Effects of initial (larval) size and host body temperature on growth in trematodes

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Abstract: For ectotherms, temperature is an important correlate of variation in body size within species. Variation in body size among related species could also be attributable in part to temperature if the different species grow under different thermal regimes. The roles of both initial (larval) size and host body temperature on final (adult) size of parasitic trematodes were investigated in a comparative analysis. Trematodes are a good model group for such a study, with almost half of known species growing at high and constant temperatures in endothermic vertebrates and the rest at lower and fluctuating temperatures in ectothermic vertebrates. The relative growth of trematodes, i.e., their growth relative to the size of their larvae, varied greatly among species. Increases in body size from the cercarial larval stage to the adult stage averaged almost 40-fold (maximum 1300-fold), whereas increases in size from the metacercarial stage to the adult stage averaged 6-fold (maximum 110-fold). There were no differences between trematodes in ectothermic hosts and trematodes in endothermic hosts with respect to these measures of relative growth, however, which suggests that host type and the thermal regime provided by the host have no effect on the growth of trematodes from larval to adult stages. In contrast, the final (adult) body size of trematodes appears to be determined to some extent by their initial (larval) size, independently of the type of host in which they developed.

Résumé : Chez les ectothermes, la température est en corrélation avec les différences de taille chez une espèce. La variation de la taille du corps chez des espèces apparentées peut aussi être attribuable en partie à la température, si les différentes espèces font leur croissance à des régimes thermiques différents. Le rôle que jouent la taille initiale (larvaire) et la température de l'hôte dans le réglage de la taille définitive (adulte) du corps des trématodes parasites a été examiné au moyen d'une analyse comparative. Les trématodes constituent un bon groupe modèle pour ce genre d'étude puisque près de la moitié des espèces connues font leur croissance à des températures élevées et constantes chez des vertébrés endothermes et les autres espèces croissent à des températures fluctuantes plus basses chez des vertébrés ectothermes. La croissance relative des trématodes, i.e. leur croissance par rapport à la taille de leurs larves, varie beaucoup d'une espèce à l'autre. De la larve cercaire jusqu'au stade adulte, l'animal augmente sa taille d'un facteur de 40 en moyenne (maximum 1300), alors que de la larve métacercaire à l'adulte, la croissance se fait selon un facteur de 6 en moyenne (maximum 110). Il n'y a pas de différence entre les trématodes parasites de vertébrés ectothermes et les trématodes parasites des vertébrés endothermes quant aux mesures de la croissance relative, ce qui laisse croire que le type d'hôte et le régime thermique de l'hôte n'influencent pas la croissance des trématodes du stade larvaire au stade adulte. En revanche, la taille définitive des trématodes (adultes) semble dépendre, jusqu'à un certain point, de la taille initiale des larves, indépendamment du type d'hôte chez lequel se fait leur développement.

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Introduction

For most organisms, body size is the single most important life-history trait, as demonstrated by its effects on fecundity, mortality, and most other key parameters determining an organism's fitness (Peters 1983; Schmidt-Nielsen 1984; Stearns 1992). The great variation in body size among species within a taxon therefore provides a quick indication of the range of life-history strategies adopted by these spe-

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cies, each determined by the specific living conditions and selection pressures they experience. Body size also varies within species as a result of plasticity in development under different environmental conditions. For instance, in ectotherms, temperature usually correlates with growth rate and maximum body size at a given developmental stage (Atkinson 1994, 1995). In a review of studies on ectothermic animals, Atkinson (1994) found that in the vast majority of cases, body size is reduced at higher temperatures despite faster growth rates. In other words, as the rearing temperature increases, animals take less and less time to attain smaller final sizes. The optimal adult body size of ectotherms is determined to a great extent by rearing temperature (Sibly and Atkinson 1994). To date, the potential of temperature to explain variation in body size among related ectotherm species has not been explored in a large-scale comparative analysis.

Parasitic helminths like trematodes (digeneans) offer a unique opportunity to conduct such a study. Approximately half of the known species of trematodes exploit endothermic

vertebrates (Gibson and Bray 1994), where the temperatures they experience are high (36–38°C in placental mammals, 39–42°C in birds) and constant. In contrast, the remaining species live in ectothermic vertebrates at temperatures that fluctuate widely around much lower mean values. Trematode species range in adult body size from less than 1 mm to several centimetres long. Could this variation be partly due to the different rearing temperatures offered by different hosts? Poulin (1997) found no significant differences in adult body size between trematode parasites of endothermic vertebrates and their relatives in ectothermic vertebrates; host body size was also shown not to correlate with trematode adult size. However, that comparison focused only on the *absolute* adult body sizes of trematodes, not on their adult body sizes *relative* to larval sizes. It may be that growth rates and relative increments in body size, rather than final adult body size per se, are affected by the body temperature of the host.

