OIKOS

Meta-analysis

A meta-analysis of how parasites affect host consumption rates

Agata Mrugała[1,2,3], **Justyna Wolinska**[1,2,3] **and Jonathan M. Jeschke**[1,2,3]

[1]Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany
[2]Department of Biology, Chemistry, Pharmacy, Institute of Biology, Freie Universität Berlin, Germany
[3]Berlin-Brandenburg Institute of Advanced Biodiversity Research, Berlin, Germany

Correspondence: Agata Mrugała (agata_mrugala@wp.pl)

Oikos
2023: e09700
doi: 10.1111/oik.09700
Subject Editor: Ellen Decaestecker
Editor-in-Chief: Dries Bonte
Accepted 13 April 2023

Parasites are known to mediate trophic interactions and can, for example, modify how consumers acquire resources. These modifications of host feeding behaviour can be imposed through three interconnected mechanisms affecting: 1) host food acquisition, 2) host food digestion or 3) host energy budgets. As a result, infected hosts may consume more, less or the same amount of food compared to their uninfected conspecifics. It is commonly assumed that infected hosts have lower consumption rates than uninfected hosts, but a comprehensive quantitative synthesis investigating the effects of parasites on host consumption rate has been lacking thus far. To fill this knowledge gap, we systematically searched for experimental studies that evaluated changes in consumption rate of infected vs uninfected hosts. In total, we extracted 158 effect sizes from 68 studies. We then performed meta-analyses of mean differences in host consumption rates and their variation. The analyses were carried out for all taxonomic groups as well as separately for vertebrate and invertebrate hosts. The main-effects meta-analyses confirmed a generally negative effect of parasites on host consumption rates; infected hosts consumed on average 25% less food than their uninfected conspecifics. In addition, there was a significant increase in the variability in host consumption rate, on average by 25%, indicating that parasites can have variable effects on the foraging behaviour of their hosts. The meta-regression models revealed that several moderator variables related to host and parasite characteristics influence host consumption rate. Experimental infection had a stronger influence on variance effects than natural infection. Parasitic infections reduced consumption rate of vertebrate hosts by 28% and

Synthesis

Parasites modify host consumption rates through direct and indirect changes to host food acquisition, digestion and energy budgets. As a result, infected hosts may consume more, less or an equal amount of food compared to uninfected conspecifics. Yet, the specific effects of parasites are often context-dependent and the underlying reasons of observed differences - difficult to determine. This meta-analysis serves as the first comprehensive overview of the effects of parasites on the host feeding capacity, sheds light on the factors contributing to the observed differences and provides novel insights on how parasites affect the variability in host feeding behaviour.

NORDIC SOCIETY OIKOS

www.oikosjournal.org

thus more strongly than those of invertebrates, which were reduced by 22%. We conclude with recommendations to facilitate future ecological research syntheses on host–parasite interactions and beyond.

Keywords: behaviour, consumer-resource interactions, feeding rate, host-parasite interaction, meta-analysis of variance, parasitic infection, phylogenetic meta-analysis

Introduction

Although usually small, short-lived and hidden within their host organisms, parasites are pervasive components of biological communities (Poulin 1999, Hatcher et al. 2012, Friesen et al. 2020). In a myriad of ways, they are able to regulate host population abundance and to mediate the dynamics of whole communities (Minchella and Scott 1991, Marcogliese 2004, Wood et al. 2007). Besides their considerable impact on host demography by direct effects on survival and reproduction, parasites may also indirectly affect interactions of their hosts with other species, via altering consumer–resource relationships. Specifically, parasites affect the efficiency of consumers in obtaining prey and the susceptibility of prey to predation (Poulin 1999, Hatcher et al. 2012). Hence, these inconspicuous members of biological communities mediate species interactions at all trophic levels and form important nodes in natural food webs (Lafferty et al. 2008, Hatcher et al. 2012, Morton and Lafferty 2022).

Parasite-induced changes in trophic interactions depend on whether the infected host is a predator or prey. For example, trophically transmitted parasites are known to affect the exposure of their infected hosts (i.e. prey) to predation, via causing changes to the activity, colouration, choice of microhabitat or predator avoidance responses (Thomas et al. 2002, Kunz and Pung 2004, Lagrue et al. 2016, de Bekker et al. 2018, Thünken et al. 2019). Although less studied, parasites may also exert considerable effects on the behaviour of consumers (e.g. predators) by changing their activity, food intake or propensity to risk-taking. For example, infection of the rusty crayfish *Faxonius rusticus* with *Microphallus* trematodes reduced rates of feeding and growth compared to uninfected individuals (Sargent et al. 2014, Reisinger and Lodge 2016). However, likely due to increased boldness induced by infection, infected crayfish had higher feeding rates than uninfected individuals in a mesocosm experiment with predatory fish (Reisinger and Lodge 2016). As suggested by the authors, the parasite-induced changes in the behaviour of rusty crayfish may further affect both macrophytes and macroinvertebrate communities (Reisinger and Lodge 2016). Considerable reduction in consumption rates was also observed in the mud crab *Eurypanopeus depressus* infected with the rhizocephalan barnacle *Loxothylacus panopei* (O'Shaughnessy et al. 2014, Toscano et al. 2014). As voracious consumers of bivalves, *E. depressus* exert top–down control within intertidal oyster reefs. Consequently, the reduction of *E. depressus* predation may modify their ecological role and cause trophic changes in these aquatic ecosystems (O'Shaughnessy et al. 2014, Toscano et al. 2014).

Parasites may also affect the feeding behaviour of other groups of consumers, for example grazers. Aquatic snails play important roles in benthic communities through their top–down control of algal and periphyton biomass, and the enhancement of primary production (Marks and Lowe 1989, Pyron and Brown 2015). The grazing behaviour of aquatic snails is especially affected by trematode parasites that use them as intermediate hosts, although available experimental studies show that grazing rates of infected snails may be higher, lower or similar to those of uninfected conspecifics. For example, infected *Littorina littorea* and *Littoraria irrorata* snails consumed up to 55% less than uninfected snails (Wood et al. 2007, Clausen et al. 2008, Morton 2018), whereas infected individuals of *Physella acuta* had higher grazing rates compared with uninfected snails (Bernot and Lamberti 2008). Furthermore, the feeding of *Lymnaea stagnalis* and *Radix lagotis* seems to be unaffected by trematode infection (Vivas Muñoz et al. 2018). As observed in the field, the algal community structure changes in response to the infection rates in snail populations (Bernot and Lamberti 2008), confirming the high ecological relevance of trematodes in structuring benthic communities.

Parasitic infections may also modify the behaviour of those consumers that play significant roles as ecosystem engineers in terrestrial ecosystems. For example, dung beetles which consume and burrow faeces contribute to suppression of various pathogens, facilitate soil aeration and fertilization, and increase the rate of nutrient cycling (Nichols et al. 2008). Their infection with nematodes considerably decreases the amount of consumed faeces and reduces the burial of faeces below the surface soil (Boze et al. 2012, Boze and Moore 2014). In contrast, nematode infection of horned passalus beetles resulted in an increase of their wood consumption by 15% (Davis and Prouty 2019). The latter result highlights that parasites may also improve an ecosystem service provided by their hosts; through, for instance, an increase in the mechanical breakdown of fallen wood and consequently in the wood decomposition rate.

