 live cercariae (Table I). All fish were left undisturbed for 2 h and then placed in 37 l aquaria labelled by treatment. After 2 days, fish were transferred to test aquaria.

Test stimuli were made by preparing 10 ml aliquots containing dechlorinated tap water only (water control group) or 10 ml of water with 150 cercariae (used for parasite-naïve and experienced treatment groups) (Table I). These test stimuli were frozen at -20° C until needed. Because freezing killed the cercariae, behavioural responses to this stimulus could only be due to innate (naïve group) or learned (experienced group) recognition of olfactory and visual cues of cercariae and not from direct attack. Four weeks following the trials, infected fish were humanely killed with an overdose of methanes tricaine sulphonate (MS222) and dissected to enumerate the metacercaria infections in exposed fish.

A grid (50 \times 50 mm) was drawn on the end panel of 24, 37 l experimental tanks using a black pen. The remaining sides were painted to prevent visual contact between neighbouring tanks. A thin plastic tube provided compressed air to dirt-magnet[®] (Jungle Laboratories Corporation, Cibola, TX, U.S.A.) sponge filters placed in the centre of each tank. A second airline hose was wedged into the rigid plastic lift tube of the filter. This second hose was used to surreptitiously introduce test stimuli. The turbulence of the airflow masked pressure changes associated with cue injection. Dye tests confirmed that water currents created by the filter quickly dispersed test stimuli throughout the test aquarium. Injection hoses were c. 2 m in length and allowed experimenters to conveniently introduce stimuli without disturbing the test subject.

Conditioned fish were placed individually into the experimental tanks and allowed to acclimate for 24 h. They were fed commercial flake food before trials began. The stimulus hose for each experimental tank was rinsed by twice withdrawing and discarding 60 ml of tank water. A third 60 ml of tank water was retained to be used later to flush test stimuli into the test aquarium. Each fish was observed for 11 min: 5 min pre-stimulus behaviour, followed immediately by 1 min of stimulus injection during which time no behaviour was recorded, followed immediately by 5 min of post-stimulus behaviour. Activity and vertical distribution were recorded because reduction in activity and movement towards the bottom are well documented behavioural responses to predation risk (Lawrence & Smith, 1989; Chivers & Smith, 1998) and parasitism risk (Poulin *et al.*, 1991; Thiemann & Wassersug, 2000). Vertical distribution was

TABLE I. Test stimuli presented for conditioning and trials ($n = 8$ per treatment)

Treatment	Conditioning stimulus	Test stimulus
Water control	10 ml dechlorinated water	10 ml dechlorinated water
Naïve	10 ml dechlorinated water	10 ml with 150 thawed (dead) cercariae
Experienced	10 ml with 50 live cercariae	10 ml with 150 thawed (dead) cercariae

recorded every 15 s (score ranged from 1 to 5, with one for the surface row and five for the bottom row). Activity was scored as the total number of grid lines crossed in 5 min.

All data were assessed for normality prior to analysis using the Shapiro–Wilk test. Host L_T were compared using one-way ANOVA. Activity levels prior to the addition of stimuli were compared with one-way ANOVA to separate possible effects that prior infection would have on host activity. Following the protocol of Wisenden & Harter (2001), the overall change in host activity and vertical distribution was determined by subtracting the pre-stimulus data from the post-stimulus data. Changes in activity and vertical distribution were compared with one-way ANOVA.

All experimental methods were reviewed and approved by the MSUM Institutional Animal Care and Use Committee (protocol number 07-T-Biol-015-N-Y-C).

RESULTS

COST OF PARASITISM EXPERIMENT

Exposure to cercariae resulted in successful infections in proportion to the number of cercariae to which fish were exposed. When fish were dissected and encysted metacercariae counted 5 weeks after exposure, mean \pm s.e. intensity for the low-exposure group was 61.7 ± 6.8 ($n = 12$) whereas mean intensity of the high-exposure group was 80.8 ± 4.5 ($n = 12$).