As implied above, the final (adult) size of a trematode will depend not only on the rate at which it grows toward that final size, but also on its initial (larval) size upon arriving in the vertebrate host. The typical life cycle of trematodes includes three different host species and several developmental stages (Kearn 1998). The first intermediate host is almost invariably a snail, in which a new batch of larvae is produced by asexual multiplication. These larvae, or cercariae, leave the snail to find their next host. They are short-lived, do not feed, and usually possess a tail for swimming. Upon entry into the second intermediate host (either an invertebrate or an ectothermic vertebrate), they shed their tail, often migrate to a specific location within the host, encyst, and become metacercariae. The metacercarial cyst consists of lipid, polysaccharide, and protein layers that isolate the metacercaria from the host (Smyth 1994). Acquisition of resources from the second intermediate host is thus not an option, and the energy reserves left from the cercarial stage will provide for metacercarial maintenance, excystment, and transition to the adult stage in the next host. In fact, the metacercarial stage is generally seen as a late addition to the trematode life cycle, involving no growth (at least in most species) but serving to prolong the infective life of the cercaria and enhance its chances of ingestion by the next host (Pearson 1972). The life cycle is completed when a metacercaria, along with the second intermediate host, is ingested by a suitable definitive host, which is either an ectothermic or endothermic vertebrate, depending on the trematode species. Eggs produced by adult worms in the definitive host are released in host faeces; larvae hatched from these eggs infect snails to begin the cycle anew. There are many variations on this basic life cycle, but for most trematodes all growth from the cercarial or metacercarial stage to the adult stage occurs within the definitive host and is subject to conditions experienced within that host. In addition to host influences on growth rate, the final (adult) size reached by a trematode may be determined, i.e., constrained, by its initial (larval) size, a possibility never tested before.

The objectives of this study were (*i*) to compare the relative growth of trematodes in ectothermic and endothermic hosts, and (*ii*) to determine whether the initial (larval) size of a trematode has any bearing on its final (adult) body size. The results will reveal which contributes most to trematode adult body size, larval size or the thermal regime during growth that is provided by the host.

Methods

Data were obtained from life-cycle studies and new species descriptions published since 1940 in the following journals: *Journal of Parasitology*, *Journal of Helminthology*, *Systematic Parasitology*, *Folia Parasitologica*, *International Journal for Parasitology*, *Zeitschrift für Parasitenkunde*, and *Proceedings of the Helminthological Society of Washington*. In addition, a few other studies from R.P.'s reprint collection also contributed to the dataset. These sources should provide a random sample of trematode species for which life-history data are available. Although thousands of trematode species have been described, most are known only from their adult stage. Three criteria were used to include trematode species in the dataset. First, data on body sizes of the adult and either the cercarial or metacercarial larval stage, or both, had to be available. Second, body-size data had to come from naturally infected host species and not from experimental infections of laboratory hosts. This is important because commonly used laboratory hosts are often immunosuppressed and thus provide unnatural growing conditions for trematodes. Third, only trematode species with the typical three-host life cycle and with hermaphroditic adults were included; schistosomes and a few other trematode taxa with atypical life cycles were thus excluded.

Methods used for the preparation and fixation of trematode specimens vary from study to study, and they can affect the accuracy of measurements of body length or width. This is not really a problem in this study, since for each trematode species we used measures of relative growth rate from one developmental stage to the next that were taken from the same study (see below). Measurements of worm sizes that we recorded from the literature were either means or the midpoints of ranges based on the examination of several individuals. The length and width (µm) of the cercaria (excluding the tail), metacercaria, and adult were recorded for each species, as well as the length and width of the metacercarial cyst (the latter two dimensions are the same in species where the cyst is spherical). Given that the worms are flat, the best measure of their body size is their surface area. This was obtained separately for cercariae, metacercariae, and adult worms, using the formula for the surface area of an ellipse, $\pi(L/2)(W/2)$, where L and W are the length and width, respectively. Similarly, the volume of the metacercarial cyst was calculated as the volume of an ellipsoid, $(\pi LW^2)/6$, where L and W are the length and width, respectively. Areas and volumes were $\log_{10}$-transformed for all analyses described below.