All in all, the existing literature suggests that infected hosts may consume more, less or an equal amount of food compared to uninfected conspecifics. The underlying reasons for observed differences are often difficult to determine, but three general interconnected mechanisms can be distinguished (Fig. 1). First, parasitic infections can decrease host ability to encounter, detect and catch prey (i.e. to acquire food). This can be due to reduction of host sensory performance. For instance, the feeding efficiency of European perch declines with increasing infection intensity of *Tylodelphys clavata* metacercariae in the vitreous humour of their eyes

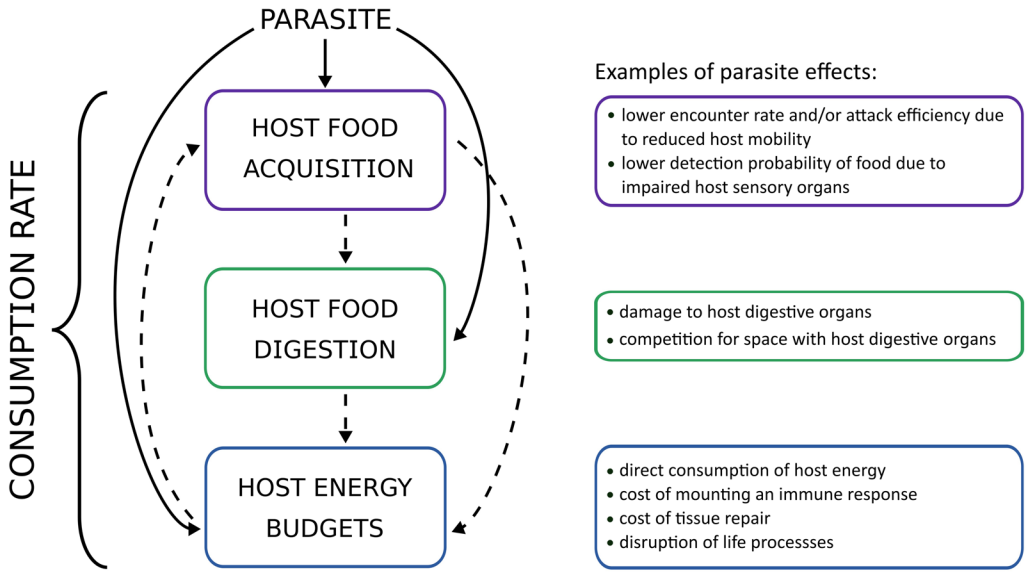

Figure 1. Parasites may affect consumption rates of their hosts through effects on host food acquisition, food digestion and energy budgets. The way in which these three mechanisms and their associated effects are related is indicated by solid (direct effects) and dashed (indirect effects) arrows.

(Vivas Muñoz et al. 2017, 2019), strongly reducing their visual sense. Furthermore, parasites can reduce host mobility, which typically reduces host encounter rate with prey and host attacking efficiency – two important determinants of consumption rate (Jeschke et al. 2002). This can be caused by parasite-induced changes to host morphology and physiology (Binning et al. 2017). Parasites that occupy host muscles, as the microsporidian *Thelohania contejeani* infecting crayfish species, may cause damage to muscle tissue and hence reduce their function (Haddaway et al. 2012). Host mobility can also be impaired by growing externa of rhizocephalan barnacle parasites that impede crab manoeuvrability in oyster reef interstices (O'Shaughnessy et al. 2014) or by gill infestation by mussel larvae (i.e. glochidia), resulting in elevated ventilation rates and reduced oxygen consumption of fish hosts (Crane et al. 2011, Horký et al. 2014).

Second, parasites can reduce host digestive capabilities either through damage to their internal organs (i.e. hepatopancreas and gastrointestinal tract) that impair their normal function (Britton et al. 2011, Sargent et al. 2014, Toscano et al. 2014) or through competition for space with the host's internal organs that may potentially reduce space for food storage (Cunningham et al. 1994, Sánchez et al. 2016). For instance, the pathological damage to the intestinal tract of common carp caused by the cestode parasite *Bothriocephalus acheilognathi* had obstructing effects on carp feeding (Britton et al. 2011), while the growth of plerocercoid larvae of the cestode *Schistocephalus solidus* in sticklebacks' body cavity largely decreased their stomach capacity (Cunningham et al. 1994).

Third, the effects of parasites on host feeding behaviour can be mediated by their impacts on host energy budgets. These may include direct energy consumption by parasites, metabolic costs of mounting an immune response or costs necessary for tissue repair and replacement (Lochmiller and Deerenberg 2000, Sadd and Schmid-Hempel 2009). These responses will be followed by reallocation of energy from certain life processes (e.g. reproduction, growth and activity) to others (Lettini and Sukhdeo 2010, Leaphart and Zelmer 2017). Consequently, the deficit of available energy may either be compensated by an increased consumption (Martin-Hernandez et al. 2011, Davis and Prouty 2019) or lead to a decline in the food intake (i.e. anorexia; Kyriazakis et al. 1998, Mercer et al. 2000, Pirhonen et al. 2003). Furthermore, the metabolic requirements of hosts might be reduced if their life processes are disrupted by parasites. For example, the trematode-induced castration of snails or bacteria-induced castration of water fleas leads to changes in energy availability that would otherwise be allocated for host reproduction (Ebert et al. 2004, Wood et al. 2007, Vivas Muñoz et al. 2018). The effects of parasites on host food consumption are additionally dependent on the amount of released energy. If the energy requirements of the parasite and the host match released energy pools, no change in the consumption rate may be observed, while the reduction in the host's energetic demands (e.g. due to disrupted reproduction) may decrease consumption rate. Moreover, if infected hosts experience insufficient levels of energy, they may compensate by an increased feeding or reduced activity (O'Shaughnessy et al. 2014, Toscano et al. 2014, Vivas Muñoz et al. 2018).

These three interconnected mechanisms advance our understanding of the potential impacts that parasitic infections can impose on host feeding behaviour. They are, however, not sufficient to explain observed differences in the magnitude and direction of those impacts. Moreover, no comprehensive quantitative synthesis investigating differences in consumption rate caused by parasitic infections is currently available. To address these issues, we performed a meta-analysis of studies that experimentally tested consumption rate of infected versus

uninfected hosts. We not only investigated mean differences, but also performed a meta-analysis of variance (Nakagawa et al. 2015, Sánchez-Tójar et al. 2020, Hasik et al. 2023), as different parasites may have variable effects on host foraging behaviour. Our analyses of infected animal hosts across taxonomic groups addressed the following questions: 1) how strong is the effect of parasitic infection on host consumption rate and on the variability in host foraging behaviour? 2) Does this effect lead to a decrease or increase in host consumption rate and in its variance? 3) Which factors explain the observed variation in effect sizes? As we expect differences in responses to parasitic infections between vertebrate and invertebrate hosts, we also performed our analyses separately for these two groups.

