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Cost of interspecific competition between trematode colonies

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Research Paper

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Abstract

In a range of trematode species, specific members of the parthenitae colony infecting the molluscan first intermediate host appear specialized for defence against co-infecting species. The evolution of such division of labour requires that co-infection entails fitness costs. Yet, this premise has very rarely been tested in species showing division of labour. Using *Himasthla elongata* (Himasthlidae) and *Renicola roscovita* (Renicolidae) infecting periwinkles *Littorina littorea* as study system, we show that the size of emerged cercariae is markedly reduced in both parasite species when competing over host resources. Cercarial longevity, on the other hand, is negatively influenced by competition only in *R. roscovita*. Season, which may impact the nutritional state of the host, also affects cercarial size, but only in *H. elongata*. Hence, our study underlines that cercarial quality is, indeed, compromised by competition, not only in the inferior *R. roscovita* (no division of labour) but also in the competitively superior *H. elongata* (division of labour).

Introduction

Different species of parasites utilizing the same host species may find themselves also infecting the same host individual and, hence, compete directly over host resources. For parasitic flatworms such as trematodes infecting a molluscan first intermediate host, the parasite–host biomass ratio is quite large, typically around 0.20 (Hechinger *et al.*, 2009). This predicts that interspecific trematode competition over host resources may be intensive, potentially affecting parasite fitness negatively. Accordingly, co-infecting colonies of larval trematodes (parthenitae) are frequently engaged in antagonistic interactions within the molluscan host, in which one species attempts to eliminate the other either directly by consumption or indirectly by producing substances that interfere with the growth and development of the competitor (Lie *et al.*, 1965; Basch *et al.*, 1970; Lim & Heyneman, 1972; Walker, 1979; Hechinger *et al.*, 2011; Leung & Poulin, 2011; Miura, 2012; Nielsen *et al.*, 2014; Garcia-Vedrenne *et al.*, 2017). In the former case, there exists a dominance hierarchy where trematodes that develop through a redial larva stage, equipped not only with a complete feeding apparatus (mouth, pharynx and stomach) but also appendages for locomotion, are competitively superior to species that develop through the largely immobile sporocyst stages lacking such structures (Sousa, 1993; Kuris & Lafferty, 1994; Galaktionov & Dobrovolskij, 2003).

During the last decade, a range of trematode species originating from three different families have been shown to have their intramolluscan redial colonies divided into two morphologically and functionally distinct groups or castes (Poulin *et al.*, 2019). The minor caste (soldiers) is primarily engaged in defending the colony against other invading parasites, whereas the considerably larger colony members are mostly engaged in producing the colony's cercarial dispersal stages (the reproductive caste). Although it is not generally accepted that these parthenitae colonies exhibit division of labour and, hence, emerge as socially organized (see Galaktionov *et al.*, 2015), available evidence suggests that the smaller colony members are those individuals mainly involved in antagonistic or predatory interactions with competitors (Hechinger *et al.*, 2011; Leung & Poulin, 2011; Miura, 2012; Nielsen *et al.*, 2014; Mouritsen & Halvorsen, 2015).

If such a predatory role by the smaller parthenitae is, indeed, an adaptation resulting from natural selection under competitive pressures from co-infecting parasite species (see Poulin *et al.*, 2019), it requires that the fitness of trematode colonies is negatively affected by co-infections. Surprisingly, this important evolutionary premise has been scrutinized in only two of the 15 socially organized systems so far identified, and demonstrated in just one of them. By using cercarial emission rate as a fitness parameter, Lloyd & Poulin (2012, 2013) found markedly reduced fitness in redial colonies of *Philophthalmus* sp. when the host snail (*Zeacumantus subcarinatus*) was shared with the competitor *Maritrema novaezealandensis*. In contrast, the cercarial production by redial colonies of *Himasthla elongata* infecting common periwinkles (*Littorina littorea*) appeared unaffected by competition from co-occurring *Renicola roscovita* colonies (Mouritsen & Andersen, 2017).