Relative growth from one developmental stage, t_1, to a subsequent stage, t_2, was calculated as (log area at t_2) – (log area at t_1). This difference was computed for three developmental periods: cercaria to metacercaria, cercaria to adult, and metacercaria to adult. The use of log-transformed data on surface areas of trematodes at different stages allows for comparisons across species without a spurious scaling effect. Relative growth computed this way measures the proportional increase in size, not the absolute growth, and can thus

be compared among species that differ widely in actual larval or adult sizes. Negative values indicate a reduction in size, zero indicates no growth, 1 indicates a 10-fold increase in size, 2 indicates a 100-fold increase, etc.
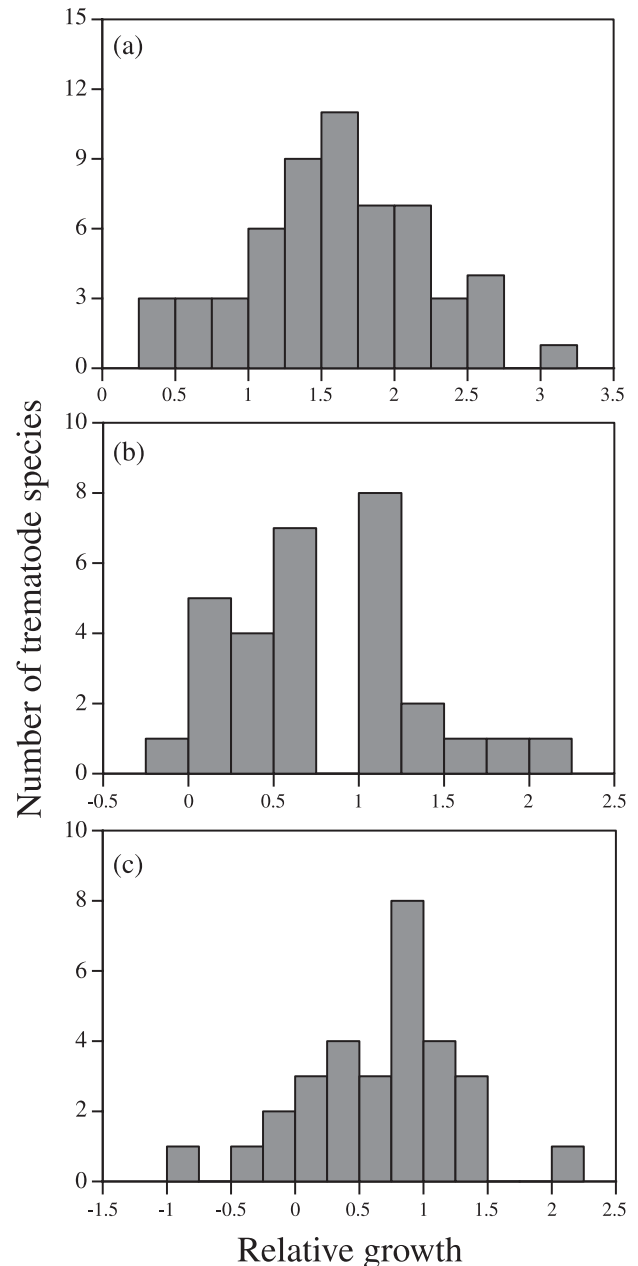
In the first instance, ANOVAs were used to compare relative growth between trematodes with ectothermic hosts and those with endothermic hosts, and Pearson's correlation coefficients were used to assess the relationships between body sizes at different developmental stages across trematode species. These statistical procedures assume that trematode species are independent, which might be true if the effect of hosts (i.e., developmental temperature) outweighs phylogenetic influences. However, similarities among trematode species due to common ancestry make them non-independent in a statistical sense, and the analyses were therefore repeated while controlling for potential phylogenetic influences. The phylogenetically independent contrasts method (see Felsenstein 1985; Harvey and Pagel 1991) was used. The phylogeny of trematodes is still not fully resolved. Here we constructed a working phylogeny using proposed relationships among families and higher taxa from Cribb et al. (2001), with additional information from the Appendix in Brooks and McLennan (1993). Independent contrasts were computed between sister taxa in the trematode phylogeny, using the Comparative Analysis by Independent Contrasts program, version 2.0 (Purvis and Rambaut 1994). Contrasts between sister taxa that differed with respect to a dichotomous variable (e.g., whether the definitive host is ectothermic or endothermic) were computed following the recommendations of Burt (1989) so that no taxon was used in more than one contrast. The mean value of these contrasts was compared with zero, as expected from the null hypothesis, using one-group two-tailed Student's t tests. Relationships between contrasts in continuous variables (surface areas of the cercaria, metacercaria, and adult worm and volume of the metacercarial cyst) were assessed using correlation forced through the origin (see Garland et al. 1992).

