# Adaptive division of growth and development between hosts in helminths with two-host life cycles

**Daniel P. Benesh,**[1,2,3] iD **James C. Chubb,**[4] **and Geoff A. Parker**[4]

[1]*Department of Molecular Parasitology, Humboldt University 10115, Berlin, Germany*

[2]*Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB) 12587, Berlin, Germany*

[3]*E-mail: dbenesh82@gmail.com*

[4]*Department of Evolution, Ecology and Behaviour, University of Liverpool, Liverpool L69 7ZB, United Kingdom*

**Parasitic worms (helminths) with complex life cycles divide growth and development between successive hosts. Using data from 597 species of acanthocephalans, cestodes, and nematodes with two-host life cycles, we found that helminths with larger intermediate hosts were more likely to infect larger, endothermic definitive hosts, although some evolutionary shifts in definitive host mass occurred without changes in intermediate host mass. Life-history theory predicts parasites to shift growth to hosts in which they can grow rapidly and/or safely. Accordingly, helminth species grew relatively less as larvae and more as adults if they infected smaller intermediate hosts and/or larger, endothermic definitive hosts. Growing larger than expected in one host, relative to host mass/endothermy, was not associated with growing less in the other host, implying a lack of cross-host trade-offs. Rather, some helminth orders had both large larvae and large adults. Within these taxa, however, size at maturity in the definitive host was unaffected by changes to larval growth, as predicted by optimality models. Parasite life-history strategies were mostly (though not entirely) consistent with theoretical expectations, suggesting that helminths adaptively divide growth and development between the multiple hosts in their complex life cycles.**

**KEY WORDS:** Acanthocephala, adaptive decoupling hypothesis, Cestoda, comparative analysis, life-history model, Nematoda.

Animals with complex life cycles occupy different niches as larvae and adults, and helminths (parasitic worms belonging to Platyhelminthes, Nematoda, or Acanthocephala) provide a remarkable example of such ontogenetic niche shifts. Helminths commonly infect different hosts in succession, exploiting one or more intermediate hosts as larvae before sexually reproducing in a definitive, or final, host (Chubb et al. 2010). Transmission is normally trophic, with a prey host being consumed by the predator next host. In the predator definitive host (DH), helminths often grow extensively, for example, the sheep tapeworm (*Moniezia* and its relatives) first infects an oribatid mite, then enters sheep DHs as larval cysts less than 0.5 mm in diameter before growing to an adult length of several meters. By contrast, other helminths, such as the pork tapeworm (*Taenia solium*) and diverse acanthocephalans, spend months growing as

larvae in the prey intermediate host (IH); some helminths even complete all their growth as larvae (Benesh et al. 2013). Parasite growth can cause host pathology through nutrient theft or tissue damage. So, what explains the diversity of helminth life-history strategies?

Life-history strategies of complex life-cycle organisms are expected to be shaped by the growth and mortality rates of larvae and adults (Werner and Gilliam 1984; Rowe and Ludwig 1991; Day and Rowe 2002). Helminths with two-host life cycles likely experience different conditions in the IH and DH, and several models explore how they should divide growth and development between hosts (Choisy et al. 2003; Parker et al. 2003, 2009; Iwasa and Wada 2006; Ball et al. 2008). These models relate fitness to body size (size is commonly proportional to fecundity in helminths; e.g., Skorping et al. 1991; Trouvé et al. 1998).
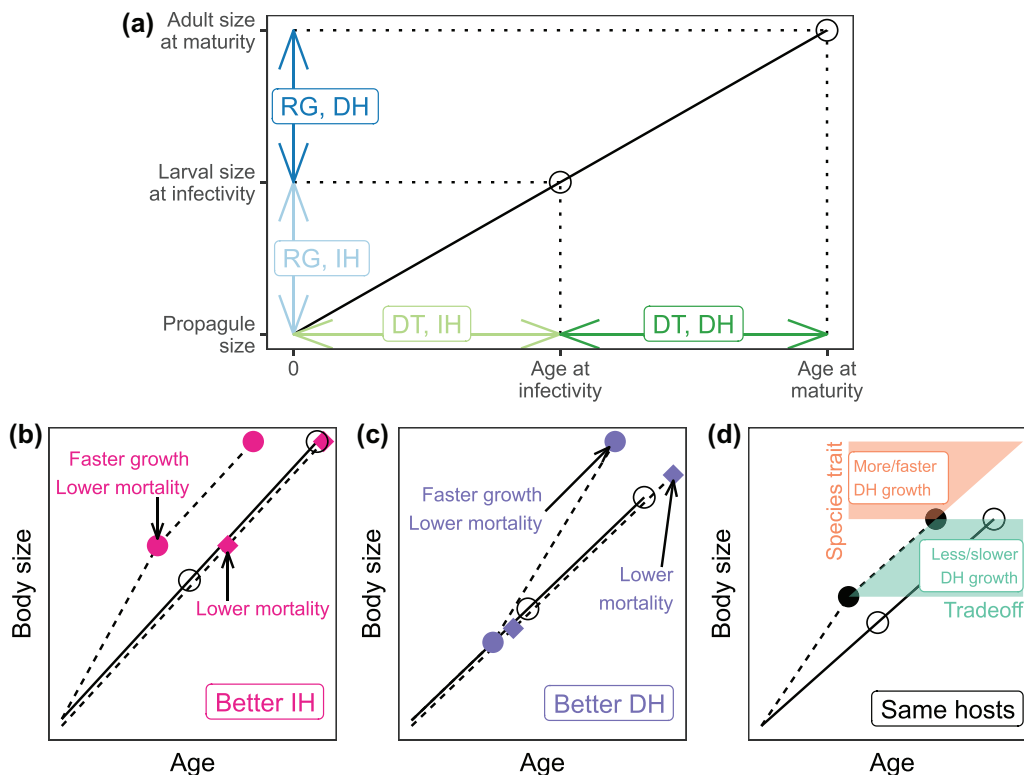
**Figure 1.** (a) Division of helminth growth and development in a two-host life cycle. Parasites grow to an infective size in the intermediate host (IH) and then to a reproductive size in the definitive host (DH). As helminths generally grow several orders of magnitude from egg to adult, often exponentially, body size is on a log scale, such that changes represent relative growth (RG). Changes in age between stages are developmental times (DT). Time spent waiting for transmission to the DH after reaching infectivity in the IH is not shown. In panels (b) to (d), filled circles and dotted lines represent changes from the baseline expectation. (b) When IHs facilitate faster parasite growth and/or lower parasite mortality, parasites are predicted to shift growth to the IH and reach larger sizes at infectivity, although this does not affect size at sexual maturity in the DH. (c) When DHs facilitate faster growth and/or lower mortality, parasites should grow to larger sizes at sexual maturity and size at infectivity in the IH may be reduced. Table A1 in the Supporting Information summarizes the theory underlying these predictions. (d) Even with the same IH and DH, some parasite species may grow faster or larger. In theory, faster-than-expected growth as larvae should not affect growth rate and maturation size as adults (decoupled stages, dotted line). Alternatively, growth could be a species-level trait (e.g., leading to more and/or faster growth in both hosts relative to expectations; final size in DH falls in orange-shaded area) or subject to cross-stage trade-offs (e.g., more/faster larval growth results in less/slower adult growth than expected; teal shaded area).

Then, they predict optimal parasite growth, given the growth and mortality rates in each host, usually assuming helminths stop growing at infectivity in the IH host and at sexual maturity in the DH. In general, higher growth rates and lower mortality rates, which may be size dependent, favor extended parasite growth in each host (Ball et al. 2008; Parker et al. 2009).

A schematic outline of helminth size and development in a two-host life cycle is shown in Figure 1a, whereas Figure 1b,c shows how changes in growth-to-mortality rate ratios (i.e., how rapidly and safely parasites can grow in each host) are predicted to affect life-history strategies. The assumptions and equations underlying these predictions are laid out in Section A in the Supporting Information ("Life-history models"), although we also note that the effect of size- or age-dependent mortality on optimal larval growth and development can be more complex than in Figure 1, depending on the model (Table A1 in the Supporting Information). First, consider worm size. Larval size at infectivity is increased by higher growth/mortality rate in the IH (Fig. 1b), whereas adult size at sexual maturity is increased by higher growth/mortality rate in the DH (Fig. 1c). Size at maturity is independent of the size attained at transmission from the IH (Fig. 1b) (Benesh et al. 2013). There is also an interaction between growth in the DH and in the IH (Parker et al. 2009): the optimal larval size is decreased by high growth/mortality rate in the DH (Fig. 1c). Developmental times can also depend on both hosts (Ball et al. 2008). The time needed to reach the size at maturity in the DH (i.e., prepatent period) can be decreased by higher growth/mortality rate in the IH and the associated in-

crease in the larval size at transmission (Fig. 1b). And because larval size is decreased by high growth/mortality rate in the DH (Parker et al. 2009), this may reduce development time in the IH (Fig. 1c).