Albeit limited, these contradictive results raise concern about either the evolutionary premise of fitness costs of competition, or the application of cercarial emission rate as the only relevant fitness parameter. As stressed by Poulin *et al.* (2019), other fitness components can be evolutionary targeted – for instance, the duration of infection rather than the parasite's immediate reproductive rate during competition events (i.e. lifetime rather than short-term reproductive success). Additional and equally relevant fitness components can be envisaged, such as the quality rather than the number of emerged cercariae. The amount of glycogen allocated to non-feeding cercariae during development will determine their functional longevity following emergence from the molluscan host and, hence, their likelihood of reaching the next host in the life cycle (Ginetsinskaya, 1988; Galaktionov & Dobrovolskij, 2003). Furthermore, the sheer size of the cercarial dispersal stage is known to correlate positively with adult body size and, in turn, the fecundity of adult worms in the definitive host (Poulin, 1997; Trouvé *et al.*, 1998; Poulin & Latham, 2003). Hence, reduced cercarial quality may have serious repercussions on the parasite's integrated lifetime reproductive success, and, insofar as cercarial quality is negatively affected by competition, natural selection may drive the evolution of a distinct redial caste dedicated to the elimination of competitors.

Here, we address this issue by revisiting the *Himasthla*–*Renicola* competition within periwinkle host snails (Mouritsen & Andersen, 2017) in order to clarify whether or not cercarial quality (size and longevity) is influenced by co-infection. Because the energy available for the parasites may be influenced by host nutritional state (e.g. Seppälä *et al.*, 2008; Mouritsen & Andersen, 2017), host size and season were also included in the analysis as potentially confounding variables.

Material and methods

Collection and acclimation of animals

Between September 2017 and January 2018, common periwinkles (*L. littorea*) were collected in the littoral zone of Knebel Vig, Denmark (56°13′41.2″N, 10°27′47.4″E). Here, the periwinkles are known to host infrapopulations of the trematodes *R. roscovita* and *H. elongata*, of which the former develops sporocysts (no division of labour) and the latter develops rediae (division of labour possible). Snails were distributed in storage containers (40 × 30 × 20 cm, approximately 25 individuals per container) kept in an illuminated temperature-controlled room. Each container was filled with 10 l of seawater that was replaced weekly (21–26 psu), an oxygen supply and a number of small rocks with microalgal films serving as food supply.

The snails were gradually acclimated after collection – that is, the water temperature in the storage containers was changed from approximately *in situ* water temperature at collection to 16°C. The final storage temperature of 16°C was chosen to minimize (1) temperature stress during the cercarial emission procedure (see below); and (2) unintentional emission of cercariae in storage containers (especially pronounced around 20°C and above; Galaktionov & Dobrovolskij, 2003). The acclimation procedure also ensured a similar starting point in terms of temperature for all snails prior to experimentation regardless of date of collection. The length of the acclimation period as well as the temperatures involved depended on the *in situ* water temperature at the point of collection. Snails collected during autumn (late September to late October) were stored for five days at *c.* 12°C, followed by five days at 16°C. Snails collected during winter (mid-December to mid-January) were stored for five days at 5°C, followed by five days at 10°C and, finally, five days at 16°C.

Following acclimation, snails single-infected by *R. roscovita* or *H. elongata* as well as snails infected by both these trematode species (double infections) were identified by shedding of cercariae. Snails were incubated individually in seawater-filled glass jars (70 ml) at *c.* 20°C under light for a few hours and emerged cercariae were species determined according to Werding (1969) under a stereomicroscope. Infected snails were then uniquely marked (numbered) and returned to infection-specific storage containers at 16°C until further treatment. When planned measurements and experiments had been performed (see below), the shell height of each snail was determined to the nearest 0.1 mm using an electronic calliper (mean/range: 23.2/17.7–29.3 mm) followed by dissection to verify infection status.