Results

Data were obtained for 57 trematode species from 24 families, although data on all variables were not available for all species; the full dataset is shown in Appendix A. Of these, 27 species used ectotherms as definitive hosts and 30 used endotherms. Relative growth from cercaria to adult varied widely across species (Fig. 1). Using back-transformation of the log-based values, the size of worms increased from less than 2-fold to more than 1300-fold from cercaria to adult, with an average increase of almost 40-fold. Relative growth from metacercaria to adult was less spectacular, with a maximum of >110-fold and a mean of about 6-fold, but was also quite variable (Fig. 1). Interestingly, in one species the adult was smaller than the metacercaria (relative growth <0). Negative values for relative growth were more common from cercaria to metacercaria; at the other extreme, the metacercaria of one species was >160-fold larger than its cercaria (Fig. 1).

There were no significant differences in relative growth from cercaria to adult ($F_{[1,55]} = 0.03$, $P = 0.873$) or from metacercaria to adult ($F_{[1,28]} = 0.08$, $P = 0.781$) between trematodes using ectothermic vertebrates as definitive hosts

Fig. 1. Frequency distribution of relative growth values among trematode species for three different periods during the life cycle, cercaria to adult (*a*), metacercaria to adult (*b*), and cercaria to metacercaria (*c*). Relative growth from one developmental stage, t_1, to a subsequent stage, t_2, was calculated as (log body surface area at t_2) – (log area at t_1); all body surface areas are calculated in square micrometres. Thus, negative values indicate a reduction in size, zero indicates no growth, 1 indicates a 10-fold increase in size, 2 indicates a 100-fold increase, etc.
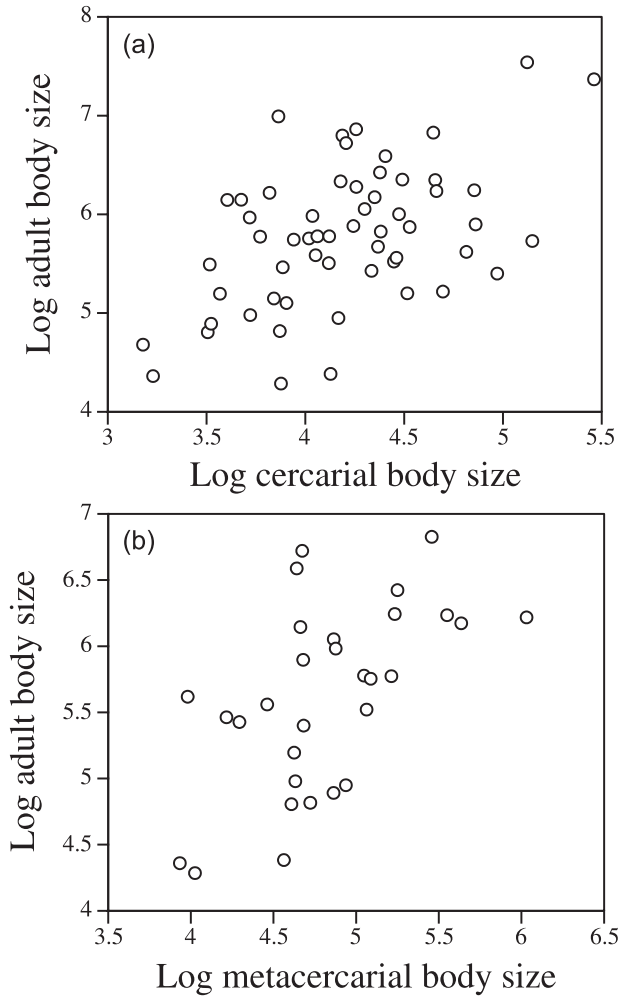

and those using endotherms. There was also no difference in relative growth from cercaria to metacercaria ($F_{[1,28]} = 0.078$, $P = 0.783$) between trematode species using invertebrates as second intermediate hosts and those using vertebrates. Actual sizes of various developmental stages did not differ between trematode species using different types of host (all $P \geq 0.45$), except in metacercarial surface area, with trematodes in ectothermic definitive hosts having

Table 1. Interspecific correlation-coefficient matrices among sizes of trematodes at different developmental stages.