Analysis of regression residuals of $\ln M$ and $\ln L_T$ showed no significant differences among fish assigned to the three treatment groups at the start of the experiment (ANOVA, $F_{2,57}$, $P > 0.05$; Fig. 1). Analysis of residuals at 17 days PI showed significant differences among treatment groups (ANOVA, $F_{2,52}$, $P < 0.001$). Control fish were significantly heavier for their L_T than the treatment groups exposed to cercariae (*post hoc* pair-wise Tukey test, $P < 0.05$). Low-infection and high-infection groups did not differ from each other (Tukey test $P > 0.05$; Fig. 1). Thus, physical condition was significantly reduced at 17 days PI to 20 or 120 cercariae, indicating a metabolic cost of parasitism.

AVOIDANCE OF THE COST OF PARASITISM EXPERIMENT

L_T did not differ among treatment groups (ANOVA, $F_{2,21}$, $P > 0.05$) and encysted metacercariae were present in all fish in the parasite-experienced treatment (mean \pm s.e. number of metacercariae per individual = 24.3 ± 1.3). Prior to the addition of stimuli, fish activity was normally distributed (Shapiro–Wilk test, $P > 0.05$) and did not significantly differ among treatments (ANOVA, $F_{2,21}$, $P > 0.05$).

Change (post-stimulus-pre-stimulus) in fish activity and change in vertical distribution conformed to a normal distribution (Shapiro–Wilk test: both, $P > 0.05$). Change in activity was significantly affected by treatment (ANOVA, $F_{2,21}$, $P < 0.05$). Experienced fish reduced activity in trials, whereas naïve fish and water-control fish increased activity (Fig. 2). Tukey *post hoc* pair-wise comparisons showed that experienced fish reduced their activity significantly more than water controls. There was no effect of treatment on change in vertical distribution (ANOVA, $F_{2,21}$, $P > 0.05$; Fig. 3).