Material and methods

Literature search

We searched for the relevant literature in the Web of Science Core Collection (WoS) following the guidelines of the PRISMA statement (Moher et al. 2010). Details of the search strategy, including numbers of assessed records at each phase of our search, are presented in the Supporting information. The primary search in WoS was performed on 27 September 2019 with the search term: (TS = ((predat* OR host) AND (parasit* OR infect*) AND ('consumption rate*' OR 'feeding rate*' OR 'feeding ecology' OR 'functional response' OR 'trophic ecology' OR 'grazing' OR 'food intake' OR 'behaviour* modification' OR 'behaviour* manipulation' OR 'feeding strategy' OR 'food density'))). Subsequently, additional papers that were not returned during primary search but were cited in the WoS-selected articles or cited the WoS-selected articles, were also checked for eligibility. This process aimed to exhaust available literature and ended on 14 August 2020. In total, we screened 3924 abstracts and assessed 859 full-text articles for inclusion in this meta-analysis. The screening of full-text articles resulted in 92 records. We further excluded 24 records, as they did not report sufficient statistical information to be included in the meta-analysis. Our final dataset consisted of 68 studies published between 1973 and 2019 (for the list of included studies see the Supporting information).

Articles were included in the meta-analysis if they met all of the following eligibility criteria:

1) The study was published in a peer-reviewed academic journal.
2) The consumption rate of the animal host was evaluated in an experimental setting with two groups: infected and uninfected (control). The infected group was derived either from natural or experimental infection. In the latter case, the experimental infection was carried out either through direct inoculation or exposure of experimental animals; both happened only once (i.e. studies with recurrent dosing were excluded). The control group could either consist of individuals known to be uninfected or hosts that underwent an experimental parasite removal through anti-parasitic treatment.
3) The animal hosts were infected either by a microparasite (i.e. bacteria, fungi, protozoans, viruses) or a macroparasite (i.e. arthropods, parasitic molluscs, helminths).
4) Both groups (infected and uninfected) consisted of different individuals (i.e. within-subject design studies were excluded).
5) The consumption rate (of a single individual or a whole group) was measured as: number of consumed prey/food items, dry/wet weight of consumed prey/plants, weight of egesta, counts of faecal pellets, percentage of gut with food content, dry matter/organic matter intake.

However, we excluded studies if:

1) Apart from an effect of the parasites on host consumption rate, the study also measured an effect of an additional factor as e.g. immune activation, predator's presence, light intensity. We excluded studies in which the effect of parasites could not be isolated from the study design.
2) The study focused on the effect of parasitoids on the consumption rate of their hosts. Parasitoids are insects that during their larval stages develop by eating the organs of their hosts, which eventually leads to the host's death (Mills 2009). Hence, parasitoids occupy an intermediate position between predators and true parasites.
3) The study examines the use of parasites as biological control agents. This includes studies in which the host is a known pest on crops, and the parasite is known to control crop pests. Due to their bias towards parasites that lower consumption rates of their hosts, such studies were excluded from this meta-analysis.

From each study, we recorded the year of publication, parasite taxonomy (phylum and species), type of parasite (macro- or microparasite), parasite life cycle (complex or direct), host taxonomy (group [vertebrate or invertebrate], class and species), details about the host (i.e. sex, age), infection type (natural or experimental), infected organ (body cavity, circulatory, digestive, muscular, sensory, whole body), prey mobility (immobile, mobile, unknown), study environment (freshwater, marine or terrestrial) and the geographic place where the experiment was performed (continent and country).

Data analysis

All analyses were performed in R ver. 4.0.3 (www.r-project.org). For the calculation of effect sizes, we extracted data either from the figures (using WebPlotDigitizer), statistics reported in the text or from the raw data (provided by the authors of one study). We used the following criteria to select data for effect sizes: 1) from studies that used functional responses to measure host consumption rates, we extracted information from three prey densities: the lowest, middle and the highest; 2) from experimental trials that tested consumption rates at

different temperatures, we only chose the temperature that was the closest to the natural temperature; 3) if consumption rate was measured multiple times over a specific period of time, only the last measurement was considered; 4) from studies that tested the effect of different infection intensities on host consumption, we extracted all data and 5) similarly, all data was extracted from studies that used either different developmental stages of hosts or different types of prey (defined in our meta-analysis as any food item eaten).

We used the bias-corrected estimator of log response ratio of group means (RR^{Δ}, hereafter referred to as: mean response; Lajeunesse 2015) to compare the effects of parasitic infection on consumption rates of infected versus uninfected hosts. This effect size estimator is calculated from the log response ratio of group means (lnRR; Hedges et al. 1999) and corrects for bias introduced by quantifying the outcomes of studies with small sample sizes. The choice of mean response ratio was also dictated by its lower sensitivity to heteroscedasticity, compared with Cohen's *D* and Hedges' *g* (Borenstein et al. 2009). The log coefficient of variation ratio (lnCVR, hereafter referred to as: variation) was used to study variance effects (Nakagawa et al. 2015). The effect sizes of lnRR and lnCVR were computed from means and standard deviations (SD) with the function *escalc* in the R package 'metafor' (Viechtbauer 2010) or from medians and quartiles with the function *metacont* in the R package 'meta' (Schwarzer 2007, Balduzzi et al. 2019), using infected and uninfected groups as treatment and control groups, respectively. Subsequently, we used the equations provided by Lajeunesse (2015) to calculate RR^{Δ} and $var(RR^{\Delta})$. The mean response and variation estimates can be interpreted as the percentage of change between the treatment and control group. Consequently, negative effect sizes represent a decrease in host consumption rate or a decrease in the variability in host consumption rate, respectively.

We performed multilevel random-effects meta-analysis with the function *rma.mv* (R package 'metafor',). We chose the random-effects model due to the large variability in experimental conditions and taxonomic groups examined in our meta-analysis. This model assumes that the effect sizes in each study are independent of each other (Thompson and Higgins 2002, Borenstein et al. 2009, Noble et al. 2017). We performed two types of models: 1) main-effects models to test for the general effect of parasitic infection on host consumption rates and 2) multilevel meta-regression models to assess the contribution of the fixed effects (moderator variables) to the magnitude and direction of the effect sizes. Each moderator variable was tested in a separate meta-regression model to account for the potential collinearity between these variables. All models were performed for the whole dataset as well as separately for vertebrates and invertebrates.