	Metacercarial surface area	Metacercarial cyst volume	Adult surface area
Across species values			
Cercarial surface area	0.202 (30)	0.107 (43)	0.506** (57)
Metacercarial surface area		0.744** (20)	0.577** (30)
Metacercarial cyst volume			0.063 (43)
Across phylogenetic contrasts			
Cercarial surface area	0.282 (24)	0.408* (30)	0.525** (41)
Metacercarial surface area		0.835** (16)	0.693** (24)
Metacercarial cyst volume			0.191 (30)

Note: Numbers in parentheses are sample sizes.
*$P < 0.05$.
**$P < 0.001$.

Fig. 2. Relationship between adult body size and both cercarial body size (*a*) and metacercarial body size (*b*) across species of trematodes. Body size is measured as body surface area (μm^2). Each data point represents a different trematode species.

cercarial stage to the metacercarial stage, there were no associations between cercarial size and either metacercarial size or cyst volume (Table 1). Both cercarial size and metacercarial size were positively and significantly correlated with adult size (Table 1, Fig. 2). There is much scatter in these relationships (Fig. 2), and the best of these two predictors (metacercarial size) explained only about 33% of the variation in adult size; still, these results suggest that larval size is an important determinant of adult size. In contrast, the volume of the metacercarial cyst, though correlated with the surface area of the metacercaria, did not relate to adult body size (Table 1).

As in the analyses across species values, analyses based on phylogenetically independent contrasts also indicate that there is no difference in relative growth from cercaria to adult ($N = 9$ contrasts, $t = 0.201$, $P = 0.846$) and from metacercaria to adult ($N = 6$ contrasts, $t = 0.146$, $P = 0.890$) between trematode taxa using ectothermic definitive hosts and their sister taxa using endotherms. There was also no difference in relative growth from cercaria to metacercaria between trematode taxa using invertebrates as second intermediate hosts and their sister taxa using vertebrates ($N = 5$ contrasts, $t = 1.345$, $P = 0.250$). In analyses across species values, trematodes in ectothermic definitive hosts had slightly but significantly larger metacercariae than those in endothermic definitive hosts; using phylogenetic contrasts, this difference does not exist ($N = 6$ contrasts, $t = 1.488$, $P = 0.197$), but five of the six contrasts showed that metacercariae in the trematode taxa using ectotherms were larger than those in their sister taxa using endotherms. There is thus a possibility that larger metacercariae are indeed associated with the use of ectothermic hosts, and that our analysis lacked the power to detect this difference. Absolute sizes of other developmental stages did not differ between sister trematode taxa using different types of host (all $P \geq 0.31$).

Except for minor differences involving the volume of the metacercarial cyst, relationships between the sizes of trematodes at different stages in their development based on phylogenetic contrasts were essentially the same as those derived from species values (Table 1). Again, both cercarial size and metacercarial size were positively and significantly correlated with adult size (Table 1), although there is again much scatter when these variables are plotted one against another (Fig. 3). The relationship between cercarial size and adult size is greatly influenced by a single outlier in the top right corner of the plot in Fig. 3. However, repeating the analysis

slightly but significantly larger metacercariae than those in endothermic definitive hosts ($F_{[1,28]} = 6.255$, $P = 0.0185$).
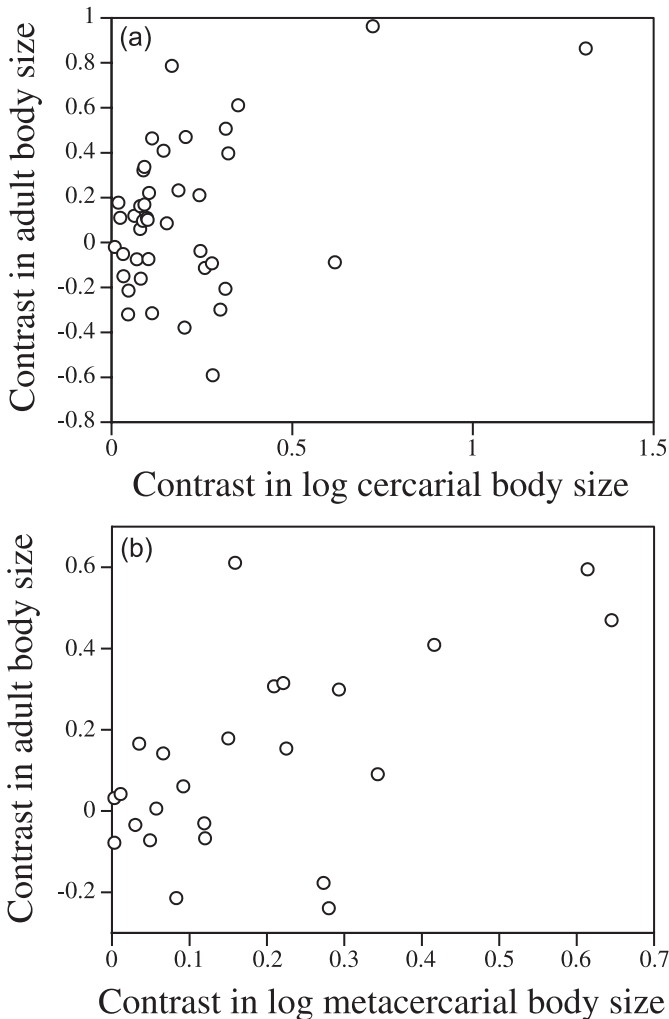
There were some relationships between the sizes of trematodes at different stages in their development (Table 1). Interestingly, although little growth is expected from the