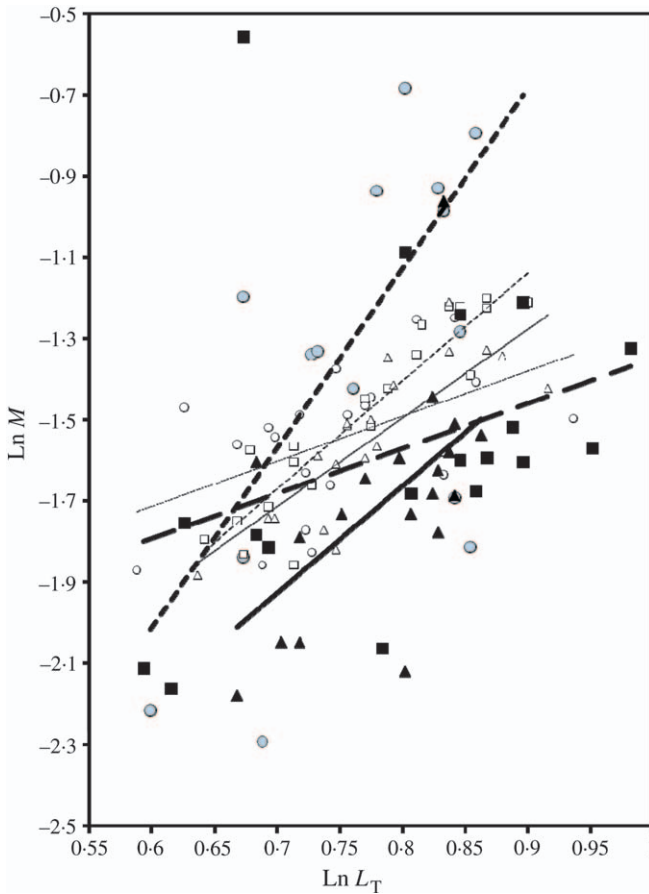


FIG. 1. The relationship between mass (M) and total length the (L_T) (ln, transformed data) of *Pimephales promelas* at the beginning (○, control; □, low-infection dose treatment; △, high-dose treatment) and at 17 days post-infection (●, control; ■, low-dose treatment; ▲, high-dose treatment). The curves were fitted by: initial control $y = 1.1110x - 2.3790$ ($r^2 = 0.2548$), initial low-dose treatment $y = 2.6607x - 3.533$ ($r^2 = 0.8573$), initial high treatment dose $y = 2.1851x - 3.2433$ ($r^2 = 0.6463$), after 17 days control $y = 4.4295x - 4.6694$ ($r^2 = 0.3755$), after 17 days low dose treatment $y = 1.1123x - 2.4595$ ($r^2 = 0.1149$) and after 17 days high-dose treatment $y = 2.6286x - 3.7666$ ($r^2 = 0.3321$).

DISCUSSION

This study demonstrated that *P. promelas* experienced a significant metabolic cost due to the developing metacercariae of *Ornithodiplostomum* sp. Moreover, fish learned to recognize and avoid parasitism risk after one exposure to cercariae.

Cercaria penetration causes injury to epidermal tissues (Poulin *et al.*, 1999) and metacercaria development leading to the encysted stage of strigeoid trematodes is associated with extensive damage to tissues (Goater *et al.*, 2005). Repairing this damage requires reallocation of metabolic resources away from somatic growth that probably contributed to the reduced growth and mass loss observed in infected fish in this study. Moreover, metabolic demand imposed

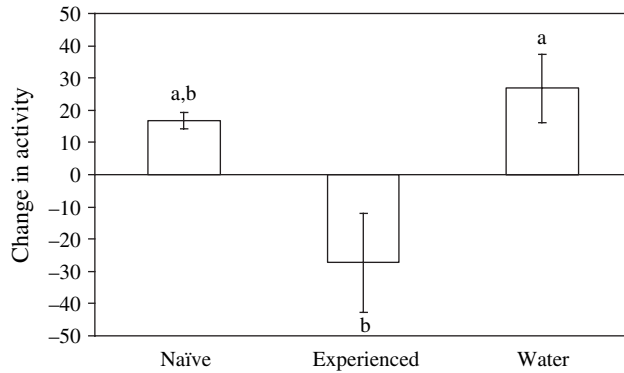


FIG. 2. Mean \pm S.E. change in activity for (1) cercariae-naïve *Pimephales promelas* in response to the odour and sight of dead cercariae, (2) cercariae-experienced *P. promelas* in response to the odour and sight of dead cercariae or (3) cercariae-naïve *P. promelas* in response to plain water (control). Shared lower case letters above bars indicate no difference ($P < 0.05$) in Tukey *post hoc* pair-wise comparisons.

by metacercaria development probably consumes the energy budget of the fish host. The growth and development of *O. ptychocheilus* metacercariae reached maxima at 1–4 weeks post-infection, corresponding to the period when the parasites are covered by a complex network of microlamellae (= modified microvilli) extending from the tegument into adjacent host tissue (Goater *et al.*, 2005). A similar pattern of growth combined with similar modifications to the tegument also occur in *Ornithodiplostomum* sp. (unpubl. obs.).

The most likely cause of the decline in *P. promelas* condition in the present experiment was recovery from the pathology of cercarial penetration and metacercarial migration, and subsequent metabolic demands of metacercariae growth and development. Sandland & Goater (2001) found no effect of infection on *P. promelas* L_T in their study of *O. ptychocheilus*. Physical condition, however, is a more sensitive measure of negative energy balance, particularly over an interval as short as 17 days. In this study, regression residuals of ln