In the main-effects model, we fitted the non-phylogenetic and phylogenetic models to investigate how both the overall effects and their level of uncertainty are influenced by non-independence due to the degree of relatedness between species. The variance–covariance matrix with phylogenetic information was constructed with the use of R packages 'rotl' (Michonneau et al. 2016) and 'ape' (Paradis and Schliep 2019) following the R script provided by Moran et al. (2021). Existing phylogenies and taxonomic information were obtained from the Open Tree of Life (Michonneau et al. 2016; for the final phylogenetic tree of all host animals, Supporting information). In the multilevel meta-regression models, however, only the phylogenetic model was used. In addition to host phylogeny, we used effect size ID, study ID, host species and parasite species as random effects in all models to account for effect- , study- and species-level non-independence (Nakagawa and Santos 2012, Noble et al. 2017). Moreover, we performed the meta-regression models for the levels of moderator variables with > 10 effect sizes to ensure sufficient statistical power. 'Unknown' levels of moderator variables were not considered in the meta-regression models.

Heterogeneity was assessed with the use of R packages 'metafor' and 'orchaRd' (Nakagawa et al. 2021). For the main-effects models, we estimated the absolute heterogeneity (Q; via function *rma.mv* in R package 'metafor') as well as total and separate relative heterogeneity for each random factor (I^2; Nakagawa and Santos 2012; via function *i2_ml* in R package 'orchaRd'). Following Higgins et al. (2003), the heterogeneity was considered as low, moderate and high if I^2 was 25, 50 and 75%, respectively. In addition to confidence intervals of the mean effect, we calculated prediction intervals that are particularly relevant in ecological meta-analyses with high heterogeneity (Nakagawa et al. 2021). The prediction interval in the random-effects model estimates the true effect that is expected for 95% of similar future studies (IntHout et al. 2016). For each meta-regression model, we obtained the residual heterogeneity Q_E, the moderator-specific heterogeneity Q_M (both via function *rma.mv* in R package 'metafor') and variance statistic $R^2_{marginal}$ (via function *r2_ml* in R package 'orchaRd'). $R^2_{marginal}$ represents the percentage of heterogeneity explained by the inclusion of each moderator variable (Nakagawa and Schielzeth 2013).

We used nine moderator variables to assess their contribution to the observed heterogeneity in the meta-regression models. They were divided into three groups, each including variables related to 1) host, 2) parasite and 3) experimental design characteristics. The variables related to host characteristics included: host group (vertebrate, invertebrate), host age (adult, juvenile) and host sex (female, male, mixed). We have also tested parasite type (macroparasite, microparasite), parasite life cycle (complex, direct) and infected organ (body cavity, circulatory, digestive, muscular, sensory, whole body) as parasite characteristics. Finally, to account for differences in experimental design that might have influenced the variation of effect sizes, we included type of infection (experimental, natural) and prey mobility (mobile, immobile) as moderator variables.

Publication bias

Selective publication of statistically significant results, a phenomenon known as publication bias or the 'file drawer problem', is an important concern in meta-analysis (Rosenthal

1979, Dickersin 2005). To visually identify a potential publication bias in our dataset, we used the funnel plot (Sterne and Egger 2001), which we calculated via the function *funnel* in the R package 'metafor' with the standard error as a measure of study size on the vertical axis. The slight asymmetry of the distribution of effect sizes on this plot suggests that some relevant studies might not have been published (Supporting information). However, the majority of points were distributed symmetrically on the funnel plot. We also quantified the publication bias using Egger's regression (Egger et al. 1997; via function *regtest* in R package 'metafor') and trim-and-fill methods (Duval and Tweedie 2000; via function *trimfill* in R package 'metafor'), where the number of missing studies was estimated as L0 and R0 estimators. The Egger's regression test indicated that effect sizes were not significantly related to their standard errors ($z = 0.59$, $p = 0.5562$), showing no significant evidence for funnel-plot asymmetry. Furthermore, adding 18 effect size estimates that were likely to be missing according to the trim-and-fill methods resulted only in a slight decrease of the mean response estimate (−0.27, 95% confidence intervals: −0.34, −0.19). As the studies used in the meta-analysis focused on effects on host consumption rates, we did not conduct publication bias tests for variation (lnCVR).

Results

Our dataset includes 158 effect sizes obtained from 68 studies, with vertebrate and invertebrate datasets containing 56 effect sizes from 30 studies and 102 effect sizes from

Table 1. Main-effects model estimates (bias-corrected estimator of log response ratio of group means[RR^{A}] and log coefficient of variation ratio [lnCVR]) and heterogeneity statistics (Q and I^2) calculated for the entire dataset and separately for vertebrates and invertebrates. Estimates are provided for non-phylogenetic (non-phylo) and phylogenetic (phylo) models. Total and separate random-effect specific heterogeneity (I^2) is expressed in percentages. Q refers to absolute heterogeneity. Round brackets contain 95% confidence intervals. Square brackets contain 95% prediction intervals. $N_{effect\ size}$ – number of effect sizes used in each model. Effect ID and Study ID refer to identifiers assigned to individual effect sizes and studies, respectively.

	Effect size	$N_{effect\ size}$ (N_{study})	Mean effect	$I^2_{Effect\ ID}$ (%)	$I^2_{Study\ ID}$ (%)	$I^2_{Host\ species}$ (%)	$I^2_{Parasite\ species}$ (%)	I^2_{Total} (%)	Q
All species	RR^{A} (non-phylo)	158 (68)	−0.22 (−0.32, −0.11) [−1.04, 0.61]	38.64	16.28	<0.001	42.72	97.64	2596.11 p < 0.0001
	RR^{A} (phylo)	158 (68)	−0.22 (−0.32, −0.11) [−1.04, 0.61]	38.64	16.28	<0.001	42.72	97.64	2596.11 p < 0.0001
	lnCVR (non-phylo)	158 (68)	0.21 (0.07, 0.35) [−0.90, 1.32]	37.98	32.67	<0.001	7.97	78.62	957.35 p < 0.0001
	lnCVR (phylo)	158 (68)	0.22 (0.04, 0.41) [−0.89, 1.34]	37.99	32.35	3.24	5.2	78.79	957.35 p < 0.0001
Vertebrates	RR^{A} (non-phylo)	56 (30)	−0.25 (−0.33, −0.16) [−0.78, 0.29]	84.34	12.09	<0.001	<0.001	96.43	665.87 p < 0.0001
	RR^{A} (phylo)	56 (30)	−0.25 (−0.33, −0.16) [−0.78, 0.29]	84.34	12.09	<0.001	<0.001	96.43	665.87 p < 0.0001
	lnCVR (non-phylo)	56 (30)	0.36 (0.10, 0.61) [−1.04, 1.75]	33.94	52.8	<0.001	<0.001	86.74	614.62 p < 0.0001
	lnCVR (phylo)	56 (30)	0.36 (0.10, 0.61) [−1.04, 1.75]	33.94	52.78	<0.001	<0.001	86.74	614.62 p < 0.0001
Invertebrates	RR^{A} (non-phylo)	102 (38)	−0.2 (−0.37, −0.03) [−1.23, 0.82]	22.31	19.52	<0.001	55.25	97.08	1810.89 p < 0.0001
	RR^{A} (phylo)	102 (38)	−0.2 (−0.37, −0.03) [−1.23, 0.82]	22.31	19.52	<0.001	55.25	97.08	1810.89 p < 0.0001
	lnCVR (non-phylo)	102 (38)	0.11 (−0.02, 0.25) [−0.70, 0.93]	43.63	<0.001	<0.001	20.37	64	313 p < 0.0001
	lnCVR (phylo)	102 (38)	0.11 (−0.02, 0.25) [−0.70, 0.93]	43.63	<0.001	<0.001	20.37	64	313 p < 0.0001

38 studies, respectively (Table 2). The vertebrate dataset includes the following host groups: amphibians (11 host species; 16 effect sizes, 6 studies), birds (3 host species; 4 effect sizes, 2 studies), fish (8 host species; 21 effect sizes, 12 studies) and mammals (5 host species; 15 effect sizes, 10 studies). The invertebrate dataset includes: crustaceans (15 host species; 60 effect sizes, 24 studies), gastropods (7 host species; 16 effect sizes, 7 studies) and insects (7 host species; 26 effect sizes, 7 studies). None of included studies concern vectors and vector-borne parasites.