Parasite growth and mortality rates can be determined by host size. In larger hosts, parasites might experience more competition (Lester and Mcvinish 2016) or be targeted by more sophisticated immune responses (Brace et al. 2017). Then again, larger hosts provide worms with more energy and/or space for growth (George-Nascimento et al. 2004; Poulin and George-Nascimento 2007; Hechinger 2013), perhaps with lower mortality, because they generally live longer (McCoy and Gilooly 2008) and may be able to tolerate large parasites. Accordingly, larger hosts, particularly endotherms (Poulin et al. 2003; Benesh et al. 2021b; but see Poulin and Latham 2003), often harbor larger worms, both within (e.g., Dezfuli et al. 2001; Barber 2005; Benesh 2010) and across parasite species (Arneberg et al. 1998; Poulin et al. 2003; Trouvé et al. 2003; Randhawa and Poulin 2009). Worms that infect large IHs might also infect large DHs, because big prey are eaten by big predators (Bersier and Kehrli 2008; Brose et al. 2019). A correlation between IH and DH size might explain why helminths with large larvae commonly have large adults (Poulin and Latham 2003; Poulin et al. 2003; Benesh and Valtonen 2007; Benesh et al. 2013). Considering both hosts jointly is essential for testing life-history predictions (Fig. 1b,c).

Variation in parasite growth and/or survival could partly reflect adaptations to efficiently exploit host resources or escape host defenses. Some adaptations may be useful in multiple hosts, such as avoiding conserved immune responses like respiratory burst (Buchmann 2014). Alternatively, there could be performance trade-offs between hosts (Gandon 2004; Hammerschmidt and Kurtz 2005). For example, trematodes (*Schistosoma mansoni*) that were experimentally selected for higher growth in the IH (cercarial production in snails) had reduced fecundity in the mouse DH (Gower and Webster 2004). Other experiments, however, have found selection at one parasite life stage (i.e., in the IH host, or in the DH) to have little impact on the other stage (Ferguson et al. 2003; Hafer-Hahmann 2019), suggesting traits in successive hosts are genetically decoupled and can evolve independently (Benesh 2016). Such decoupling is likelier on a longer, macroevolutionary scale, as selection and mutation break down cross-stage pleiotropy over time (Ebenman 1992; Moran 1994). Host generalism in helminths provides an example; the diversity of host species infected at one life stage does not limit the hosts infected at the next stage (Benesh et al. 2021a). Whether helminth growth in consecutive hosts is decoupled or constrained by performance trade-offs has not been tested (Fig. 1d).

We used a compilation of acanthocephalan, cestode, and nematode life cycles to test hypotheses about parasite life-history strategies. First, we examined whether worms that infected large IHs were more likely to infect large, endothermic DHs. Second, we investigated whether parasite growth and development changed with host "quality" as predicted by life-history theory (Fig. 1b,c). Third, we tested whether overperformance in one host was associated with underperformance in the other host (Fig. 1d). Our analysis is the first to explore how IH and DH traits together shape helminth life histories.

## Methods
### PARASITE LIFE-HISTORY AND HOST TRAITS
Parasite growth and development were obtained from a life-cycle database for acanthocephalans, cestodes, and nematodes (Benesh et al. 2017). The database does not include trematodes, whose life cycles usually include an asexually reproducing larval stage that is not trophically transmitted. We focused on species with two-host cycles (which were the most common), so we considered growth and development at two life stages: first IH and second DH. Note that stage refers to the "host in the cycle," not ontogenetic stages within hosts (like, e.g., acanthor, acanthella, cystacanth).

There were 634 species in the life-cycle database with two-host life cycles, but 16 had cycles that are only partially known, for example, larvae in the IH have been reported, but the DH is not known with certainty. We also excluded some cestodes, like *Echinococcus* spp., that asexually reproduce as larvae (21 species). In these species, growth in the DH is hard to quantify, because the initial size depends on how many asexual clones from the larval stage establish infection.

We converted parasite lengths and widths to biovolumes based on a stage's shape (e.g., volume of a cylinder for thread-like worms, an ellipsoid for eggs, or a ribbon for flatworms). Helminth biovolumes can overestimate mass (Llopis-Belenguer et al. 2018). Nevertheless, they are reasonable proxies, as our biovolume estimates scaled closely with masses predicted from length-mass allometries for cestodes (Benesh et al. 2013), acanthocephalans (Benesh et al. 2009), and nematodes (Andrássy 1956). In the dioecious acanthocephalans and nematodes, we used female size to calculate adult growth because it determines fecundity. Total growth in a life stage is the difference between final size and initial size. Helminths generally grow several orders of magnitude from egg to adult, often exponentially (Hutchison 1958; Crompton 1972; Halvorsen and Skorping 1982), so instead of *total* growth, we largely focused on *relative* growth, the log fold change in parasite size in a host: ln(final size/initial size).

Developmental times were the days until infectivity (for IHs) or sexual maturity (for DHs; the prepatent period).

Development is temperature dependent, so we expressed it in degree days (Trudgill et al. 2005): $D \times (T - B)$, where $D$ is developmental time in days, $T$ is the temperature at which development was observed, and $B$ is a baseline temperature below which development does not occur (assumed to be 5°C). When stages had multiple measurements for body size or developmental time, we calculated averages.

Host masses were obtained from over 130 sources (see Benesh et al. 2021b), some of the most important being Pantheria (Jones et al. 2009), Fishbase (Froese and Pauly 2022), EltonTraits (Wilman et al. 2014), EOL (Parr et al. 2014), and a food web compilation (Brose et al. 2019). We converted dry and ash-free dry masses to wet mass by assuming body water contents of 70% and 90%, respectively (Ricciardi and Bourget 1998; Block 2003). Parasites often infect multiple host species at a given life stage, so we calculated the average host mass for each stage. We considered a life stage to infect endotherms if it predominantly infects mammals or birds.

## IMPUTATION OF MISSING DATA

The analysis included 597 species. Most had an estimate for DH mass (98%), but fewer had IH masses (64%). Growth and developmental times were available for 35% and 20% of larval and adult stages, respectively. Just 81 (14%) species had no missing data, although most (82%) had a growth or developmental time estimate for one life stage. To make full use of the data and limit potential biases, we imputed missing host and parasite traits (Nakagawa and Freckleton 2008). The imputation procedure was described previously (Benesh et al. 2021b), so we only present it briefly.

We fitted Bayesian multivariate mixed models with taxonomic random effects (Hadfield and Nakagawa 2010). Taxonomy is a strong predictor of host body masses and parasite life history and is therefore useful in imputation (Penone et al. 2014). Further, multivariate models account for the correlations among response variables. We fitted separate models to impute host masses and parasite traits (body length, width, development time, and temperature at each life stage). Host and parasite traits were not used to impute each other because propagule stages (free eggs or larvae) lack associated host traits. A large dataset of animal body sizes ($n = 71{,}443$) was used to impute the missing masses for hosts in the life-cycle database. The models' posterior distributions were randomly sampled to generate 100 imputed datasets (Van Buuren 2018). Models predicted observed data well and made plausible predictions for cases with missing data (see Supporting Information A in Benesh et al. 2021b).

Results were comparable with and without imputation. Analyses with imputation are presumably less biased, so we present them in the main text, whereas the unimputed results are in Section D in the Supporting Information.

## ANALYSES

We tested hypotheses with multivariate mixed models (MCMCglmm R package; Hadfield 2010). Multivariate models include covariance between response variables, and can therefore test hypotheses about correlations, before and after controlling for other effects. To account for shared ancestry, we acquired parasite taxonomies from the Open Tree Taxonomy (Rees and Cranston 2017) and included taxonomic levels in the mixed models as nested random effects (Hadfield and Nakagawa 2010). Explained variance was estimated according to Nakagawa and Schielzeth (2013).

## HOST QUALITY: BIG IH, BIG DH?

Big predators usually consume big prey, so parasites with large IHs likely have large DHs. We fitted models with IH and DH masses as response variables, before and after adding parasite taxonomy as random effects. We also modeled taxonomic covariances to assess whether worm taxa with large IHs also have large DHs. To evaluate taxonomic covariance, we started with a model including parasite phylum and class, then we sequentially added order, family, and genus (root to tip), examining the variance and covariance in host masses at each step. Also, because the three helminth groups in our data (acanthocephalans, cestodes, and nematodes) evolved complex life cycles independently, we checked whether they differed in average host masses by moving parasite phylum out of the random effects and into the fixed effects.

Parasites grow larger in endothermic hosts (Benesh et al. 2021b), so we tested whether parasites with larger IHs were more likely to be transmitted to endotherms. We fitted a logistic regression with DH endothermy as response variable and IH mass as predictor.