Fig. 3. Relationship between adult body size and both cercarial body size (*a*) and metacercarial body size (*b*) across species of trematodes. Body size is measured as body surface area (μm^2). Each data point represents an independent phylogenetic contrast between sister taxa in the trematode phylogeny.

after excluding this point still gives a positive relationship ($r = 0.393$, $N = 40$, $P = 0.014$). Thus, larval trematode size, measured at either the cercarial or the metacercarial stage, remains a significant determinant of adult body size even after the possible confounding influence of phylogeny is controlled for.

Discussion

The relationship between external temperature and within-species variation in body size in ectothermic organisms is so widespread that it can be seen as a biological law (Atkinson 1994). At the interspecific level, the role of temperature in determining variation in body size among species is not as clear. Parasitic trematodes are an ideal group of ectotherms for such an investigation, since they grow inside either an ectothermic definitive host or an endothermic one. Our results, however, suggest that host type and the thermal regime provided by the host had no effect on the relative growth of

trematodes from larval to adult stages. Instead, the final (adult) body size of trematodes appeared to be determined to some extent by their initial (larval) size, independently of the type of host in which they developed. Larval size did not explain a substantial portion of the variation in adult size, and possibly other influential factors are involved; the type of definitive host used, and the rearing temperature experienced inside that host, do not appear to figure among them, however. These results add weight to the view that the biology of parasites is not necessarily determined by that of their hosts (Brooks and McLennan 1993).

There was a weak tendency for trematode species using ectothermic definitive hosts to have larger metacercariae than trematodes using endothermic hosts. Given that the adult body sizes of trematodes do not differ between species using ectotherms and species using endotherms (see also Poulin 1997), this would suggest that trematodes in endotherms must increase their size to a greater extent than trematodes in ectotherms to make up for their smaller initial size. The difference in metacercarial body size was not supported by analyses of independent contrasts, however, and there was no hint of a difference in relative growth between trematodes in ectothermic and endothermic hosts. Thus, the suggestion of host effects on trematode growth and size finds no support in our results, which are based only on data from a small number of trematode species because so few life cycle studies are available. Given that these few species cover a broad range of taxa, the results are most likely valid.

Ectothermic and endothermic vertebrate definitive hosts differ with respect to factors other than body temperature, and these may obscure any effect of rearing temperature on trematode growth. For instance, endothermic birds and mammals have higher metabolic rates than ectothermic fish, amphibians, and reptiles, and therefore require a higher intake of nutrients and energy. It is possible that trematodes in birds and mammals have access to more food simply because their hosts ingest food in greater quantity or of higher quality. Trematodes do not feed on host food, however, although intestinal trematodes do sometimes include host gut contents in their diet (Roberts and Janovy 1996). They feed mainly on blood, as well as tissue and mucus from the wall of their habitat (gut, bile ducts, urinary bladder, etc.). Differences in the amount of resources available to trematodes in ectothermic and endothermic hosts may therefore be too small to matter. Other potential differences between ectothermic and endothermic hosts include the efficiency of host immune responses, but nothing is known about how these may influence parasite body size.