Main-effects models

All main-effects models showed negative effects in mean response models and positive effects in variation models, indicating a lower consumption rate of infected versus uninfected hosts overall, but an increase in the variability in host consumption rate due to parasitic infections (Table 1, Fig. 2). Heterogeneity could be resolved by phylogeny only in both general variation models, in which the 95% confidence intervals overlapped with zero (Table 1). Total heterogeneity I^2 was high in all mean response models (> 96%; Table 1), which is in line with the expected high levels of heterogeneity due to the system-specific nature of ecological phenomena (Senior et al. 2016). Indeed, despite the overall negative effect of parasites on host consumption rate, almost one third of all mean effect sizes was positive. In the variation models, total heterogeneity I^2 was moderate to high (64–87%; Table 1). These results are consistent with the expected lower levels of heterogeneity in variation compared to mean response models (Sánchez-Tójar et al. 2020). The high heterogeneity among effect sizes was also indicated by the wide prediction intervals overlapping with zero (Table 1, Fig. 2). The I^2 estimates for random effects varied across models (Table 1).

The general main-effects meta-analysis indicated that infected hosts consume on average 25% less food than their uninfected conspecifics. Similarly, the infection with parasites increased variability in host consumption rate on average by 25% (phylogenetic model; non-phylogenetic model: 23%). Moreover, parasitic infection leads to stronger decrease in consumption rate of vertebrate hosts (both models: 28%) compared to invertebrate hosts (both models: 22%). The increase in variance is also larger in vertebrate (both models: 43%) than in invertebrate hosts (both models: 12%).

Meta-regression models

The difference between vertebrate and invertebrate hosts explained only a negligible amount of heterogeneity among mean response estimates ($R^2_{marginal} = 0.20\%$), although moderator-specific heterogeneity indicated that 'host group' significantly influenced effect sizes (Table 2). The 95% confidence intervals did not overlap with zero for any host group, and a higher decrease of mean consumption rates was observed for vertebrate hosts (Table 3). In the variation model, however, 'host group' explained some amount of heterogeneity ($R^2_{marginal} = 4.40\%$; Table 2). The 95% confidence intervals did not overlap with zero for the vertebrates, with

Table 2. Heterogeneity statistics testing contribution of moderator variables to variation in effect sizes (RR^{Δ} and lnCVR) calculated for the entire dataset: residual heterogeneity (Q_E), moderator explained heterogeneity (Q_M) and the estimated percentage of heterogeneity explained by the moderators ($R^2_{marginal}$). Degrees of freedom (df) are provided for Q_E and Q_M. The levels of each moderator variable are provided in Table 3.

	Moderator variable	RR^{Δ}			lnCVR		
		Q_E (residual)	Q_M (moderator)	$R^2_{marginal}$ [%]	Q_E (residual)	Q_M (moderator)	$R^2_{marginal}$ [%]
Host characteristics	Host group	2476.76 (df = 156) p < 0.0001	16.6 (df = 2) p = 0.0002	0.2	927.62 (df = 156) p < 0.0001	13.19 (df = 2) p = 0.0014	4.4
	Host age	2567.65 (df = 150) p < 0.0001	16.81 (df = 2) p = 0.0002	0.63	899.31 (df = 150) p < 0.0001	6.17 (df = 2) p = 0.0456	3.89
	Host sex	2293.49 (df = 129) p < 0.0001	18.63 (df = 3) p = 0.0003	3.84	803.34 (df = 129) p < 0.0001	9.84 (df = 3) p = 0.0200	2.8
Parasite characteristics	Parasite type	2401.72 (df = 156) p < 0.0001	19.16 (df = 2) p < 0.0001	3.58	937.36 (df = 156) p < 0.0001	9.96 (df = 2) p = 0.0069	3.9
	Life cycle	2586.71 (df = 156) p < 0.0001	17.26 (df = 2) p = 0.0002	0.9	951.61 (df = 156) p < 0.0001	11.83 (df = 2) p = 0.0027	3.01
	Infected organ	2326.73 (df = 148) p < 0.0001	15.96 (df = 5) p = 0.0070	1.42	846.95 (df = 148) p < 0.0001	10.95 (df = 5) p = 0.0524	3.77
Experimental design	Infection type	2516.6 (df = 156) p < 0.0001	15.51 (df = 2) p = 0.0004	2.45	940.96 (df = 156) p < 0.0001	12.14 (df = 2) p = 0.0023	3.4
	Prey mobility	2345.7 (df = 152) p < 0.0001	14.98 (df = 2) p = 0.0006	<0.00	932.27 (df = 152) p < 0.0001	5.42 (df = 2) p = 0.0664	1.13

the variation estimates for vertebrates being three times as high as for invertebrates (Table 3), suggesting that parasitic infection significantly increases the variability in consumption rate of vertebrate hosts.

Among other moderator variables related to host characteristics, 'host age' contributed to the observed heterogeneity in all mean response models (Table 2, Supporting information), with infected adult individuals having lower consumption rates than juveniles (Table 3, Supporting information). Furthermore, 'host age' explained a considerable amount of heterogeneity in all variation models (Table 2, Supporting information), with a significantly higher variation in feeding behaviour observed for adult hosts (Table 3, Supporting information). 'Host sex' influenced mean response estimates in the general and invertebrate models ($R^2_{marginal}$ = 3.84% and $R^2_{marginal}$ = 4.73%, respectively; Table 2, Supporting information), indicating that significantly lower consumption rates may be especially observed in experiments with mixed-sex groups (Table 3, Supporting information). Some heterogeneity was, moreover, explained by 'host sex' in the general variation model ($R^2_{marginal}$ = 3.89%; Supporting information), with the highest variability exhibited also by mixed-sex groups (Table 3).