Cercarial dimensions

Himasthla elongata and *R. roscovita* cercariae for size measurements were obtained by incubating infected snails individually in seawater-filled glass jars at 22°C for 3 h. Water and shed cercariae were then poured into Petri dishes and placed in an oven at 60°C for 1 h in order to heat-kill the trematode larvae. Corresponding body length (tail excluded) and width of 20 haphazardly chosen cercariae from each individual trematode colony (i.e. 20 *Himasthla* and 20 *Renicola* cercariae from double-infected hosts) were then measured under a stereomicroscope (×80) using an ocular micrometre. Also, the diameter of the relatively large ventral sucker of all *H. elongata* cercariae was measured. This procedure was carried out for infected snails collected both during autumn and winter, and, in total, 1620 cercariae from 20 single-infecting *Himasthla* colonies (14 in autumn, six in winter), 25 single-infecting *Renicola* colonies (ten in autumn, 15 in winter) and ten double infections (six in autumn, four in winter) were measured.

The exclusion of the tail in body measurements is justified because it is lost prior to metacercarial formation, and, hence, it is the tail-less cercarial body that transforms into the adult worm and determines its fecundity (our focus, see Introduction). Moreover, due to the high energy content of the tail that determines cercarial swimming stamina (Lawson & Wilson, 1980; Ginetsinskaya, 1988), properties of the tail will be an integral part of cercarial longevity (see below).

Cercarial longevity

Cercariae for survival experiments were obtained as described above. Petri dishes containing emerged cercariae (average age: 1.5 h) were subsequently placed in a temperature-controlled room at 24°C and inspected under a stereomicroscope for presence of irreversibly grounded cercariae every second hour. Irreversibly grounded and, hence, functionally dead cercariae were defined as individuals found on the bottom of the dish that either (1) presented markedly reduced tail movements; (2) had lost their tail; or (3) laid motionless. After 12 h, the total number of cercariae present in each Petri dish was recorded. Prior to the cercarial counts, host snails were measured (as above) and returned to their storage containers.

The above protocol was conducted for infected snails collected both during autumn and winter in order to account for different nutritional states of host snails. In total, 16 single-infecting *Himasthla* colonies (11 in autumn, five in winter), 17 single-