The positive relationship between larval (either cercarial or metacercarial) size and adult size across trematode species suggests that the initial body size when the trematode enters a definitive host determines to a large extent what final size will be reached. In contrast, in a comparative study of schistosome trematodes parasitic in mammalian definitive hosts, Loker (1983) found an almost significant *negative* correlation between adult size and cercarial size (though his analysis did not account for potential phylogenetic effects). Schistosomes are unusual trematodes in many respects; in particular, they have a two-host life cycle in which cercariae penetrate the definitive host directly. They have no metacercarial stage, and the cercariae assume a greater role in

dispersion than in other trematodes. This may have led to a range of trade-offs between cercarial size and other life-history traits (Loker 1983). In the three-host trematodes investigated here, these trade-offs would be different.

For instance, there might be a trade-off between the number and size of cercariae produced asexually within the first intermediate host (snail) if cercarial size is a key determinant of adult body size. Despite the potential for certain trematode species to increase their body size 100- or 1000-fold relative to their cercarial or metacercarial size, our results show that having larger larvae still provides a head start toward a larger adult body size. Adult body size is the main determinant of reproductive output, in terms of egg number or size, in trematodes (Poulin 1997; Trouvé et al. 1998) as well as other parasitic organisms (Poulin 1998). We might thus expect investments in cercarial production to be balanced between high numbers, to increase transmission success, and large size, which ensures higher rates of future reproduction. The hypothesized trade-off between the number and size of cercariae produced assumes, of course, that the potential effects of the size and diet of snail hosts are standardized in comparisons among trematode species. No such trade-off exists among schistosomes (Loker 1983), but this has not been explored among other trematodes with the typical three-host cycle.

Improving the head start toward a large adult size in other ways than by compromising the number of cercariae produced should also be strongly favoured by selection. Indeed, although cercarial size does not correlate with metacercarial size, the relative growth between these developmental stages is generally positive and produces, on average, an almost 5-fold increase in size. This occurs in spite of the very limited opportunities for obtaining resources from the second intermediate host in which the cercaria-to-metacercaria transition takes place.

The factors determining the body size of parasitic animals have been elucidated in other groups. For instance, in analyses controlling for phylogenetic effects in ectoparasites of fish, which are exposed to external water temperatures, taxa inhabiting high latitudes tend to have larger adult body sizes than their relatives from warmer waters (Poulin 1995, 1996, 1998). For internal parasites, like nematodes, space restrictions may be more important, and indeed host body size is often a correlate of parasite body size (Morand et al. 1996). No such correlation exists for trematodes, however (Poulin 1997). It is well documented that there is variation in adult morphology among conspecific trematodes growing in different host species (Blankespoor 1974; Bray and des Clers 1992; Pérez Ponce de León 1995). The present results do not exclude the possibility that host effects shape trematode growth, but they rule out host endothermy per se as a determinant of adult trematode size, suggesting instead that adult body size is mainly an extrapolation of larval size.

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Appendix A

Table A1. Data on the 57 trematode species included in the analysis.