Among moderator variables related to parasite characteristics, 'parasite type' explained variable amounts of heterogeneity in all mean response models (Table 2, Supporting information). The highest amount of heterogeneity was explained in invertebrate mean response model ($R^2_{marginal}$ = 11.55%; Supporting information), indicating that infection with macroparasites may likely lead to significant decreases in mean host consumption of invertebrate hosts (Supporting information). 'Parasite type' explained also variable amounts of heterogeneity in general and vertebrate variation models ($R^2_{marginal}$ = 3.90% and $R^2_{marginal}$ = 5.11%, respectively; Table 2, Supporting information), suggesting that infection with microparasites increases variability in host consumption rate (Table 3, Supporting information). Type of infected organ contributed to the overall heterogeneity in general and vertebrate mean response models ($R^2_{marginal}$ = 1.42% and $R^2_{marginal}$ = 5.68%, respectively; Table 2, Supporting information), in which the significant result was obtained for body cavity and digestive organs in general (Table 3) and circulatory organs and whole body for vertebrates (Supporting information). 'Infected organ' explained also some heterogeneity in the vertebrate variation model ($R^2_{marginal}$ = 3.00%; Supporting information), suggesting that infection of circulatory organs increases variability of host consumption rate (Supporting information).

'Life cycle' explained some amount of heterogeneity in the general and invertebrate mean response models ($R^2_{marginal}$ = 0.90% and $R^2_{marginal}$ = 2.00%, respectively; Table 2, Supporting information). In the invertebrate model, the mean response estimate for parasites with complex life cycles was more than two times higher and its 95% confidence intervals did not overlap with zero (Supporting information). Furthermore, 'life cycle' explained some amount of heterogeneity in the general variation model ($R^2_{marginal}$ = 3.01%; Table 2). The variation estimates for direct life cycle was higher and its 95% confidence intervals did not overlap with zero (Table 3), suggesting that parasites with direct life cycles may cause significant increases in behavioural or physiological variability of infected hosts.

Among moderator variables related to experimental design, the type of infection explained variable amount of

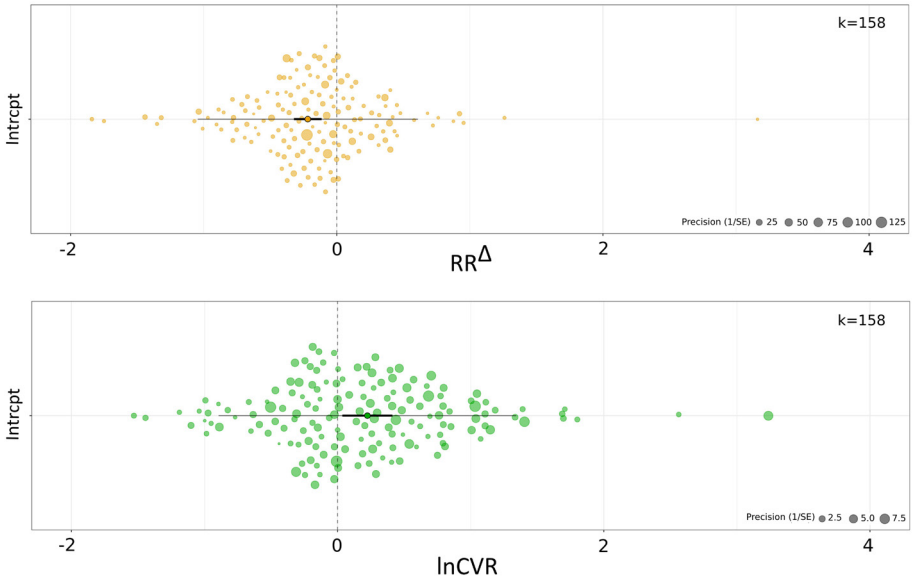

Figure 2. Main-effects phylogenetic model estimates for the entire dataset presented as orchard plots (Nakagawa et al. 2021). (A) mean response (RR^{Δ}) and (B) variation (lnCVR). Central circles with branches represent mean effect sizes. Branches indicate 95% confidence intervals (thicker) and prediction intervals (thinner). Bubbles represent individual effect sizes scaled by their precision (i.e. the inverse of sampling standard error). k refers to the number of effect sizes.

Table 3. Effect size estimates (RR^{Δ} and lnCVR) for each level of tested moderator variables calculated for the entire dataset. Confidence intervals that do not overlap with zero are indicated in bold. $N_{effect\ size}$ – the number of effect sizes, and N_{study} – the number of studies. n/a indicates estimates that were omitted in the analyses due to a low number of effect sizes ($N_{effect\ size} < 10$).

	Moderator variable	Level	$N_{effect\ size}$	N_{study}	RR^{Δ} estimate	lnCVR estimate
Host characteristics	Host group	invertebrate	102	38	**−0.20 (−0.34, −0.07)**	0.12 (−0.05, 0.29)
		vertebrate	56	30	**−0.24 (−0.41, −0.07)**	**0.36 (0.15, 0.57)**
	Host age	adult	111	49	**−0.24 (−0.37, −0.12)**	**0.32 (0.05, 0.60)**
		juvenile	41	16	−0.17 (−0.37, 0.03)	0.07 (−0.28, 0.42)
	Host sex	female	28	13	**−0.24 (−0.45, −0.03)**	0.11 (−0.21, 0.43)
		male	29	15	−0.07 (−0.27, 0.13)	0.22 (−0.09, 0.54)
		mixed	75	40	**−0.28 (−0.42, −0.14)**	**0.34 (0.12, 0.55)**
Parasite characteristics	Parasite type	macroparasite	96	47	**−0.27 (−0.39, −0.14)**	0.15 (−0.04, 0.34)
		microparasite	62	21	−0.11 (−0.29, 0.08)	**0.38 (0.13, 0.62)**
	Life cycle	complex	60	26	**−0.27 (−0.43, −0.10)**	0.10 (−0.12, 0.31)
		direct	98	42	**−0.18 (−0.32, −0.05)**	**0.30 (0.12, 0.47)**
	Infected organ	body cavity	36	17	**−0.26 (−0.49, −0.030**	0.13 (−0.18, 0.43)
		circulatory	11	9	−0.31 (−0.65, 0.02)	**0.57 (0.15, 0.99)**
		digestive	39	22	**−0.23 (−0.41, −0.04)**	0.20 (−0.07, 0.47)
		muscular	16	5	−0.11 (−0.50, 0.28)	0.32 (−0.17, 0.81)
		sensory	5	4	n/a	n/a
		whole body	51	11	−0.18 (−0.45, 0.10)	0.27 (−0.06, 0.60)
Experimental design	Infection type	experimental	77	33	−0.15 (−0.30, 0.01)	**0.33 (0.13, 0.52)**
		natural	81	37	**−0.28 (−0.43, −0.13)**	0.12 (−0.06, 0.30)
	Prey mobility	mobile	72	25	**−0.22 (−0.39, −0.05)**	0.15 (−0.13, 0.43)
		immobile	82	43	**−0.21 (−0.34, −0.09)**	**0.27 (0.04, 0.50)**

heterogeneity in the general and invertebrate mean response models ($R^2_{marginal} = 2.45\%$ and $R^2_{marginal} = 5.34\%$, respectively; Table 2, Supporting information), indicating that natural infections may have a stronger influence on host consumption rates of invertebrates (Supporting information). Moreover, 'infection type' explained also some amounts of heterogeneity in the general variation model ($R^2_{marginal} = 3.40\%$; Table 2), suggesting that experimental infection may lead to significant increases in the variation of feeding behaviour (Table 3). Prey mobility explained some amounts of heterogeneity in vertebrate and invertebrate mean response models ($R^2_{marginal} = 2.56\%$ and $R^2_{marginal} = 2.17\%$, respectively; Supporting information); indicating that feeding on mobile prey can lead to lower consumption rates of infected hosts (Supporting information). This moderator variable did not explain the overall heterogeneity in variation models (Table 2, Supporting information).