## PARASITE LIFE-HISTORY STRATEGIES: DIVISION OF GROWTH AND DEVELOPMENT WITH SHIFTS IN HOST QUALITY

We fitted taxonomic models with six parasite traits as response variables: relative growth in IH and DH, developmental time in IH and DH, and size and age at maturity (Fig. 1a). We modeled *relative* growth, but *absolute* body size likely determines infectivity (Froelick et al. 2021) or fecundity (Skorping et al. 1991; Trouvé et al. 1998). Absolute growth can be inferred from the models. Absolute and relative growths in the IH are nearly equivalent; both are essentially determined by final larval size, because propagules tend to be consistently small across species. Similarly, adult size is generally much larger than larval size, so absolute growth in the DH is approximated by size at maturity. To explore how parasite life-history strategies change with host quality, we added host traits as fixed effects (IH mass, DH mass, and DH endothermy), and we checked their interactions. Finally, we moved
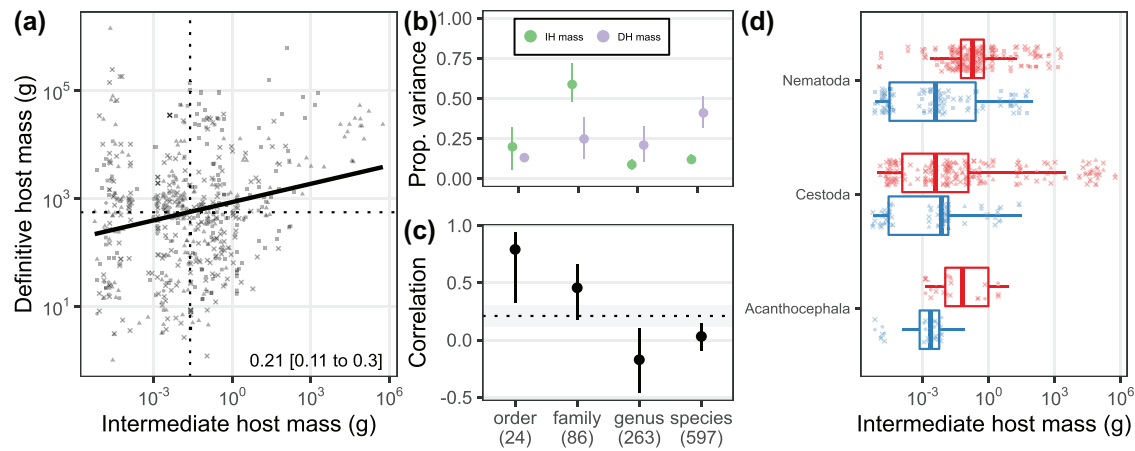
**Figure 2.** (a) Intermediate versus definitive host mass (IH and DH), (b) the proportion of variance in host mass explained by parasite taxonomic level, (c) the correlation between IH mass and DH mass at each taxonomic level, and (d) IH masses for parasite species with endotherm (red) or ectotherm DHs (blue). The correlation coefficient [95% CI] of the regression line in panel (a) is given on the plot and is represented as a horizontal dotted line in panel (c). Variances in panel (b) and covariances in panel (c), and their 95% CIs, were estimated with multivariate mixed models in which taxonomic levels were added root to tip, for example, order-level (co)variance represents orders with large/small hosts relative to their class, then families that infect large/small hosts relative to their order, and so forth. The taxon-level correlations in panel (c) are plotted in Figure C2 in the Supporting Information. The number of taxa at each level is stated in parentheses. Point shapes in panels (a) and (d) differentiate the three parasite groups; imputed data (averages from 100 imputations) are plotted as Xs.

helminth group (acanthocephalan, cestode, nematode) from the random to the fixed effects.

### LARVAL VERSUS ADULT LIFE-HISTORY STRATEGIES: TRADE-OFFS?

We examined the covariance between parasite life-history traits before and after accounting for parasite group, host masses, and endothermy. For instance, growth and developmental time are expected to be correlated, but if this is caused by prolonged growth in bigger hosts, then the correlation may disappear after accounting for host mass. Correlations can also be driven by taxonomy, as, all else equal, some taxa grow and develop longer than others. To evaluate taxonomic correlations, we started with a model including parasite phylum and class, and then we sequentially added lower taxonomic levels: orders, then families, and finally genera (root to tip). This quantifies taxon-level covariance after accounting for higher level taxonomy, for example, whether families that have large larvae for their order/class also have large adults. An example of how trait correlations were deconstructed is shown in Figure C1 in the Supporting Information.

We examined whether covariances between larval and adult traits supported optimality models or hinted at cross-stage trade-offs. Some correlations are expected under both scenarios. For example, short larval development may be associated with prolonged adult development, either because infecting high-quality DHs favors spending less time in the IH (Fig. 1b,c) or because

rapid larval development is traded off against slower adult development (Fig. 1d). Other cross-stage correlations, however, should distinguish optimality and trade-off scenarios. For example, larval growth is not predicted to alter the optimal adult reproductive size (Fig. 1b), such that a given increase in larval growth should result in an equal decrease in adult growth, that is, a slope of −1 in a regression of relative growth in IH versus DH. A slope less than −1 would indicate that adult growth decreases more than expected with additional larval growth, that is, a trade-off (Fig. 1d).

## Results

### HOST QUALITY: LARGE IHs ARE ASSOCIATED WITH LARGE, ENDOTHERMIC DHs

Helminths with large IHs tended to infect larger DHs; a doubling of IH mass was associated with an 8% (95% CI: 4–11) increase in DH mass (Fig. 2a). A doubling of IH mass also increased the odds of infecting an endotherm DH 88% (40–252), 5% (0–10), and 23% (16–31) in acanthocephalans, cestodes, and nematodes, respectively (logistic regression, $P < 0.001$; Fig. 2d).

IH and DH masses ranged over 11 and six orders of magnitude. Host masses did not differ across the three helminth groups (likelihood ratio test adding parasite phylum to fixed effects, $P > 0.08$), but they did vary at other taxonomic levels. Parasite taxonomy explained more of the variation in IH mass than in DH mass (88% vs. 64%). Parasite order combined with family
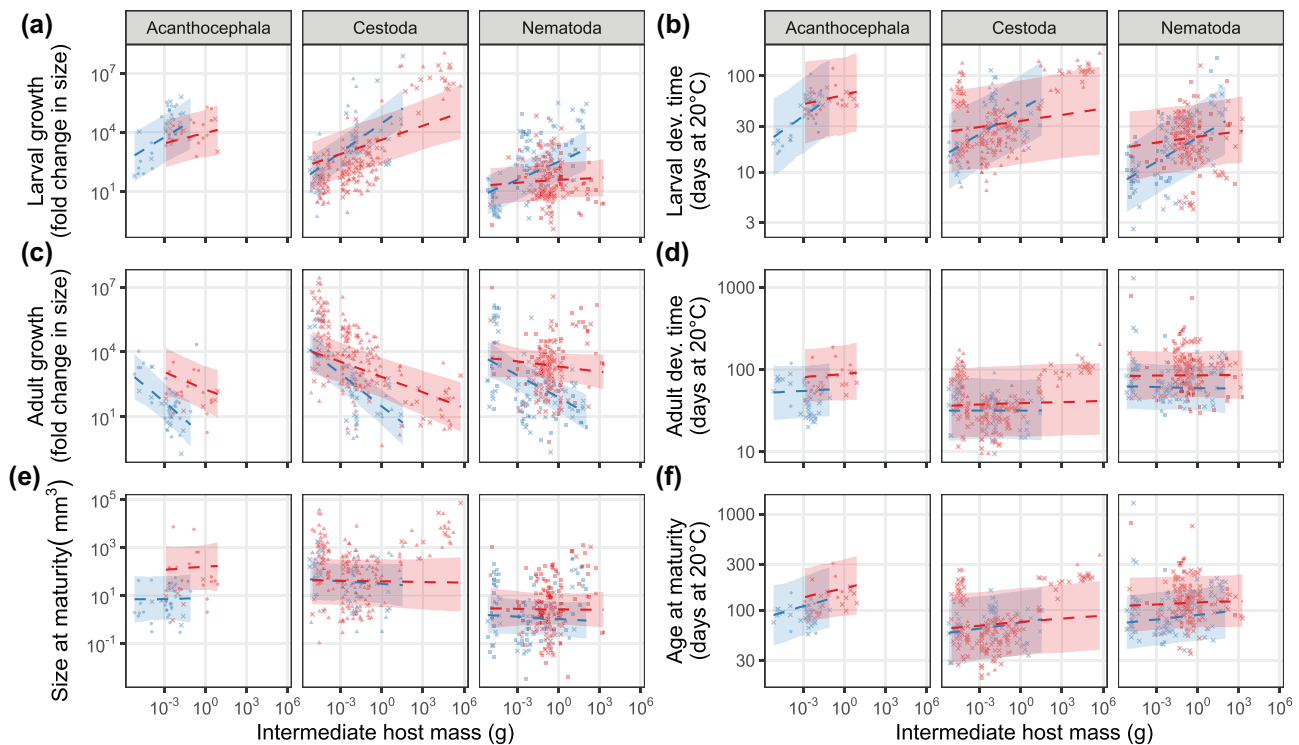
**Figure 3.** (a) Larval growth, (b) larval developmental time, (c) adult growth, (d) adult developmental time, (e) size at maturity, and (f) age at maturity as a function of intermediate host mass. Blue and red points represent species with ectotherm or endotherm definitive hosts, respectively. Lines and 95% credible intervals were estimated with mixed models accounting for parasite taxonomy. Missing data were imputed; averages from 100 imputations of the *y*-axis variable are plotted as Xs.

explained 79% of the variation in IH mass versus 38% for DH mass, whereas 62% of the variation in DH mass was among and within genera versus 21% for IH mass (Fig. 2b). Consequently, IH and DH mass were correlated at the order and family level, but genus-level shifts in DH mass were not associated with changes in IH mass (Fig. 2c).