	Cercarial surface area (μm^2)	Metacercarial surface area (μm^2)	Metacercarial cyst volume (μm^3)	Adult surface area (μm^2)	Intermediate host[a]	Definitive host[b]
Allocreadium fasciatusi	1 508.0	—	5 884 962.4	47 852.9	1	1
Allocreadium handiai	71 534.2	171 003.6	10 248 869.1	1 754 332.3	1	1
Allocreadium ictaluri	16 081.1	47 124.0	9 202 793.6	5 260 216.5	1	1
Ascocotyle pachycystis	3 204.4	40 543.9	7 672 467.9	63 904.9	2	2
Brachylaima ruminae	22 431.0	431 071.5	—	1 493 526.9	1	2
Bunoderella metteri	44 414.4	286 270.4	72 776 123.2	6 707 316.0	1	1
Caecincola latostoma	6 936.7	—	2 224 973.3	140 140.5	2	1
Cardiocephalus longicollis	288 922.0	—	—	23 326 380.0	2	2
Cephalogonimus salamandrus	15 079.7	—	1 132 383.4	2 158 354.6	2	1
Cephalogonimus vesicaudus	17 517.6	—	1 047 200.0	760 466.7	2	1
Cephalophallus obscurus	13 430.3	36 442.6	4 914 509.6	24 190.3	1	2
Cephalouterina dicamptodoni	13 201.0	111 420.0	22 836 399.3	599 888.5	1	1
Conspicuum icteridorum	7 304.2	—	4 290 744.9	9 817 500.0	1	2
Cryptogonimus spinorum	8 011.1	—	14 358 871.3	126 174.5	2	1
Curtuteria australis	140 900.8	—	6 370 641.2	537 213.6	1	2
Diplostomum baeri	5 899.1	163 363.2	—	593 762.4	2	2
Dollfusinus frontalis	23 884.8	177 535.0	—	2 657 195.1	1	2
Echinostoma ilocanum	15 382.6	—	547 517.2	6 275 110.4	1	2
Euryhelmis squamula	11 260.7	—	65 450 000.0	384 846.0	2	2
Genarchopsis goppo	10 420.7	122 522.4	—	569 415.0	1	1
Gigantocotyle explanatum	132 839.4	—	5 203 733.2	34 653 026.1	1	2
Glypthelmins pennsylvaniensis	5 222.1	—	22 449 350.0	926 835.6	1	1
Haematoloechus coloradensis	11 506.1	—	2 572 446.8	600 403.7	1	1
Hemiurus luehei	3 337.9	72 889.0	—	77 754.6	1	1
Holorchis pycnoporus	10 869.9	75 227.2	—	961 262.8	1	1
Lacunovermis conspicuus	14 702.7	86 527.5	—	89 146.8	1	2
Macroderoides spiniferus	24 103.9	—	3 605 182.9	668 532.5	2	1
Meiogymnophallus multigemmulus	7 539.8	10 597.4	—	19 314.6	1	2
Monorchis parvus	5 258.3	42 831.0	1 150 349.2	95 426.1	1	1
Mosesia chordeilesia	7 690.6	16 422.7	3 534 964.4	290 481.8	1	2
Neopechona cablei	28 902.7	28 902.7	—	363 247.5	1	1
Nezpercella lewisi	46 030.7	353 997.8	20 613 844.4	1 716 099.0	2	1
Notocotylus gippyensis	45 356.8	—	1 893 759.3	2 223 467.4	1	2
Notocotylus tadornae	33 693.7	—	1 629 514.4	743 302.6	1	2
Opisthioglyphe locellus	21 618.2	19 635.0	1 949 820.9	267 036.0	1	2
Ornithodiplostomum ptychocheilus	3 694.5	42 117.1	35 340 054.8	157 109.1	2	2
Paramacroderoides echinus	28 071.0	115 629.7	26 246 183.0	332 318.4	2	1
Paryphostomum radiatum	25 427.3	43 674.5	2 412 748.8	3 885 373.8	2	2
Paryphostomum segregatum	18 101.5	—	958 933.6	1 894 227.7	2	2
Petasiger novemdecim	8 733.6	—	633 392.4	553 992.9	2	2
Petasiger variospinsus	65 349.2	9 544.2	601 448.8	415 845.7	2	2
Pharyngostomoides adenocephala	4 727.1	—	—	1 406 062.4	1	2
Pharyngostomoides procyonis	3 278.7	—	—	310 429.3	1	2
Phyllodistomum bufonis	18 064.2	—	3 053 635.2	7 257 096.0	1	1
Plagioporus hypentelii	49 662.4	—	6 981 469.3	165 002.3	1	1
Plagioporus shawi	19 939.1	73 077.2	3 808 303.5	1 130 976.0	1	1
Plagiorchis neomidis	32 792.0	—	4 251 946.7	158 247.9	1	2
Plagitura salamandra	30 993.8	—	733 040.0	2 247 814.8	1	1
Pleurogenoides ovatus	6 591.9	1 070 539.5	—	1 652 290.2	1	1
Pleurogonius malaclemys	93 600.0	48 108.9	18 816 613.2	251 147.4	1	1
Prosthodendrium anaplocami	1 693.5	8 572.6	65 450.0	22 972.9	1	2
Psilostomum magniovum	72 834.9	47 792.0	11 064 524.4	790 858.5	1	2

Table A1 (*concluded*).

	Cercarial surface area (μm^2)	Metacercarial surface area (μm^2)	Metacercarial cyst volume (μm^3)	Adult surface area (μm^2)	Intermediate host[a]	Definitive host[b]
Pygidiopsis ardeae	7 422.0	52 778.9	3 901 867.2	65 659.4	2	2
Renicola lavi	29 794.1	—	—	1 001 385.0	2	2
Strigea elegans	4 029.1	45 945.9	39 316 076.8	1 399 582.8	2	2
Telogaster opisthorchis	23 326.4	—	8 181 250.0	470 061.9	2	1
Textrema hopkinsi	13 141.3	—	33 974 347.3	319 642.1	2	1

[a]1, invertebrate; 2, vertebrate.
[b]1, ectotherm; 2, endotherm.