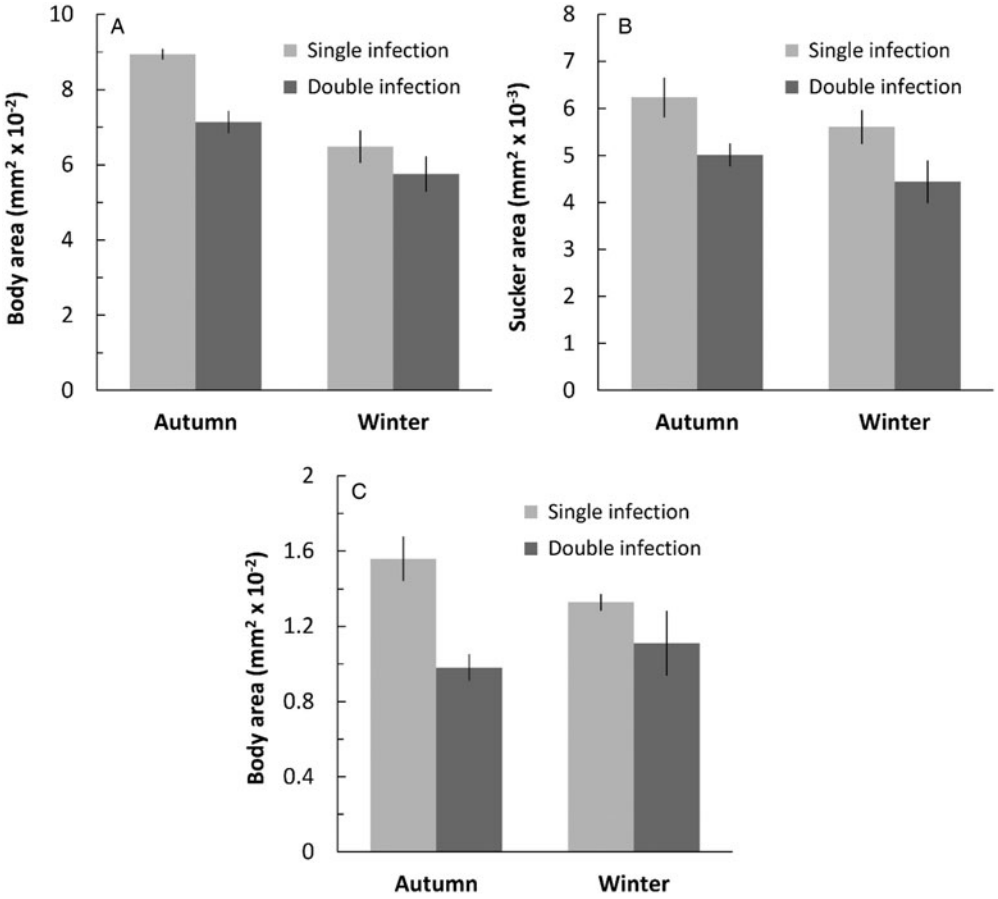

Fig. 1. Body dimensions (mean of mean ± standard error) of cercariae emerging from single- and double-infected periwinkles *Littorina littorea* during autumn (September–October) and winter (December–January). (A) Projected body area ($mm^2 \times 10^{-2}$) of *Himasthla elongata* cercariae; (B) ventral sucker area ($mm^2 \times 10^{-3}$) of *H. elongata* cercariae; (C) projected body area ($mm^2 \times 10^{-2}$) of *Renicola roscovita* cercariae. $N_{Himasthla,\ autumn}$: single/double = 14/6; $N_{Himasthla,\ winter}$: single/double = 6/4; $N_{Renicola,\ autumn}$: single/double = 10/6; $N_{Renicola,\ winter}$: single/double = 15/4.

infecting *Renicola* colonies (five in autumn, 12 in winter) and eight double infections (five in autumn, three in winter) were processed. On average, the longevity of 75.4 ± 14.4 (standard error) cercariae from each individual trematode colony was monitored.

Data analyses

All statistical analyses were carried out using Statistical Package for the Social Sciences (IBM SPSS 24.0; IBM Corporation, New York). The influence of competition (single-/double-infected), season (autumn/winter) and host size (shell height) on cercarial dimensions were analysed using ANCOVA (analysis of covariance), entering host size as covariate. The mean projected body area (length × width) and mean ventral sucker area across cercariae within individual colonies were used as the unit of analysis. Hence, mean values depicted in figures represent mean of mean. A similar ANCOVA model was applied for cercarial longevity by interring LT50 values (time passed at the point of 50% mortality) as the unit of analysis. Two separate ANCOVAs were conducted, one for each of the two trematode species involved (*H. elongata* and *R. roscovita*). LT50 values were obtained from cercarial survival curves elaborated for each individual trematode colony processed.

Preliminary full-model ANCOVAs were executed to evaluate the significance of two- and three-way interactions. As none of these interaction terms were statistically significant, neither regarding cercarial dimensions ($P \geq 0.188$) nor cercarial longevity ($P \geq 0.576$), we only present summary statistics from reduced-model ANCOVAs, including interaction mean squares and associated degrees of freedom in the error variance. All analyses were preceded by tests of homogeneity of error variance (Levene's test) and evaluation of normality. Because equality of error variance was violated in the case of *Renicola* body size, these data were rank-transformed prior to analysis in order to meet requirements. In any case, all mean values reported on in the following are based on untransformed data.

Results

Cercarial dimensions

The projected body area of *H. elongata* cercariae was significantly affected by both competition and season, whereas host size was uninfluential (fig. 1a, table 1). When the host snail was co-infected by *R. roscovita*, emerging *H. elongata* cercariae were roughly 20% smaller than cercariae emerging from a host infected solely by *Himasthla*. Similarly, cercariae emerging during winter were about 24% smaller than those emerging during autumn. On the other hand, the size of the ventral sucker was affected statistically only by competition; season as well as host size appeared uninfluential (fig. 1b, table 1). Interestingly, competition

Table 1. Summary statistics of reduced-model ANCOVAs, including body size (projected area) or ventral sucker area of *Himasthla elongata* or *Renicola roscovita* cercariae as dependent variable, competition (single/double infection) and season (autumn/winter) as independent fixed factors, and host size (shell height of *Littorina littorea*) as a covariate.