## PARASITE LIFE-HISTORY STRATEGIES: ADAPTIVE DIVISION OF GROWTH BETWEEN HOSTS

Parasites with two-host life cycles amassed nearly all their total biovolume in the DH (99% [94%–99%] in average-sized hosts; Fig. B1 in the Supporting Information). Relative growth, however, was more evenly split (46% [36%–57%] in the DH); an average helminth grew 384-fold (75–1585) in the DH and 1000-fold (103–10,393) in the IH. But this varied among parasite groups, with acanthocephalans growing relatively more in the IH and nematodes more in the DH (Fig. B1 in the Supporting Information). Although the CIs were wide, an average helminth developed longer in its DH than its IH (57 [26–122] vs. 33 [14–78] days at 20°C) with slightly slower relative growth (0.17 [0.06–0.43] vs. 0.24 [0.09–0.62]; Fig. B2 in the Supporting Information), because relative growth rates slowed with size and age

(i.e., it takes helminths longer to grow from 1 to 10 mg than from 0.1 to 1 mg; Fig. B4 in the Supporting Information).

Host traits had significant associations with both larval and adult life history ($R^2_{m}$ in Table 1). The trends were rather consistent in acanthocephalans, cestodes, and nematodes, because allowing parasite group by host trait interactions only accounted for an additional 0%–2% of the total trait variance ($R^2_{c}$ in Table 1). However, parasite growth and development varied among lower level taxa, particularly families (Fig. C3 in the Supporting Information), both before and after accounting for host traits (Table 1). Parasite families characterized by high/low growth and long/short development are given in Tables C1–C3 in the Supporting Information.

Bigger IHs were associated with more larval growth and development (Fig. 3a,b) and relatively less adult growth (Fig. 3c). IH mass did not clearly affect prepatent periods (Fig. 3d) or size at maturity (Fig. 3e), although prolonged larval development in larger IHs slightly increased age at maturity (Fig. 3f). Species with bigger DHs did not grow less as larvae (Fig. 4a,b), but they grew slightly more as adults (Fig. 4c,d). A doubling of DH mass was associated with a 17% (11–23) and 3% (2–4) increase in helminth size and age at maturity, respectively (Fig. 4e,f).
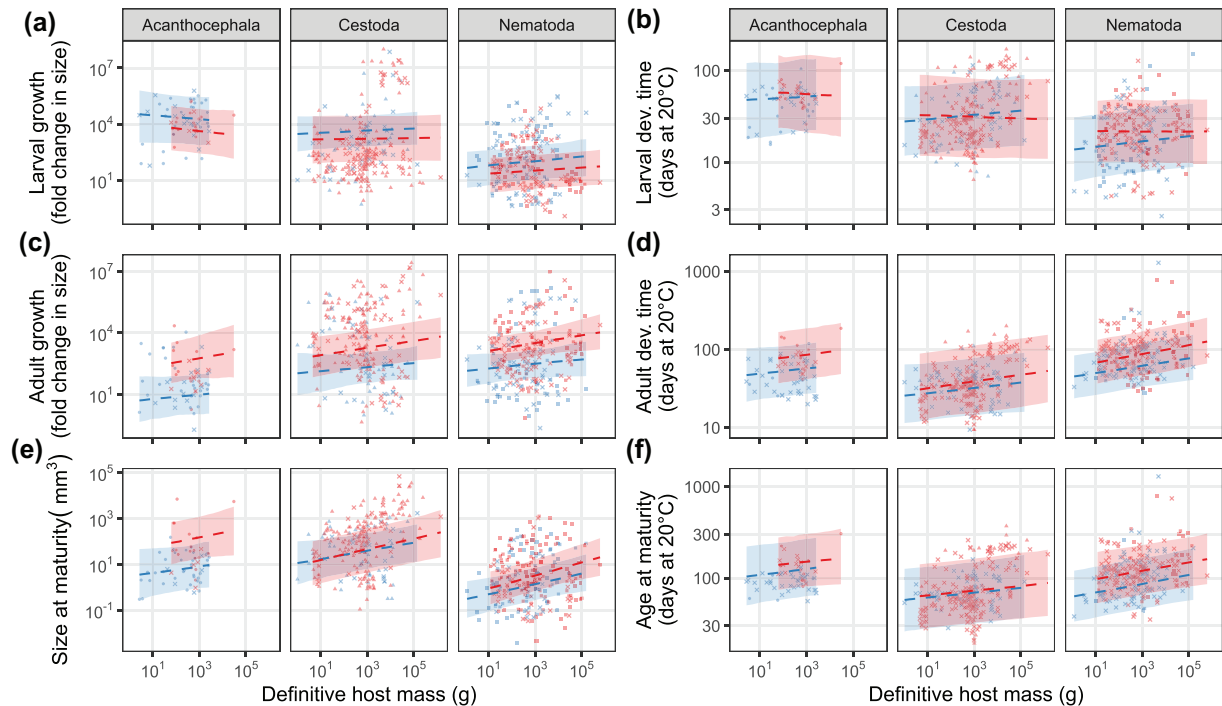
**Figure 4.** (a) Larval growth, (b) larval developmental time, (c) adult growth, (d) adult developmental time, (e) size at maturity, and (f) age at maturity as a function of definitive host mass. Blue and red points represent species with ectotherm or endotherm definitive hosts, respectively. Lines and 95% credible intervals were estimated with mixed models accounting for parasite taxonomy. Missing data were imputed; averages from 100 imputations of the *y*-axis variable are plotted as Xs.

Relative growth rates, as both larvae and adults, did not vary with host mass (Fig. B2 in the Supporting Information).

Helminths with an endotherm DH grew more as adults (1386-fold [243–5672] vs. 105-fold [21–493]; Fig. 4c), maturing at larger sizes, at least in acanthocephalans and nematodes (Fig. 4e). They also grew less as larvae compared to those with an ectotherm DH (517-fold [55–5869] vs. 2149-fold [245–22,905] for average-sized hosts), particularly in larger IHs (Fig. 3a).

In summary, trends in Figures 3 and 4 were qualitatively consistent with theoretical expectations—parasites with smaller IHs and larger endothermic DHs grew less as larvae and more as adults—with two exceptions (Table 2). First, better conditions in the IH did not reduce prepatent periods in the DH (Fig. 3d). Second, better conditions in the DH did not decrease developmental times in the IH (Fig. 4b), nor were larger DHs associated with reduced larval growth (Fig. 4a).

## LARVAL VERSUS ADULT LIFE-HISTORY STRATEGIES: NO CROSS-STAGE TRADE-OFFS

The correlation between larval growth and developmental time weakened from 0.60 to 0.41 after including host traits in the model, suggesting some parasites grow larger and longer because they infect bigger IHs (Fig. 5a). By contrast, the same correlation

at the adult stage strengthened, suggesting that the parasites that grow more, relative to the size/endothermy of their DH, also have longer prepatent periods (Fig. 5b). Even after accounting for host traits, some parasite taxa grew more/less than expected. Larval growth and development covaried mainly among orders and families (Fig. 5a). Adult growth and development covaried among families too, but there was also significant covariance among genera (Fig. 5b).