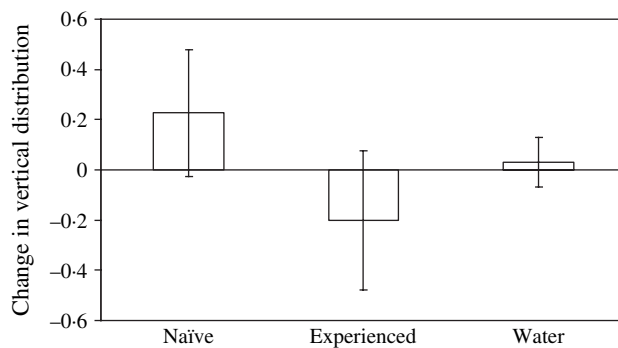


FIG. 3. Mean \pm S.E. change in vertical distribution for (1) cercariae-naïve *Pimephales promelas* in response to the odour and sight of dead cercariae, (2) cercariae-experienced *P. promelas* in response to the odour and sight of dead cercariae or (3) cercariae-naïve *P. promelas* in response to plain water (control).

M and $\ln L_T$ were used. Even when physical condition is estimated crudely by condition factor K ($K = 100ML_T^{-3}$), significant decline in condition in bluegill sunfish *Lepomis macrochirus* Rafinesque is correlated with infections of more than 50 metacercariae of blackspot *Uvulifer ambloplites* (Lemly & Esch, 1984).

Metacercaria development (size, time to encystment and time to size reduction) of *O. ptychocheilus* is affected at high levels of infection by intraspecific competition for finite resources of the host (Sandland & Goater, 2000). *Ornithodiplostomum ptychocheilus* metacercariae resulting from high-intensity exposure (average of 116 metacercariae per fish) grew and developed more slowly than metacercariae from relatively low-intensity exposure (average of 29 metacercariae per fish) because of food limitation (Sandland & Goater, 2000). Intraspecific food competition occurs among metacercariae because they are either unable to sequester more host tissue, or the host is able to limit parasite access to its tissues. In the current study, there was no evidence from fish condition of intraspecific competition between low (61.7% infectivity \times exposure to 20 cercariae = 12 metacercariae) and high (80.6% infectivity \times exposure to 120 cercariae = 97 metacercariae) exposure treatments. This suggests that as few as 12 metacercariae were sufficient to put experimental *P. promelas* into a negative energy budget and that additional metacercariae had no additive effect.

Parasite avoidance behaviours are well documented and have been previously observed in other fish and parasite systems (Poulin & FitzGerald, 1989; Karvonen *et al.*, 2004), but the mechanisms for detection (specifically for the avoidance of cercariae) are poorly understood. The present study is the first to show that fishes can detect cues associated with trematode cercariae, remember them and avoid them in future encounters. A single exposure to cercariae is sufficient to alter future responses of *P. promelas* to chemical and visual indicators of parasitism risk. Behavioural response was manifest as a reduction in activity, a behavioural strategy that has been shown to reduce the risk of parasite exposure in the other studies (Poulin *et al.*, 1991; Thiemann & Wassersug, 2000). Parasite-naïve fish did not reduce activity in response to thawed (dead) cercariae and their behavioural response did not differ from control fish. This latter finding suggests that naïve *P. promelas* do not innately recognize the general odour or sight of cercariae as indicators of parasitism risk. These results agree with those of Poulin *et al.* (1999) and Thiemann & Wassersug (2000) in that behavioural response to parasitism risk is similar in kind to behavioural responses to predator risk.

