

# Avian cestodes affect the behaviour of their intermediate host *Artemia parthenogenetica*: An experimental study

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## Abstract

The brine shrimp *Artemia parthenogenetica* (Crustacea, Branchiopoda) is intermediate host for several cestode species whose final hosts are waterbirds. Previous field studies have shown that brine shrimps infected with cestodes have a bright red colour and are spatially segregated in the water column. However, the ethological mechanisms explaining such field observations are unknown. Changes in appearance and behaviour induced by trophically transmitted parasites have been shown to increase the risk of predation by the final host. In this experimental study, we compared the behaviour of uninfected *Artemia* and those infected by avian cestodes. We found that parasitised individuals behave differently from unparasitised ones in several ways. In contrast to uninfected individuals, infected brine shrimps were photophilous and showed increased surface-swimming behaviour. These observations suggest that the modified behaviour (in addition to the bright red colour of the majority of the infected individuals) results in infected brine shrimps becoming more vulnerable to avian final hosts, which facilitates parasite transmission. We discuss our results in terms of the adaptive nature of behavioural changes and their potential implications for the hypersaline ecosystem.

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## 1. Introduction

The parasite manipulation of host behaviour is currently a widely studied phenomenon because of its ecological and evolutionary significance (see Combes, 1991, 2001; Poulin, 1995, 1998; Moore, 2002; Thomas et al., 2005; Jog and Watve, 2005). Recent studies emphasise the importance of gathering empirical data from diverse host–parasite systems (Thomas et al., 2005; Klein, 2005; Hurd, 2005; Rigaud and Haine, 2005; Poulin et al., 2005; Ponton et al., 2006). Cases when two or more trophically transmitted parasites co-occur in the same host population and one or more of them manipulate host behaviour are of particular interest because of the complexity and the diversity of interspecific interactions (e.g. Thomas et al., 1998; Cézilly et al., 2000; Babirat et al., 2004; Haine et al., 2005; Rigaud and Haine, 2005; Kostadinova and Mavrodieva, 2005). Parasite-induced alterations in the host behaviour may have major implications at the

ecosystem level (Combes, 1996; Thomas et al., 1999; Thomas and Renaud, 2001; Mouritsen and Poulin, 2005; Thompson et al., 2005) but this remains a largely unexplored area.

Among the trophically transmitted avian helminths, most previous studies on parasite-induced behavioural modifications in invertebrate intermediate hosts have focussed on trematodes (e.g. Helluy, 1983, 1984; Thomas et al., 1995; Babirat et al., 2004; Kostadinova and Mavrodieva, 2005) and acanthocephalans (e.g. Hindsbo, 1972; Moore, 1983; Cézilly et al., 2000). Studies on parasite manipulation in invertebrates infected with larval cestodes are few (Graham, 1963; Hurd and Fogo, 1991; Yan et al., 1994).

Brine shrimps of the genus *Artemia* (Branchiopoda: Anostraca) act as intermediate hosts for 13 species of avian cestodes; their parasitic transmission depends on predation by birds (see review in Georgiev et al., 2005). Cestodes have been reported to induce changes in colour and spatial distribution of infected brine shrimps in the field; these alterations are suspected to be associated with behavioural modifications following infection (Gabrion et al., 1982; Thiéry et al., 1990; Sánchez et al., 2006a). However, the effect of larval cestodes on *Artemia* behaviour has never been assessed. In this study, we explore possible causes of

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parasite-induced spatial segregation and colour change observed in the field by examining the behaviour of naturally infected and uninfected brine shrimps in the laboratory. Since making the upstream host more visible to predators is believed to be a major mechanism facilitating parasite transmission along food chains (Combes, 2001), we quantify the light/dark microhabitat preference and measure time spent at the water surface to test the prediction that infected brine shrimps become more vulnerable to aquatic birds. We also test the hypothesis that the association between the high cestode burden and the red colour of brine shrimps is due to the increased time spent at the surface (resulting in accumulation of photoprotective carotenoids, see Sánchez et al., 2006a). In addition, cestodes have been suggested to increase the buoyancy of infected *Artemia* by increasing their lipid content (Amat et al., 1991) and therefore surfacing behaviour could easily be confounded with negative geotaxis. Thus, we designed an experiment to separate the effects of phototaxis and geotaxis and to evaluate whether photophily or changes in buoyancy are responsible for surfacing behaviour; for this purpose, we used light stimuli to drive the movement of brine shrimp in the water column. Finally, we discuss the potential effect of cestodes on salt pan communities through their influence on *Artemia* behaviour.