Across life stages, more larval growth and development was associated with less adult growth (Fig. 6a,b) but larger sizes at maturity (Fig. 6e,f), implying adult growth decreased disproportionately with larval growth (Fig. 6a). The slopes were −0.65 (−0.71 to −0.59) and −0.66 (−0.74 to −0.58) before and after accounting for host traits, implying that a doubling of larval growth decreased adult growth by ∼37% instead of a proportionate 50%. Slopes were closer to −1 after accounting for parasite order (family-level: −0.71 [−0.95 to −0.47]; genus-level: −0.88 [−1.18 to −0.60]; Fig. C5 in the Supporting Information), indicating that some orders grow extensively as both larvae and adults, but within those taxa, additional larval growth decreases adult growth roughly proportionately. Consequently, there were no clear correlations between larval growth/development and maturation size after controlling for host traits and higher taxonomy (Fig. 6e,f). Prolonged larval growth and development did
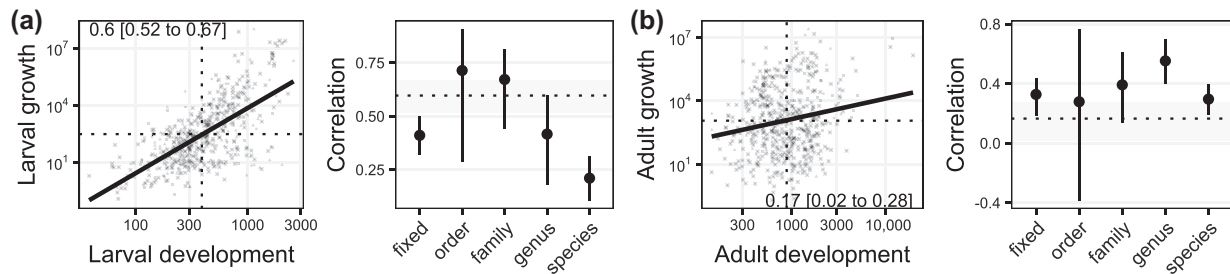
**Figure 5.** Helminth growth (fold change) versus developmental time (degree days) in (a) intermediate hosts and (b) definitive hosts. The left subplots are raw, species-level relationships, and the correlation coefficient [95% credible interval] is given on the plot. These coefficients are also depicted as dotted horizontal lines on the right subplots, which show how correlations change after adding fixed effects (host mass, endothermy, and parasite group) and then taxonomic levels from root to tip. For instance, family-level covariance was estimated after accounting for fixed effects and higher taxonomy, genus-level covariance was estimated after controlling for family-level covariance, and so on. These correlations are visualized in Figure C4 in the Supporting Information. Covariances and their 95% CIs were estimated with multivariate mixed models accounting for missing data; imputed data (averages from 100 imputations) are plotted as Xs. Point shapes differentiate the three parasite groups as in Figures 2–4.
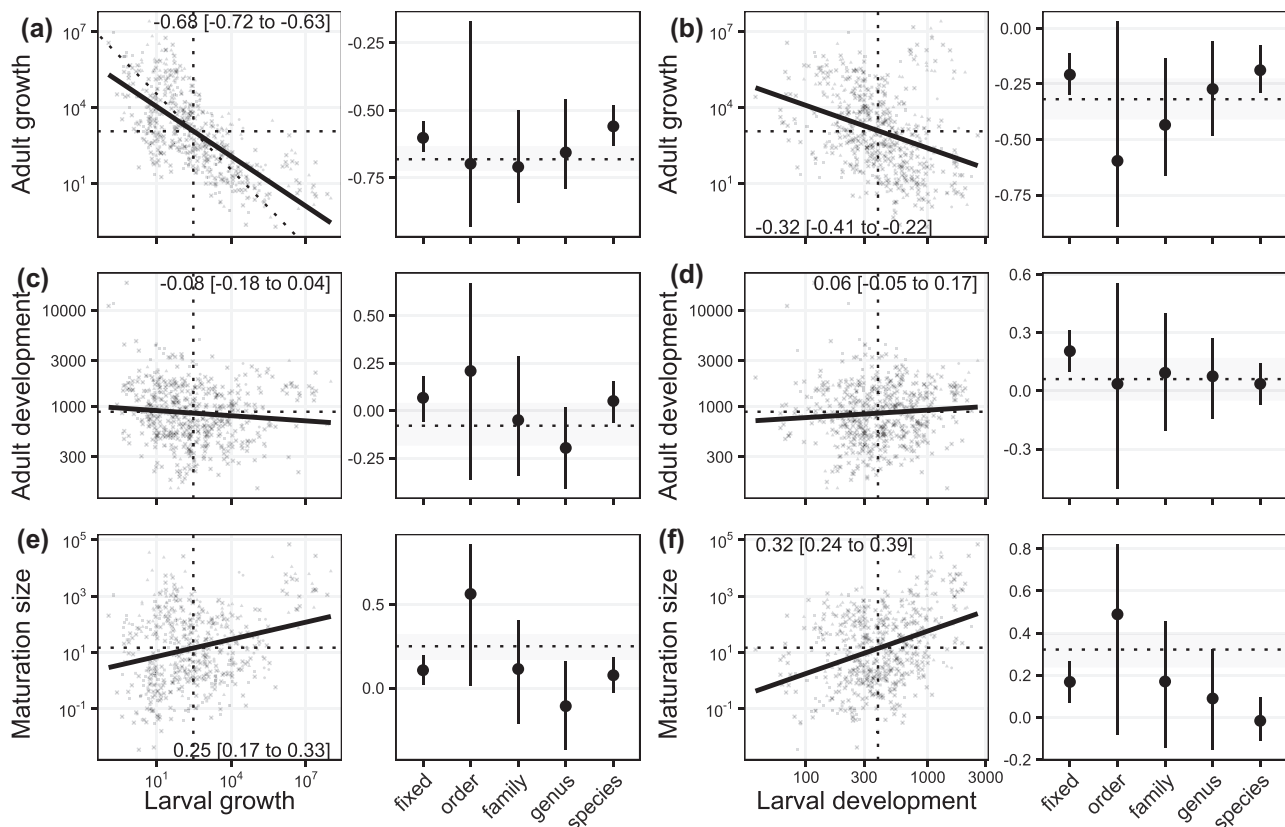


**Figure 6.** Covariances between larval growth and development and three components of adult fitness: (a, b) adult growth, (c, d) prepatent period, and (e, f) size at maturity. Growth and developmental times are expressed as fold change and degree days, respectively. In panel (a), the dotted diagonal line has a slope of −1 and represents the case where larval growth reduces adult growth proportionally. Plot elements as in Figure 5. Covariances from each model are plotted in Figures C5 and C6 in the Supporting Information.

not reduce prepatent periods (Fig. 6c,d) and was associated with slower adult growth (Fig. B3 in the Supporting Information), because growth rates generally decreased in bigger, older parasites (Fig. B4 in the Supporting Information).

In summary, rapid or prolonged growth in one host was not traded off with that in the other host (Table 3). Rather, parasite orders characterized by long larval growth and development tended to grow proportionally more than expected as adults and

**Table 1.** Multivariate mixed models (Gaussian errors, identity link) examining parasite relative growth (RG) and developmental time (DT) in intermediate hosts (IH) and definitive hosts (DH) for 597 parasite species with two-host life cycles.

| Model | Growth RG IH (n = 364) $R^2_m$ | $R^2_c$ | RG DH (n = 379) $R^2_m$ | $R^2_c$ | Size at Maturity (n = 494) $R^2_m$ | $R^2_c$ | Developmental Time DT IH (n = 277) $R^2_m$ | $R^2_c$ | DT DH (n = 167) $R^2_m$ | $R^2_c$ | Age at Maturity (n = 105) $R^2_m$ | $R^2_c$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxonomic random effects | – | 0.85 | – | 0.64 | – | 0.67 | – | 0.87 | – | 0.88 | – | 0.87 |
| + host traits | 0.09 | 0.84 | 0.19 | 0.64 | 0.06 | 0.71 | 0.06 | 0.87 | 0.06 | 0.89 | 0.07 | 0.89 |
| + host traits interactions | 0.10 | 0.84 | 0.22 | 0.64 | 0.07 | 0.71 | 0.09 | 0.87 | 0.06 | 0.89 | 0.07 | 0.89 |
| + host traits × parasite group | 0.44 | 0.86 | 0.34 | 0.65 | 0.34 | 0.75 | 0.28 | 0.87 | 0.27 | 0.90 | 0.24 | 0.89 |

*Note:* The initial model included parasite taxonomy as nested random effects. Then, we added host traits (IH mass, DH mass, and DH endothermy) and their interactions. Finally, we tested whether the effects of host traits were consistent across parasite groups (acanthocephalans, cestodes, and nematodes). Marginal $R^2$ ($R^2_m$) represents the variation explained by fixed effects, while conditional $R^2$ ($R^2_c$) represents that explained by random and fixed effects combined. The difference between $R^2_c$ and $R^2_m$ is the variation attributed to parasite taxonomy.

achieved larger sizes at maturity, implying some taxa grow large in both their hosts. On the other hand, within those taxa, the families and genera characterized by larger larvae did not have larger adults, which is consistent with optimality models.