Discussion

General patterns in mean consumption rates and its variance

Our meta-analyses of mean and variance provide the first comprehensive overview of the effects of parasitic infections on the consumption rates of animal hosts and attempt to shed light on the potential factors and mechanisms contributing to the observed variability. Across existing experimental studies, a range of variable outcomes have been observed, with substantial differences in their direction and magnitude. The main-effects models in our meta-analyses indicated that while parasitic infections affect host consumption rates on average negatively, the parasites may also increase the variability in host consumption rates.

Studied effects of parasites on host behaviour usually concern the mean behavioural differences between infected versus uninfected hosts, as exemplified by the mean changes in host consumption rates. Some parasites, however, may also affect the variability in the foraging behaviour and thus consumption rate of their hosts. Indeed, host consumption rate may be affected through direct and indirect changes to host food acquisition, digestion or energy budgets (Fig. 1). As illustrated by our analysis, parasitic infections do not only affect mean changes in host consumption rates but also its variability. The changes inflicted on host life processes are often interconnected and develop in different directions, hence they will likely be followed by variable effects on host consumption rates. Specifically, infected hosts may be more likely to adapt their foraging and feeding behaviour to satisfy their nutritional needs. The meta-analysis of variance could, therefore, reveal hidden effects of parasites and broaden our understanding of biological processes (Nakagawa et al. 2015, Sánchez-Tójar et al. 2020, Hasik et al. 2023).

The effects of parasites on host behaviour, and especially its variability, have been so far rarely considered in ecological meta-analyses. A recent meta-analysis by Hasik et al. (2023) investigated how parasites affect predation and herbivory of infected consumers. The authors observed a considerable variation in interaction outcomes, and in contrast to our study, the parasites did not have a significant effect on the mean and variance responses. These differences are most likely caused by the discrepancies in the design of the meta-analyses and the number of included studies, i.e. we applied stricter inclusion criteria excluding studies with biological control agents, used another estimator for

mean response, and collected a larger number of studies. Yet, some patterns resemble each other. For instance, our findings confirm the non-significant increase in the variance response of infected predators and herbivores signalled in Hasik et al. (2023). Our meta-analysis, focusing on a specific type of host-species interactions, provides a more in-depth understanding of this topic and as such complements the study by Hasik et al. (2023).

Factors explaining observed variation in effect sizes

We expected that vertebrate and invertebrate hosts may display differential responses in their foraging behaviour following parasitic infection. The size difference between invertebrate hosts and their parasites is smaller, hence invertebrate hosts may not only be easier to manipulate but also fewer parasites may already be sufficient to modify host behaviour. In turn, the effects on vertebrates may be rather proportional to parasite load (Poulin and Thomas 1999). Yet our meta-analysis suggested that parasite effects might be stronger on vertebrate hosts, for which we observed a stronger decrease in mean consumption rate. Furthermore, more insight was provided by separate meta-regressions on vertebrate and invertebrate datasets with 'parasite type' (macroparasite versus microparasite) as moderator variable. In vertebrate hosts, even though both parasite types contributed similarly to the decreases in mean consumption rates, the variability in consumption rates appeared to be significantly affected by microparasites. For invertebrate hosts, we noted that macroparasites have a stronger effect on mean consumption rates, compared with microparasites. This confirms our predictions that the smaller size difference between the host and its parasite may lead to stronger effects on invertebrate consumption rates.

The way in which parasites affect host behaviour may be also associated with host characteristics, such as age and size. For example, meta-analysis on the effects of parasites on host performance indicated stronger decrease in performance of juvenile hosts (McElroy and De Buron 2014). Indeed, the performance of infected juvenile vertebrates may be constrained through their ongoing development. Herrel and Gibb (2006) noted that while juvenile vertebrates are able to show levels of locomotory performance similar to those of adults, it is, however, not the case for foraging performance. Hence, the performance cost generated by parasitic infections, especially on host foraging behaviour, may be greater for juveniles (Herrel and Gibb 2006, McElroy and De Buron 2014). In our meta-analyses, host age explained only moderate amounts of variation, with infected adult hosts exhibiting lower consumption rates. However, this age group also showed a significantly higher variance in consumption rate, especially among invertebrate hosts. Experimental studies comparing consumption rates of different life stages of vertebrate and invertebrate hosts could provide critical information to explain the observed results.

Energetic requirements and costs imposed by parasites affecting host metabolism may be different for females and males, particularly because energetic costs of reproduction typically increase female metabolic rates. Higher energetic requirements coupled with costs of bearing parasitic infections may together impose a heavier burden on females than on males, leading likely to the observed sex differences. In the available studies, for example, lower consumption rates of infected female, but not male, individuals were reported for different host species, including beetles (Shea 2005), gammarids (Fielding et al. 2003, Labaude et al. 2017), crabs (Pérez-Miguel et al. 2017) and birds (Tompkins et al. 2001), although one study reported that infected female periwinkle consumed more green algae compared with their infected male conspecifics (Clausen et al. 2008). In our meta-analyses parasitic infections significantly lowered consumption rates of females and mixed-sex groups, suggesting that consumption rate of infected females may be indeed more severely affected than that of infected males.

As the infection proceeds, the magnitude and direction of pathological effects on affected hosts may fluctuate. Hence, the intensity of parasitic infection (Goater and Ward 1992, Yin et al. 2015) as well as time since exposure to parasites (Khaldi et al. 2009, Bacela-Spychalska et al. 2014, Yin et al. 2018) may both determine the effects of parasites on host consumption rates. Due to an insufficient amount of data, we could not directly investigate these factors in our meta-analyses. Instead, we examined whether the type of infection (experimental vs natural) affected consumption rates of infected hosts, as this moderator variable partially accounts for these two factors. Not only the intensity of infection may be stronger in experimentally infected individuals, but also experimentally infected hosts will usually acquire the infection much earlier compared to naturally infected individuals (Sargent et al. 2014). Indeed, an earlier meta-analysis of parasite effects on host performance revealed that experimental infections had larger negative effects than did natural infections (McElroy and De Buron 2014). In our study, invertebrate hosts naturally infected with parasites showed stronger decreases in mean consumption rates compared to experimentally infected hosts. The experimental infections were, however, observed to cause significant increases in the variability in host consumption rate, indicating that infection conditions have considerably varied among experimental studies.

