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Trematodes with a reproductive division of labour: heterophyids also have a soldier caste and early infections reveal how colonies become structured

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ABSTRACT

Recent findings have extended the documentation of complex sociality to the Platyhelminthes, describing the existence of a reproductive division of labour involving a soldier caste among the parthenitae of trematode parasites. However, all species examined to date occupy high positions in trematode inter-specific dominance hierarchies and belong to two closely related families, the Echinostomatidae and the Philophthalmidae (Superfamily Echinostomatoidea). Further, the two species documented as lacking soldiers also belong to the Echinostomatidae. Here, we examine four species of intermediate dominance, all belonging to the family Heterophyidae (Superfamily Opisthorchioidea): *Euhaplorchis californiensis*, *Phocitrema ovale*, *Pygidiopsis spindalis* and *Stictodora hancocki*, all of which infect the California horn snail, *Cerithideopsis californica* (= *Cerithidea californica*). We quantify morphology, distribution and behaviour of rediae from fully developed colonies. We also provide information on colony structure for three developing heterophyid colonies to better understand colony development. We discuss the implications of our findings, particularly with respect to how they suggest alternatives to the conclusions of other researchers concerning the nature of trematode sociality. Our analyses of morphological, distributional and behavioural patterns of developed colonies indicate that these heterophyid trematodes have a non-reproductive caste whose function is defence of the colony from invading trematodes. Hence, a soldier caste occurs for species lower in dominance hierarchies than previously known, and is present in at least two superfamilies of digenean trematodes, suggesting that selection for a soldier caste may be much more common among the Trematoda than previously recognised.

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1. Introduction

A complex social system has recently been documented in digenean trematodes (Hechinger et al., 2011; Leung and Poulin, 2011; Miura, 2012; Nielsen et al., 2014; Garcia-Vedrenne et al., 2016). As in the most complex animal societies (e.g., several types of insects (e.g., Wilson, 1971; Aoki, 1977; Crespi, 1992; Kent and Simpson, 1992; reviewed in Myles, 1999), snapping shrimp (Duffy, 1996), and naked mole-rats, (Jarvis et al., 1981)), the parthenita stages of some trematode species live in colonies with

morphologically and behaviourally distinct reproductive and non-reproductive castes (Hechinger et al., 2011; Leung and Poulin, 2011; Miura, 2012; Nielsen et al., 2014; Garcia-Vedrenne et al., 2016). Although the non-reproducing caste might have some other roles (e.g., Lloyd and Poulin, 2012; Galaktionov et al., 2015), it is clear that a major role is defence of colonies (Hechinger et al., 2011; Miura, 2012; Mouritsen and Halvorsen, 2015; Garcia-Vedrenne et al., 2016).

Digenean trematode colonies are formed in the first intermediate host, usually a mollusk. The colony is initiated by a single founder larva (miracidium) that infects the host, metamorphoses and clonally produces large numbers of daughter parthenitae. Some trematode species have rediae: parthenitae that possess a muscu-

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lar pharynx and a gut. Other species have sporocysts, which lack a pharynx and gut. Both kinds of parthenitae produce more parthenitae and then dispersive offspring (cercariae), which leave the colony to infect the next host in the life cycle. Once established, the colony blocks host reproduction and takes control of the host's energy allocation to serve the needs of the colony, primarily diverting energy to parasite reproduction (Rothchild and Clay, 1952; Kuris, 1974; Baudoin, 1975; Hechinger et al., 2009; Lafferty and Kuris, 2009). The colony commonly occupies the gonad and/or digestive gland of the host, taking up a large portion of the host's soft tissue (10–50%) (e.g., Hurst, 1927; Bernot and Lamberti, 2008; Hechinger et al., 2009). Given their extensive use and control of host resources, such conditions would lead to intense competition should another trematode invade the same molluscan host.

Typically, when two trematode species infect the same host, one kills the other. These antagonistic interactions are hierarchical. Dominant species fend off invasions or displace established colonies of subordinate species. This displacement may be via chemical mechanisms (known for some species with sporocysts (Basch et al., 1969; Walker, 1979)), but it most commonly occurs via predation by rediae (Lim and Heyneman, 1972; Lie, 1973; Combes, 1982; Kuris, 1990; Sousa, 1993). Until recently, this antagonism had been considered to occur via the actions of "totipotent" rediae, those that both reproduce and defend the colony (Lim and Heyneman, 1972; Lie, 1973; Kuris, 1990; Sousa, 1993; but see Lie, 1969).