## Discussion

Life-history theory predicts that complex life-cycle parasites should shift growth and development to hosts where they have better survival and/or faster growth (Ball et al. 2008; Parker et al. 2009), like large endotherms (Poulin et al. 2003; Poulin and George-Nascimento 2007; Benesh et al. 2021b). Helminths with large IHs grew relatively more as larvae and less as adults, whereas helminths with large and/or endothermic DHs grew relatively less as larvae (when the DH was an endotherm) and more as adults, achieving larger sizes at maturity. Moreover, species that grew larger than expected as larvae did not grow less than expected as adults (or vice versa). Overall, results were consistent with parasites shifting growth from relatively "poor" to "good" hosts (i.e., those with better growth/mortality ratios).

The IHs in two-host life cycles spanned 11 orders of magnitude in body mass. Much of this diversity arose long ago, among parasite orders and families. Parasite lineages exploiting larger IHs also infected larger, endothermic DHs, which was expected because large endotherms tend to consume larger prey (Brose et al. 2019). However, prey usually have multiple predators (Digel et al. 2011), so a given IH could transmit parasites to various DHs (Park 2019; Benesh et al. 2021a). This may explain shifts in DH mass among genera that occurred without corresponding changes in IH mass. The apparent conservatism of IHs compared to DHs could reflect nonadaptive (e.g., genetic or developmental constraints) or adaptive processes (e.g., selection against switching IH or for switching DH species). In any case, this seems to affect parasite life-history strategies, as larval growth varied at deeper taxonomic levels than adult growth.

Larger hosts have longer average life spans (McCoy and Gilloly 2008) and higher metabolism (especially endotherms; Brown et al. 2004), which presumably favors parasite growth by reducing mortality and/or increasing growth rates (Parker et al. 2009). Helminths, on average, completed 99% of their *total* growth in the DH, in which they achieve faster *absolute* growth rates. But *relative* growth rates were comparable in IHs and DHs and did not increase with host mass. Relative growth rates were also similar in ecto- and endotherms after adjusting for temperature. Unadjusted growth rates, however, are slightly higher in endotherms (Benesh et al. 2021b), which probably favors the larger sizes at maturity observed in acanthocephalans and nematodes infecting endothermic DHs. Nevertheless, increased para-

**Table 2.** Predicted evolutionary change in relative growth (RG) and developmental time (DT) when helminths infect better intermediate (IH) or definitive (DH) hosts.

| Parasite Life-History Trait | Better IH (Larger IH Mass) | | Better DH (Larger and Endothermic DH) | |
|---|---|---|---|---|
| | Predicted (Fig. 1b; Table A1 in the Supporting Information) | Observed | Predicted (Fig. 1c; Table A1 in the Supporting Information) | Observed |
| RG IH | Increase* | Increase (Fig. 3a) | Decrease | Decreased with endotherm DH (Fig. 4a), but unaffected by DH mass |
| DT IH | If larval growth is faster, may increase or decrease. If mortality rate lower, increase*. | Increase (Fig. 3b) | Decrease | Unaffected by DH mass or endothermy (Fig. 4b) |
| RG DH | Decrease | Decrease (Fig. 3c) | Increase | Increased with DH mass and endothermy (Fig. 4c) |
| DT DH | Decrease | Unaffected (Fig. 3d) | Increase | Increased with DH mass and endothermy (Fig. 4d) |
| Size maturity | Unaffected | Unaffected (Fig. 3e) | Increase | Increased with DH mass; endothermy effect varied among parasite groups (Fig. 4e) |
| Age maturity | Uncertain because DT IH may increase or decrease. | Increase (Fig. 3f) | Increase | Increased with DH mass; endothermy effect varied among parasite groups (Fig. 4f) |

*Note*: Better hosts are those in which parasites can grow fast and safe (i.e., a high ratio of growth to mortality rate; see Section A in the Supporting Information). Larval predictions relate to increased growth rate and/or decreased mortality rate before growth arrest in the IH; changes in mortality rate after growth arrest can affect predictions marked with *. Proxies of host quality in our analysis were host mass and endothermy.

**Table 3.** Expected and observed covariances between larval and adult traits.

| Life-History Change | Expected from Theory | Expected with Cross-Stage Trade-Offs | Observed |
|---|---|---|---|
| **More larval RG** | | | |
| | Proportionate decrease in adult RG, slope = −1 | More than proportionate decrease in adult RG, slope < −1 | Slope > −1 until accounting for higher taxonomy and ~ −1 thereafter (Fig. 6a and Fig. C5a in the Supporting Information) |
| | Shorter adult DT | Longer adult DT | No correlation (Fig. 6c and Fig. C5b in the Supporting Information) |
| | Unchanged adult RGR | Slower adult RGR | Slower (Fig. B3 in the Supporting Information) due to decelerating relative growth rate with size and age (Fig. B4 in the Supporting Information) |
| | Unchanged MS | Smaller MS | Larger MS until accounting for higher taxonomy, no correlation thereafter (Fig. 6E and Fig. C5c in the Supporting Information) |
| **Shorter larval DT** | | | |
| | Because shorter larval DT associated with smaller larval sizes (Fig. 5a), more adult RG expected | Less adult RG | More adult RG (Fig. 6b and Fig. C6a in the Supporting Information) |
| | Because shorter larval DT associated with smaller larval sizes (Fig. 5a), longer adult DT expected | Longer adult DT | Longer DT after accounting for host traits, but no correlation after accounting for taxonomy (Fig. 6d and Fig. C6b in the Supporting Information) |
| | Unchanged adult RGR | Slower adult RGR | Faster (Fig. B3 in the Supporting Information) due to decelerating relative growth rate with size and age (Fig. B4 in the Supporting Information) |
| | Unchanged MS | Smaller MS | Smaller MS until accounting for higher taxonomy, no correlation thereafter (Fig. 6F and Fig. C6c in the Supporting Information) |

*Note*: We examined how two larval traits (relative growth [RG] and developmental times [DT] in intermediate hosts) were correlated with four components of adult fitness (RG, prepatent period [DT], relative growth rate [RGR], and maturation size [MS] in definitive hosts). We contrasted two scenarios: (i) traits evolve as expected from optimality models (Fig. 1b,c) or (ii) traits are subject to constraints, either because performance in one host is traded off against performance in the other host or because some parasites grow consistently more/longer in both hosts (Fig. 1d).

site growth in larger hosts largely stemmed from longer development, not faster growth. The costs of protracted development depend on mortality, so perhaps parasite mortality decreases with host mass, despite heightened competition among parasites in larger hosts (Poulin and George-Nascimento 2007; Lester and Mcvinish 2016) and/or better immune responses (Brace et al. 2017). Even in similar-sized hosts, some parasite taxa grew larger than others (including groups with human- [Taeniidae, Dracunculidae] and livestock-infecting [Anoplocephalidae, *Stephanurus*] species), raising the possibility that these taxa have lower mortality rates.

For helminths with two-host life cycles, growth is shaped not only by conditions in their current host but also by those in their other host. For example, parasites with ectotherm DHs grew more in IHs, particularly in larger IHs that may be able to tolerate larger parasites (Benesh 2011; Weinersmith et al. 2014). Then again, parasites with larger DHs did not reduce larval growth, perhaps because small larvae ingested by big DHs have lower establishment rates (Poulin 2010; Froelick et al. 2021). This was one of the few trends deviating from theoretical expectations. Another was that more larval growth and development in larger IHs did not shorten prepatent periods in DHs. This partly reflects larger, older larvae growing slower in the DH because relative growth rate decelerated with size and age. Despite slower growth, delayed reproduction could still be favored if larger larvae have higher survival in the DH (Gemmill et al. 1999). Larger, more developed larvae often have higher survival in the next host in intraspecific experiments (Rosen and Dick 1983; Tierney and Crompton 1992; Benesh and Hafer 2012; but see Keymer 1981; Janwan et al. 2011; Benesh 2019), but they tend to mature earlier (Mead and Olsen 1971; Rietschel 1973; Stigge and Bolek 2015) and grow to an expected adult size (Steinauer and Nickol 2003), suggesting the boost in viability from larval growth is not sufficient to favor delayed reproduction. Whether the extensive interspecific variation in larval size is positively associated with survival in the DH is unknown (i.e., in the notation from Section A in the Supporting Information, whether $p_j$ decreases with $W_d$), but if it is, then helminth species with the biggest larvae would be expected to delay maturation until reaching a larger, more fecund size.