	Body area				Sucker area			
Source	df	F	*P*	Partial η^2	df	F	*P*	Partial η^2
Himasthla								
Competition	1	19.736	**<0.0005**	0.432	1	5.065	**0.033**	0.163
Season	1	45.382	**<0.0005**	0.636	1	1.556	0.223	0.056
Host size	1	0.001	0.977	<0.0005	1	0.109	0.744	0.004
Error	26				26			
Renicola								
Competition	1	15.671	**<0.0005**	0.336				
Season	1	0.386	0.539	0.012				
Host size	1	1.546	0.223	0.048				
Error	31							

Statistically significant effects are indicated by *P*-values in bold. Partial η^2 denotes effect size, i.e. the proportion of variance explained.

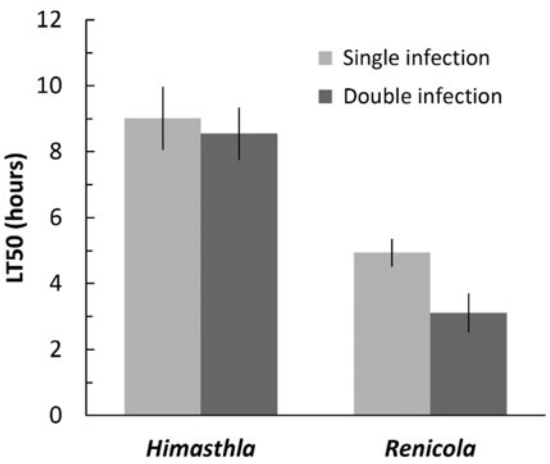

Fig. 2. Survival rates (LT50) of *Himasthla elongata* and *Renicola roscovita* cercariae from single- and double-infected periwinkles *Littorina littorea*. $N_{Himasthla}$: single/double = 16/8; $N_{Renicola}$: single/double = 17/8.

Table 2. Summary statistics of reduced-model ANCOVAs, including survival (LT50) of *Himasthla elongata* or *Renicola roscovita* cercariae as dependent variable, competition (single/double infection) and season (autumn/winter) as independent fixed factors, and host size (shell height of *Littorina littorea*) as a covariate.

	LT50			
Source	df	F	*P*	Partial η^2
Himasthla				
Competition	1	0.052	0.821	0.003
Season	1	1.218	0.283	0.057
Host size	1	0.006	0.937	<0.0005
Error	20			
Renicola				
Competition	1	6.896	**0.016**	0.247
Season	1	0.212	0.650	0.010
Host size	1	2.142	0.158	0.093
Error	21			

Statistically significant effects are indicated by *P*-values in bold. Partial η^2 denotes effect size, i.e. the proportion of variance explained.

explained considerably more variation in cercarial body size (43%) than in sucker size (16%) (table 1).

Similar to *H. elongata*, the body size of *R. roscovita* was strongly negatively affected by competition (28% reduction), whereas host size had no bearing (fig. 1c, table 1). Opposite to *H. elongata*, however, no significant effect of season could be demonstrated on the cercarial size of *Renicola*.

Cercarial longevity

The functional longevity (LT50) of *H. elongata* cercariae was affected neither by competition, season or host size (fig. 2, table 2). In contrast, the longevity of *R. roscovita* cercariae was significantly negatively affected by competition with *H. elongata* (table 2). Competition reduced renicolid longevity by 37%, explaining about 25% of the variation in the species' functional lifespan (table 2).

Overall, the functional longevity of *H. elongata* cercariae was 2–3-fold greater than that of *R. roscovita* cercariae (fig. 2). This substantially longer lifespan of *Himasthla* was highly significant for single infections (Student's *t*-test, $t_{20.7} = 3.901$, $P = 0.001$) as well as double infections ($t_{14} = 5.513$, $P < 0.0005$).