However, recent studies have shown that several trematode species have a division of labour involving a caste of non-reproducing soldiers that are specialised for defence (Hechinger et al., 2011; Leung and Poulin, 2011; Miura, 2012; Nielsen et al., 2014; Garcia-Vedrenne et al., 2016). Despite being smaller than reproductives, soldiers have relatively large pharynxes to attack and kill invaders. Only soldiers readily attack heterospecific and even conspecific enemies. The small size of these soldiers likely facilitates dispersion throughout the host body, supported by the fact that soldiers are more active and disproportionately common in areas of the host where invasions occur. Small rediae have been long observed in trematode infections (e.g., Stunkard, 1930; Kuntz and Chandler, 1956). However, small rediae are classically considered solely as being immature reproductives that are generated early in colony development, to periodically replace dying reproductives, and to permit colony growth as the host body increases in size. The discovery that these small rediae are not solely immatures, and sometimes represent a soldier caste, has expanded our perspective on the nature of trematode infections in first intermediate hosts and opened up new research avenues examining the ecology and evolution of complex sociality.

Hechinger et al. (2011) predicted that soldier castes would most likely evolve in trematode taxa that are typically dominant in interspecific hierarchies. To adequately test this and other hypotheses concerning the evolution of sociality among trematode species, it is necessary to quantify social structure for trematode species encompassing a range of dominance positions and that are spread throughout the trematode phylogenetic tree. Despite there being over 150 families of Trematoda (Cribb and Bray, 2011), all trematodes so far examined for social structure belong to two closely related digenean families: Echinostomatidae and Philophthalmidae (Superfamily Echinostomatoidea) (Hechinger et al., 2011; Leung and Poulin, 2011; Miura, 2012; Nielsen et al., 2014; Garcia-Vedrenne et al., 2016). Echinostomoids tend to occupy high positions in trematode dominance hierarchies (Lim and Heyneman, 1972; Lie, 1973; Kuris, 1990). This restricted taxonomic sampling also includes the two species explicitly shown to lack soldiers (Garcia-Vedrenne et al., 2016). Colony social structure has not been examined for species in any of the other trematode superfamilies.

Here, we examine four trematode species that belong to the Family Heterophyidae of the Superfamily Opisthorchioidea (*Euhaplorchis californiensis*, *Phocitremonoides ovale*, *Pygidiopsoidea spindalis* and *Stictodora hancocki*). These species form colonies in the California horn snail, *Cerithideopsis californica* (= *Cerithidea californica*). The California horn snail is host for a diverse trematode guild that is characterised by a fairly well-resolved interspecific dominance hierarchy (Kuris, 1990; Sousa, 1993; Hechinger, 2010). Five of the most dominant species in this hierarchy (all in the Superfamily Echinostomatoidea) have been documented to have soldiers. The heterophyids studied herein have an intermediate position in the dominance hierarchy (they are subordinate to the echinostomatids and philophthalmids, but can eliminate or prevent infections of other, more subordinate, species in the guild (Kuris, 1990)). We also compare colony structure of a few recent, developing heterophyid colonies to fully developed colonies to shed light on the nature of colony development. We discuss the implications of our results, including alternative interpretations concerning the nature of trematode sociality. Our analysis of morphology, distribution, behaviour and colony development of these four heterophyid species indicates that they also have a soldier caste, and that trematode caste structure takes time to develop, becoming more pronounced with colony age.

2. Materials and methods

2.1. Study system and sample collection

California horn snails, *Cerithideopsis californica* (= *Cerithidea californica*), (Potamididae) were collected from Carpinteria Salt Marsh, Santa Barbara County, California, USA between July 2013 and May 2016. Snails were maintained in the laboratory for up to 7 weeks in mesh bags on running sea water tables until processing. Some infections were identified by inducing cercaria emergence, and then dissected. In other cases, the snails were dissected and, if infected with the appropriate species, immediately processed. We identified trematode species following Martin (1972) and additional unpublished observations.

We examined the four species that belong to the family Heterophyidae: *E. californiensis* (EUHA), *P. ovale* (PHOC), *P. spindalis* (PYGI), and *S. hancocki* (STIC). For simplicity and clarity, we will refer to each species by the codes formed by the first four letters of their genus, as above.

2.2. Redia morphology and distribution

Snails were collected between July 2013 and October 2015. We targeted three to five colonies (snails) for each of the study species. All the trematode colonies examined were producing cercariae. We followed the methods described in Garcia-Vedrenne et al. (2016). Briefly, we dissected snails by carefully cracking the shell with a hammer and divided the body into three different regions: mantle, basal visceral mass (middle), and the gonad/digestive gland. To ensure unbiased sampling of individuals to depict size-frequency distributions, we used a grid and random numbers to randomly sample approximately 30 rediae from each snail region. Sampled rediae were killed by immersion in hot water, fixed in 70% ethanol and mounted in glycerine. Digital pictures were taken with a Lumenera Infinity 3 camera mounted on an Olympus BX60 compound microscope. We measured body length and width to the nearest micron; we also measured pharynx width and length. We calculated total body and pharynx volumes by approximation to a cylinder.

We assigned each individual to a morph category based on the presence or absence of developing offspring, regardless of size.

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