Species with larger larvae matured as slightly larger adults (Poulin and Latham 2003; Poulin et al. 2003; Benesh and Valtonen 2007; Benesh et al. 2013), partly because species with large IHs often have large, endothermic DHs, but also because some parasite taxa, particularly orders, just have large body sizes. Order-level differences may suggest that some parasite lineages have adaptations that facilitate growth and survival in both the IH and the DH, or, alternatively, that lineages long ago established a "bauplan" with larger sizes across all life stages. Within orders, however, parasite families and genera with larger larvae

did not mature at bigger-than-expected sizes and, accordingly, adult growth decreased about proportionately with larval growth. This is consistent with optimality models, and inconsistent with cross-stage growth trade-offs (Gandon 2004; Gower and Webster 2004), suggesting a degree of decoupling between larvae and adults. This dovetails with the independence of thermal sensitivities (Morley 2012; Phillips et al. 2022) and host specificity across parasite life stages (Benesh et al. 2021a), as well as the genetic decoupling observed in some selection experiments with helminths (Hafer-Hahmann 2019). More broadly, evolutionary decoupling between life stages may be common in complex life-cycle organisms, including marine invertebrates (Aguirre et al. 2014), insects (Herrig et al. 2021), and amphibians (Goedert and Calsbeek 2019; Fabre et al. 2020).

Parasites with complex life cycles are expected to spend more time in the hosts in which they can grow large, fast, and/or safely. Accordingly, helminths with two-host cycles grew relatively less as larvae and more as adults when they infected smaller IHs and larger, endothermic DHs. Moreover, helminths that grew more than expected in the IH did not grow less than expected in the DH. Rather, some lineages were characterized by large sizes as both larvae and adults. Within these taxa, however, size at sexual maturity was unrelated to larval growth, as predicted by life-history models. Most (but not all) trends were consistent with optimality models, suggesting that helminths adaptively divide growth and development between hosts.

## AUTHOR CONTRIBUTIONS

### CONFLICT OF INTEREST
The authors declare no conflict of interest.

## DATA ARCHIVING
Life-cycle data were published here: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.1680. Species-level data are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.6hdr7sr3k (Benesh 2022). Data and code to reproduce our analyses can be found here: https://github.com/dbenesh82/division_helminth_growth_devo.

## DEDICATION

One of the authors, Jimmy Chubb, died soon after this article was submitted, after a career of over 60 years in parasitological research. DPB and GAP dedicate this study to his memory and will greatly miss him as a colleague and friend.

## LITERATURE CITED

Aguirre, J., Blows, M.W. & Marshall, D.J. (2014) The genetic covariance between life cycle stages separated by metamorphosis. *Proc. R. Soc. B Biol. Sci.*, 281, 20141091.

Andrássy, I. (1956) Die Rauminhalts- und Gewichtsbestimmung der Faden-würmer (Nematoden). *Acta Zool. Hungarica*, 2, 1–5.

Arneberg, P., Skorping, A. & Read, A.F. (1998) Parasite abundance, body size, life histories, and the energetic equivalence rule. *American Naturalist*, 151, 497–513.

Ball, M.A., Parker, G.A. & Chubb, J.C. (2008) The evolution of complex life cycles when parasite mortality is size- or time-dependent. *Journal of Theoretical Biology*, 253, 202–214.

Barber, I. (2005) Parasites grow larger in faster growing fish hosts. *International Journal for Parasitology*, 35, 137–143.

Benesh, D.P. (2010) Developmental inflexibility of larval tapeworms in response to resource variation. *International Journal for Parasitology*, 40, 487–497.

———. (2011) Intensity-dependent host mortality: what can it tell us about larval growth strategies in complex life cycle helminths? *Parasitology*, 138, 913–925.

———. (2016) Autonomy and integration in complex parasite life cycles. *Parasitology*, 143, 1824–1846.

———. (2019) Crowding in the first intermediate host does not affect infection probability in the second host in two helminths. *Journal of Helminthology*, 2, 172–176.

———. (2022) Data from: adaptive division of growth and development between hosts in helminths with two-host life cycles. *Dryad, Dataset*, https://doi.org/10.5061/dryad.6hdr7sr3k.

Benesh, D.P. & Valtonen, E.T. (2007) Sexual differences in larval life history traits of acanthocephalan cystacanths. *International Journal for Parasitology*, 37, 191–198.

Benesh, D.P. & Hafer, N. (2012) Growth and ontogeny of the tapeworm *Schistocephalus solidus* in its copepod first host affects performance in its stickleback second intermediate host. *Parasit. Vectors*, 5, 90.

Benesh, D.P., Seppälä, O. & Valtonen, E.T. (2009) Acanthocephalan size and sex affect the modification of intermediate host colouration. *Parasitology*, 136, 847–854.

Benesh, D.P., Chubb, J.C. & Parker, G.A. (2013) Complex life cycles: why refrain from growth before reproduction in the adult niche? *American Naturalist*, 181, 39–51.

Benesh, D.P., Lafferty, K.D. & Kuris, A. (2017) A life cycle database for parasitic acanthocephalans, cestodes, and nematodes. *Ecology*, 98, 882.

Benesh, D.P., Parker, G.A., Chubb, J.C. & Lafferty, K. (2021a) Trade-offs with growth limit host range in complex life-cycle helminths. *American Naturalist*, 197, E40–E54.

Benesh, D.P., Parker, G. & Chubb, J.C. (2021b) Life-cycle complexity in helminths: what are the benefits? *Evolution; Internation Journal of Organic Evolution*, 75, 1936–1952.

Bersier, L.F. & Kehrli, P. (2008) The signature of phylogenetic constraints on food-web structure. *Ecol. Complex*, 5, 132–139.

Block, W. (2003) Water or ice?—the challenge for invertebrate cold survival. *Science Progress*, 86, 77–101.

Brace, A.J., Lajeunesse, M.J., Ardia, D.R., Hawley, D.M., Adelman, J.S., Buchanan, K.L., Fair, J.M., Grindstaff, J.L., Matson, K.D. & Martin, L.B. (2017) Costs of immune responses are related to host body size and lifespan. *J. Exp. Zool. Part A Ecol. Integr. Physiol.*, 327, 254–261.

Brose, U., Archambault, P., Barnes, A.D., Bersier, L.F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A., et al. (2019) Predator traits determine food-web architecture across ecosystems. *Nature Ecology & Evolution*, 3, 919–927.

Brown, J., Gillooly, J., Allen, A., Savage, V. & West, G. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

Buchmann, K. (2014) Evolution of innate immunity: clues from invertebrates via fish to mammals. *Frontiers in immunology*, 5, 459.

Choisy, M., Brown, S.P., Lafferty, K.D. & Thomas, F. (2003) Evolution of trophic transmission in parasites: why add intermediate hosts? *American Naturalist*, 162, 172–181.

Chubb, J.C., Ball, M.A. & Parker, G.A. (2010) Living in intermediate hosts: evolutionary adaptations in larval helminths. *Trends in Parasitology*, 26, 93–102.

Crompton, D.W. (1972) The growth of *Moniliformis dubius* (Acanthocephala) in the intestine of male rats. *Journal of Experimental Biology*, 56, 19–29.

Day, T. & Rowe, L. (2002) Developmental thresholds and the evolution of reaction norms for age and size at life-history transitions. *American Naturalist*, 159, 338–350.

Dezfuli, B.S., Giari, L. & Poulin, R. (2001) Costs of intraspecific and inter-specific host sharing in acanthocephalan cystacanths. *Parasitology*, 122, 483–489.

Digel, C., Riede, J.O. & Brose, U. (2011) Body sizes, cumulative and allometric degree distributions across natural food webs. *Oikos*, 120, 503–509.

Ebenman, B. (1992) Evolution in organisms that change their niches during the life cycle. *American Naturalist*, 139, 990–1021.

Fabre, A.C., Bardua, C., Bon, M., Clavel, J., Felice, R.N., Streicher, J.W., Bonnel, J., Stanley, E.L., Blackburn, D.C. & Goswami, A. (2020) Metamorphosis shapes cranial diversity and rate of evolution in salamanders. *Nature Ecology & Evolution*, 4, 1129–1140.

Ferguson, H.M., Mackinnon, M.J., Chan, B.H. & Read, A.F. (2003) Mosquito mortality and the evolution of malaria virulence. *Evolution; Internation Journal of Organic Evolution*, 57, 2792–2804.

Froelick, S., Gramolini, L. & Benesh, D.P. (2021) Comparative analysis of helminth infectivity: growth in intermediate hosts increases establishment rates in the next host. *Proc. R. Soc. B Biol. Sci.*, 288, 20210142.

Froese, R. & Pauly, D. (2022) FishBase. Available via www.fishbase.org.

Gandon, S. (2004) Evolution of multihost parasites. *Evolution; Internation Journal of Organic Evolution*, 58, 455–469.

Gemmill, A.W., Skorping, A. & Read, A.F. (1999) Optimal timing of first reproduction in parasitic nematodes. *Journal of Evolutionary Biology*, 12, 1148–1156.

George-Nascimento, M., Muñoz, G., Marquet, P.A. & Poulin, R. (2004) Testing the energetic equivalence rule with helminth endoparasites of vertebrates. *Ecol. Lett.*, 7, 527–531.

Goedert, D. & Calsbeek, R. (2019) Experimental evidence that metamorphosis alleviates genomic conflict. *American Naturalist*, 194, 356–366.