Discussion

The present results demonstrate that intramolluscan competition between trematode colonies may negatively affect size and longevity, and, thus, the quality of the emerged cercarial dispersal stages. However, these effects appear species-specific.

Cercariae emerging from *H. elongata* colonies co-occurring with *R. roscovita* were significantly smaller than those emerging from single infections. Similarly, the size of emerged *Himasthla* cercariae was smaller during winter when host food (mainly green algae) is scarce than during autumn when food is more abundant. Together, this suggests that colonies of *H. elongata* respond to nutrient limitation – either as a consequence of interspecific exploitative competition or reduced host food availability – by reducing the size of the already large dispersal stages (fig. 1). In contrast, cercarial longevity was unaffected by both competition and seasonally induced energy shortage, maintaining the already extraordinary long lifespan (fig. 2). Hence, under nutritional stress *H. elongata* appears to launch a transmission strategy that prioritizes the probability of reaching the next host in the life cycle by producing the same amount of dispersal stages (see Mouritsen & Andersen, 2017) with unchanged energy density (i.e. unchanged longevity, this study) at the expense of cercarial size. Although larger cercariae may release greater fecundity among the resulting adult worms (Poulin, 1997; Trouvé *et al.*, 1998; Poulin & Latham, 2003), this promise of future egg reproduction is worthless if the transmission to second intermediate hosts fails.

The impact of competition and season on overall body size of emerged *Himasthla* cercariae was mirrored also in the size of the ventral sucker as a relatively rigid and perhaps more true-to-scale structure than the remaining body. Statistically, however, this was only significant for competition (table 1). Considering the limited sample size, this may, in the case of season, be due to a type II error. On the other hand, suckers are formed early during cercarial ontogenesis (Galaktionov & Dobrovolskij, 2003) and, therefore, less likely to correlate tightly with the availability of host food at the point of emergence: cercariae emitted by the snails collected in winter may have been formed from redial germ balls already during late autumn.

Like *H. elongata*, interspecific competition reduced the body size of cercariae that emerged from *R. roscovita* colonies. As opposed to *H. elongata*, also the longevity of the *Renicola* cercariae was reduced under competition. Because competition also has a marked negative effect on cercarial production in *Renicola* (Mouritsen & Andersen, 2017), *R. roscovita* colonies appear particularly sensitive to competitive interactions; the dispersal stages are affected negatively both quantitatively and qualitatively, which is bound to cause a substantial reduction in transmission success. That competition also negatively impacts renicolid cercarial quality, underlining that *H. elongata* does not diminish *R. roscovita* fitness solely through direct predation (see present Introduction and discussion in Mouritsen & Andersen, 2017).

Opposite to *H. elongata*, there was no seasonal effect on the size of *R. roscovita* cercariae emerging from double-infected snails. Nor was cercarial longevity affected by season. Together, this suggests that the condition of the host (or the food available to the host) at the point of shedding has little bearing on renicolid cercarial quality, in agreement with similar findings on also the number of emerged cercariae (see Mouritsen & Andersen, 2017). The pattern may follow from the fact that the entire renicolid sporocyst colony, as well as the contained cercariae, are formed more or less simultaneously early during infection (Wright, 1956; Galaktionov & Dobrovolskij, 2003; Galaktionov *et al.*, 2015), and, hence, cercariae shed by winter snails are likely to have developed to maturity earlier during the season.

Clearly, intramolluscan competition between co-infecting *H. elongata* and *R. roscovita* involves significant fitness losses to both parties. *Renicola roscovita* is especially afflicted, as the quantity as well as the quality of dispersal stages is reduced. However, also the fitness of the generally competitively superior *H. elongata* colonies is negatively influenced: cercarial quality in terms of body size is reduced, which is likely to affect this parasite's lifetime reproductive success (see Introduction). Aside from emphasizing that the number of dispersal stages is not the only relevant fitness parameter in colonies of larval trematodes, our study demonstrates that the evolutionary premise for natural selection to maintain and further optimize a distinct group of defenders in redial colonies of *H. elongata* is, indeed, in place.

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Conflicts of interest. None.

Ethical standards. The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals.

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