A reduction in activity may not always be the most appropriate behavioural response to the risk of cercarial infection if cercariae can be avoided altogether by avoiding the area. For example, rainbow trout *Onchorhynchus mykiss* (Walbaum) avoid cercariae by moving away from the source (Karvonen *et al.*, 2004). Increased activity may allow hosts to reduce infection by dislodging cercariae that have contacted the host but not yet attached and penetrated. Tadpoles of green frogs *Rana clamitans* show an explosive increase in activity when they encounter cercariae of *Echinostoma trivolvis* (Koprivnikar *et al.*, 2006). Immobilized tadpoles showed higher rates of infection than active tadpoles. Similarly, *Bufo americanus* and *Rana sylvatica* tadpoles perform burst swimming to escape attack by cercariae of *Ribeiroia* and *Echinostoma* (Taylor *et al.*, 2004). This appears to be another parallel between behavioural responses

to risk of predation and risk of parasitism. Flight (increased activity) can evade either form of risk if the risk is localized. When surrounded by risk, as in the present study or in studies of responses to chemical alarm cues (Chivers & Smith, 1998), then reduction in activity is an appropriate response.

An alternative explanation for these data is that reduced activity levels of infected fish were induced by the prior infection. Metacercariae-induced changes in fish behaviour are well known and include both increases and decreases in the activity of infected individuals (Barber *et al.*, 2000). Infected fish, however, did not differ in activity from non-infected fish during the pre-stimulus period. Further, *P. promelas* infected with *O. ptychocheilus* showed no reduction in overall activity (Shirakashi & Goater, 2005). Although the possibility of metacercariae-induced reduction in *P. promelas* activity cannot be dismissed entirely, the present data support the notion that the marked reduction in activity observed in experienced fish is probably a learned response to the test stimuli and not a by-product of infection.

Pair-wise comparisons between naïve and experienced fish in their reduction in activity failed to surpass the threshold of statistical significance. This is in part due to small sample size but in part due also to a decrease in activity by some parasite-naïve *P. promelas*. Control fish did not decrease activity. These data indicate that parasite-naïve fish detected a novel odour in the test stimulus and were cautious but not fearful. Because there was no evidence of an increase in activity (compared to water control fish), parasite-naïve fish did not perceive the cercariae as a source of food.

Aquatic, free-living cercariae use a variety of environmental cues to recognize the presence of a potential host (Haas, 1994). Specifically, turbulence, caused by host activity, is a good indicator of host presence (Haas, 1994). Therefore, reduced activity in the presence of visual and olfactory indicators of free-swimming cercariae leads to reduced parasitism risk (Poulin *et al.*, 1999). Concomitantly, reduction in activity reduces exposure to predation risk (Mathis & Smith, 1993). Thiemann & Wassersug (2000) showed that tadpoles of *R. sylvatica* and *R. clamitans* evaluate the risk of parasitism and predation independently and respond by additively adjusting the intensity of a single behavioural response, reduction in activity. Activity reduction in their study occurred in proportion to the degree of risk. Because predators pose a greater threat to tadpole survival than parasites, the degree of reduction of tadpole activity was reduced in the presence of parasites, yet reduced significantly further when tadpoles were also confronted with predators (Thiemann & Wassersug, 2000). Reduction in tadpole activity is an adaptive response to parasitism that parallels a similar yet stronger response to predation.

Wild *P. promelas* in natural populations should favour moving to the substratum to avoid parasites because cercariae tend to position themselves close to the water surface (Haas, 1994). This would be a second parallel between antipredator and antiparasite behavioural responses. Movement towards the substratum is a behavioural response to risk of predation that has been recorded in *P. promelas* exposed to predator cues and chemical alarm cues in skin extract (Lawrence & Smith, 1989; Chivers & Smith, 1998). In the present study, however, there was no effect of treatment on change in vertical distribution. Future work needs to examine this phenomenon more closely.

Predation risk and parasitism risk share certain features that make activity reduction a behavioural stratagem that reduces exposure to both risks. Predation risk differs from parasitism risk in that predation is an absolute loss of fitness, whereas fitness consequences of parasitism may be negligible and delayed past reproductive age. Behavioural trade offs between parasitism risk and other behaviours (*e.g.* foraging and reproduction) are likely to differ in scale and nature from trade offs between those same behaviours and predation risk. Parasite threat-sensitive behavioural decision-making is an area for future study.

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