Gower, C.M. & Webster, J.P. (2004) Fitness of indirectly transmitted pathogens: restraint and constraint. *Evolution; Internation Journal of Organic Evolution*, 58, 1178–1184.

Hadfield, J. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.*, 33, 1–22.

Hadfield, J.D. & Nakagawa, S. (2010) General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, 23, 494–508.

Hafer-Hahmann, N. (2019) Experimental evolution of parasitic host manipulation. *Proc. R. Soc. B Biol. Sci.*, 286, 20182413.

Halvorsen, O. & Skorping, A. (1982) The influence of temperature on growth and development of the nematode *Elaphostrongylus rangiferi* in the gastropods *Arianta arbustorum* and *Euconulus fulvus*. *Oikos*, 38, 285–290.

Hammerschmidt, K. & Kurtz, J. (2005) Evolutionary implications of the adaptation to different immune systems in a parasite with a complex life cycle. *Proc. R. Soc. B Biol. Sci.*, 272, 2511–2518.

Hechinger, R.F. (2013) A metabolic and body-size scaling framework for parasite within-host abundance, biomass, and energy flux. *American Naturalist*, 182, 234–248.

Herrig, D.K., Vertacnik, K.L., Kohrs, A.R. & Linnen, C.R. (2021) Support for the adaptive decoupling hypothesis from whole-transcriptome profiles of a hypermetamorphic and sexually dimorphic insect, *Neodiprion lecontei*. *Molecular Ecology*, 30, 4551–4566.

Hutchison, W.M. (1958) Studies on *Hydatigera taeniaeformis* I. Growth of the larval stage. *Journal of Parasitology*, 44, 574–582.

Iwasa, Y. & Wada, G. (2006) Complex life cycle and body sizes at life-history transitions for macroparasites. *Evol. Ecol. Res.*, 8, 1427–1443.

Janwan, P., Intapan, P.M., Sanpool, O., Sadaow, L., Thanchomnang, T. & Maleewong, W. (2011) Growth and development of *Gnathostoma spinigerum* (Nematoda: Gnathostomatidae) larvae in *Mesocyclops aspericornis* (Cyclopoida: Cyclopidae). *Parasit. Vectors*, 4, 93.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., et al. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90, 2648–2648.

Keymer, A. (1981) Population dynamics of *Hymenolepis diminuta* in the intermediate host. *J. Anim. Ecol.*, 50, 941–950.

Lester, R.J.G. & Mcvinish, R. (2016) Does moving up a food chain increase aggregation in parasites? *Journal of the Royal Society, Interface*, 13, 20160102.

Llopis-Belenguer, C., Blasco-Costa, I. & Balbuena, J.A. (2018) Evaluation of three methods for biomass estimation in small invertebrates, using three large disparate parasite species as model organisms. *Science Reports*, 8, 3897.

McCoy, M.W. & Gillooly, J.F. (2008) Predicting natural mortality rates of plants and animals. *Ecol. Lett.*, 11, 710–716.

Mead, R.W. & Olsen, O.W. (1971) The life cycle and development of *Ophiotaenia filaroides* (La Rue, 1919) (Protocephala: Proteocephalidae). *Journal of Parasitology*, 57, 869–874.

Moran, N.A. (1994) Adaptation and constraint in the complex life cycles of animals. *Annu. Rev. Ecol. Syst.*, 25, 573–600.

Morley, N.J. (2012) Thermodynamics of miracidial survival and metabolism. *Parasitology*, 139, 1640–1651.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.

Nakagawa, S. & Freckleton, R.P. (2008) Missing inaction: the dangers of ignoring missing data. *Trends in Ecology & Evolution*, 23, 592–596.

Park, A.W. (2019) Food web structure selects for parasite host range. *Proc. R. Soc. B Biol. Sci.*, 286, 20191277.

Parker, G.A., Chubb, J.C., Ball, M.A. & Roberts, G.N. (2003) Evolution of complex life cycles in helminth parasites. *Nature*, 425, 480–484.

Parker, G.A., Ball, M.A. & Chubb, J.C. (2009) To grow or not to grow? Intermediate and paratenic hosts as helminth life cycle strategies. *Journal of Theoretical Biology*, 258, 135–147.

Parr, C.S., Wilson, N., Leary, P., Schulz, K.S., Lans, K., Walley, L., Hammock, J.A., Goddard, A., Rice, J., Studer, M., et al. (2014) The Encyclopedia of Life v2: providing global access to knowledge about life on Earth. *Biodivers. Data J.*, 2, e1079.

Penone, C., Davidson, A.D., Shoemaker, K.T., Di Marco, M., Rondinini, C., Brooks, T.M., Young, B.E., Graham, C.H. & Costa, G.C. (2014) Imputation of missing data in life-history traits datasets: which approach performs the best? *Methods in Ecology and Evolution*, 5, 961–970.

Phillips, J.A., Vargas Soto, J.S., Pawar, S., Koprivnikar, J., Benesh, D.P. & Molnár, P.K. (2022) The effects of phylogeny, habitat, and host characteristics on the thermal sensitivity of helminth development. *Proc. R. Soc. B Biol. Sci.*, 289, 20211878.

Poulin, R. (2010) The selection of experimental doses and their importance for parasite success in metacercarial infection studies. *Parasitology*, 137, 889–898.

Poulin, R. & Latham, A.D.M. (2003) Effects of initial (larval) size and host body temperature on growth in trematodes. *Canadian Journal of Zoology*, 81, 574–581.

Poulin, R. & George-Nascimento, M. (2007) The scaling of total parasite biomass with host body mass. *International Journal for Parasitology*, 37, 359–364.

Poulin, R., Wise, M. & Moore, J. (2003) A comparative analysis of adult body size and its correlates in acanthocephalan parasites. *International Journal for Parasitology*, 33, 799–805.

Randhawa, H.S. & Poulin, R. (2009) Determinants and consequences of interspecific body size variation in tetraphyllidean tapeworms. *Oecologia*, 161, 759–769.

Rees, J.A. & Cranston, K. (2017) Automated assembly of a reference taxonomy for phylogenetic data synthesis. *Biodivers. Data J.*, 5, e12581.

Ricciardi, A. & Bourget, E. (1998) Weight-to-weight conversion factors for marine benthic macroinvertebrates. *Mar. Ecol. Prog. Ser.*, 171, 245–251.

Rietschel, G. (1973) Untersuchungen zur Entwicklung einiger in Krähen (Corvidae) vorkommender Nematoden. *Zeitschrift Fur Parasitenkunde*, 42, 243–250.

Rosen, R. & Dick, T.A. (1983) Development and infectivity of the procercoid of *Triaenophorus crassus* Forel and mortality of the first intermediate host. *Canadian Journal of Zoology*, 61, 2120–2128.

Rowe, L. & Ludwig, D. (1991) Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology*, 72, 413–427.

Skorping, A., Read, A. & Keymer, A. (1991) Life history covariation in intestinal nematodes of mammals. *Oikos*, 60, 365–372.

Steinauer, M.L. & Nickol, B.B. (2003) Effect of cystacanth body size on adult success. *Journal of Parasitology*, 89, 251–254.

Stigge, H.A. & Bolek, M.G. (2015) The alteration of life history traits and increased success of *Halipegus eccentricus* through the use of a paratenic host: a comparative study. *Journal of Parasitology*, 101, 658–665.

Tierney, J. & Crompton, D. (1992) Infectivity of plerocercoids of *Schistocephalus solidus* (Cestoda: Ligulidae) and fecundity of the adults in an experimental definitive host, *Gallus gallus*. *Journal of Parasitology*, 78, 1049–1054.

Trouvé, S., Sasal, P., Jourdane, J., Renaud, F. & Morand, S. (1998) The evolution of life-history traits in parasitic and free-living platyhelminthes: a new perspective. *Oecologia*, 115, 370–378.

Trouvé, S., Morand, S. & Gabrion, C. (2003) Asexual multiplication of larval parasitic worms: a predictor of adult life-history traits in Taeniidae? *Parasitology Research*, 89, 81–88.

Trudgill, D.L., Honek, A., Li, D. & Van Straalen, N.M. (2005) Thermal time – concepts and utility. *Annals of Applied Biology*, 146, 1–14.

Van Buuren, S. (2018) Flexible imputation of missing data. CRC Press, Boca Raton, FL.

Weinersmith, K.L., Warinner, C.B., Tan, V., Harris, D.J., Mora, A.B., Kuris, A.M., Lafferty, K.D. & Hechinger, R.F. (2014) A lack of crowding? Body size does not decrease with density for two behavior-manipulating parasites. *Integrative and Comparative Biology*, 54, 184–192.

Werner, E. & Gilliam, J. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.*, 15, 393–425.

Wilman, H., B, J., S, J., de, L.R.C., R, M. & J, W. (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.

Associate Editor: S. Foitzik
Handling Editor: T. Chapman

## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementry Information