## 2. Material and methods

### 2.1. The host–parasite system

Brine shrimps *Artemia* are well-studied crustaceans with a near worldwide distribution inhabiting extreme hypersaline environments such as salt lakes, coastal lagoons and salt pans (Persoone et al., 1980; Abatzopoulos et al., 2002). *Artemia* tends to be the dominant invertebrate in number and biomass in the places where it occurs (e.g. Sánchez et al., 2006b). In our study area, *Artemia* is intermediate host for 8 species of cyclophyllidean tapeworms; their adults infect several species of waterbirds, including shorebirds, flamingos, gulls and grebes (Georgiev et al., 2005). The prevalence of the cestode infection in brine shrimps is av. 27% (Georgiev et al., 2005), locally reaching up to 90% (unpublished data). Brine shrimps become infected by consuming cestode eggs (containing a larva termed an oncosphere) released into the water with the faeces of the definitive hosts. Brine shrimps are non-selective filter feeders consuming particles in suspension (Reeve, 1963a,b) ranging 6.8–27.5  $\mu\text{m}$  (Fernández, 2001). The oncosphere (20  $\mu\text{m}$  in diameter for *Flamingolepis liguloides*, see Robert and Gabrion, 1991) penetrates through the intestine wall into the hemocoel where it develops into a cysticercoïd (cestode larval stage containing scolex). The life cycle continues when an infected *Artemia* is predated by the final host.

### 2.2. Sampling, rearing and determination of infection status

Based on the observation that red colour in *Artemia* is associated with cestode parasitism (Thiéry et al., 1990; Robert and Gabrion, 1991; Amat et al., 1991; Sánchez et al., 2006a), we selected 50 red and 50 transparent *Artemia parthenogenetica*

in the field in order to compare the behaviour of infected versus non-infected individuals. *A. parthenogenetica* are frequently reared in the laboratory in conditions free of parasites (Hontoria and Amat, 1992), when the intense red colour of infected individuals found in the field has never been observed (F. Amat, personal communication). We selected adult individuals of the same size in order to control for age as these two variables are correlated (F. Amat, personal communication). We collected the samples with a net of 0.1 mm mesh from an evaporation pond of intermediate salinity at an industrial salt pan in the Odiel Marshes (SW Spain, 37°17'N, 06°55'W) in November 2003 (see Sánchez et al., 2006b, for details of the study area).

In the laboratory, on the day of collection, brine shrimps were introduced into a tank, 50 (length)  $\times$  10 (height)  $\times$  30 (width) cm, filled to within 1 cm of the top with water from the pond and under a natural photoperiod. After 24 h, we conducted a series of three different behavioural tests (see below) on each of the 100 individuals, one by one, alternating groups of 10 red and 10 transparent individuals. Once all the tests were finished, brine shrimps were killed by heating to 80 °C and preserved in 70% ethanol for identification of parasites (see Georgiev et al., 2005 for methods of cestode species identification).

### 2.3. Behavioural tests

#### 2.3.1. Experiment 1: light/darkness choice

This experiment was carried out with a petri dish divided into dark and light halves. We used black plastic to cover one half of the dish and illuminated the other half with a cold light source to prevent a thermal gradient. Each *Artemia* was individually placed in the middle of the dish and after 1 min we recorded its position. We then repeated the experiment covering the opposite side of the petri dish in order to confirm the light/dark preference. In cases in which the response of brine shrimp changed between the two trials (only 4 of 100 cases), we repeated the experiment. The light/dark preference was scored as a dichotomous variable. We used  $\chi^2$  tests to compare the response to light between transparent uninfected, transparent infected, and red infected individuals. When over 20% of the expected values in the contingency table were less than 5, we performed Fisher exact tests.

#### 2.3.2. Experiment 2: time at water surface

This experiment was carried out in a white shallow (50 (length)  $\times$  10 (height)  $\times$  30 (width) cm) tank that allowed light to penetrate the entire water column from above. Each *Artemia* was introduced individually into the tank. After 1 min, we recorded the time (in seconds, s) spent within 1 cm of water surface during the following 30 s. We used Kruskal–Wallis test for comparisons of median time at the water surface between transparent uninfected, transparent infected and red infected brine shrimps. For determining which pairs of groups were different, we performed multiple-comparison post hoc tests (Siegel and Castellan, 1988).

#### 2.3.3. Experiment 3: ability to descend in the water column

This was designed to separate the effects of phototaxis and geotaxis (and also the effects of the negative geotaxis and the

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