Recommendations for future research

Ultimately, the results provided by moderator variables in meta-regression analysis may not only broaden our understanding of the specific causes driving the observed effects of parasites on host consumption rate, but may also provide useful guidelines for conducting experimental studies. If strong effects on heterogeneity are yielded by a particular moderator variable, all categories of this variable (e.g. both sexes from 'host sex' moderator variable) should be considered in the experimental design. In addition to the moderator variables that were tested in our meta-analysis, there might be other variables that influence consumption rate of infected hosts. For example, food deprivation period may be

crucial; individuals deprived of food usually consume more compared with fed individuals (Khan et al. 2003). However, as reported by Bass and Weis (1999), prolonged food deprivation may cause declines in animal activity levels to conserve energy, and hence lower its predatory capacity. The effect of parasites may also vary depending on their developmental stage. As exemplified by the trophically transmitted acanthocephalan parasites developing in amphipods, the effects on hosts differ with regard to the actual stage of the parasite: non-infective acanthella or infective cystacanth (Bethel and Holmes 1974, Franceschi et al. 2008, Dianne et al. 2011, Dianne et al. 2014). Moreover, potential moderator variables may include those characterizing external conditions, such as temperature. Changes in ambient temperature may affect host metabolic rate and thus consumption rate. Elevated temperature led, for example, to further increases in consumption rates of infected hosts (Laverty et al. 2017) or, in turn, counteracted the declines in consumption rates imposed by parasitic infections (Larsen and Mouritsen 2009, Labaude et al. 2017). Finally, the effects of parasites on host behaviour may also depend on how similar the experimental and natural conditions are. Designing experiments reflecting natural environmental conditions of studied host–parasite systems may reveal otherwise undetectable effects (Anaya-Rojas et al. 2019).

Lastly, we would like to provide recommendations for researchers to support future ecological meta-analyses. The power of meta-analyses depends on the number of used effect sizes. These are, unfortunately, often not possible to derive due to the underreporting of key statistical metrics. As highlighted by Parker et al. (2016), under-reporting concerns about half of published articles. In our case, we had to exclude 24 studies (>25%) due to the lack of such crucial statistical metrics as measures of data dispersion or sample sizes. Furthermore, incomplete reporting of the details of experimental design, including in our case the information about host, parasite or prey characteristics, hinders the use of related moderator variables. Therefore, we would like to encourage researchers to include a more thorough reporting of methods, results and data in their publications. We believe, quoting Harrison (2011), that it "should not add significantly to the burden of writing up a research article and will add value to the work by allowing its ready incorporation to a meta-analysis if required." We would also like to point out the taxonomic bias, i.e. focusing repeatedly on the same model species, that may hinder research synthesis (Poulin and Maure 2015). Also in our meta-analysis, certain host groups were underrepresented in the dataset; there were no studies on reptiles, our dataset included only three bird species, whereas mammals were represented solely by rodents and ruminants. Furthermore, around 30% of studies on crustaceans in our dataset focused on *Gammarus* spp. infected by acanthocephalans. In addition, due to an exclusion of pest insects infected by biological control agents, studies on insects are also inadequately represented in our meta-analysis. We would, therefore, recommend designing empirical studies that focus on underrepresented host and parasite species.

Conclusions

1) While infected hosts consume on average 25% less food than uninfected conspecifics, almost one third of all mean effect sizes in our meta-analysis were positive. The specific effects of parasite infections on the foraging behaviour and consumption rate of hosts are thus context-dependent.
2) Infection with parasites resulted in a 25% increase in the variability in host consumption rates. The meta-analysis of variance, therefore, provides an important insight into the hidden effects of parasites on host behaviour.
3) A smaller size difference between a host and its parasite may lead to stronger impacts induced by infection. Indeed, if both parasite types are considered separately, macroparasites seem to affect consumption rates of infected invertebrate hosts to a greater extent than microparasites.
4) The strength of parasite effects on host foraging behaviour and consumption rate may differ with regard to the infection type (i.e. experimental vs natural infections). In fact, experimental infections resulted in higher variability in host consumption rate, suggesting that empirical approaches using this infection type may yield more variable results.

Acknowledgements – AM thanks Chunlong Liu for useful tips about conducting a meta-analysis and IGB's Parasite Discussion Club for brainstorming about the preliminary results of this manuscript. Open Access funding enabled and organized by Projekt DEAL.
Funding – AM was supported by a Humboldt Research Fellowship.

Author contributions

Agata Mrugała: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Justyna Wolinska**: Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Visualization (supporting); Writing – review and editing (equal). **Jonathan M. Jeschke**: Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Supervision (lead); Visualization (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.jsxksn0fw (Mrugała et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Anaya-Rojas, J. M., Best, R. J., Brunner, F. S., Eizaguirre, C., Leal, M. C., Melián, C. J., Seehausen O. and Matthews, B. 2019. An experimental test of how parasites of predators can influence trophic cascades and ecosystem functioning. – Ecology 100: e02744.

Bacela-Spychalska, K., Rigaud, T. and Wattier, R. A. 2014. A co-invasive microsporidian parasite that reduces the predatory behaviour of its host *Dikerogammarus villosus* (Crustacea, Amphipoda). – Parasitology 141: 254–258.

Balduzzi, S., Rücker, G. and Schwarzer, G. 2019. How to perform a meta-analysis with R: a practical tutorial. – Evid. Based Ment. Health 22: 153–160.

Bass, C. S. and Weis, J. S. 1999. Behavioral changes in the grass shrimp, *Palaemonetes pugio* (Holthuis), induced by the parasitic isopod, *Probopyrus pandalicola* (Packard). – J. Exp. Mar. Biol. Ecol. 241: 223–233.

Bernot, R. J. and Lamberti, G. A. 2008. Indirect effects of a parasite on a benthic community: an experiment with trematodes, snails and periphyton. – Freshwater Biol. 53: 322–329.

Bethel, W. M. and Holmes, J. C. 1974. Correlation of development of altered evasive behavior in *Gammarus lacustris* (Amphipoda) harboring cystacanths of *Polymorphus paradoxus* (Acanthocephala) with infectivity to the definitive host. – J. Parasitol. 60: 272–274.

Binning, S. A., Shaw, A. K. and Roche, D. G. 2017. Parasites and host performance: incorporating infection into our understanding of animal movement. – Integr. Comp. Biol. 57: 267–280.

Borenstein, M., Hedges, L. V., Higgins, J. P. T. and Rothstein, H. R. 2009. Introduction to meta-analysis. – John Wiley & Sons.

Boze, B. G. and Moore, J. 2014. The effect of a nematode parasite on feeding and dung-burying behavior of an ecosystem engineer. – Am. Zool. 54: 177–183.

Boze, B. G., Hernandez, A. D., Huffman, M. A. and Moore, J. 2012. Parasites and dung beetles as ecosystem engineers in a forest ecosystem. – J. Insect Behav. 25: 352–361.

Britton, J. R., Pegg, J. and Williams, C. 2011. Pathological and ecological host consequences of infection by an introduced fish parasite. – PLoS One 6: e26365.

Clausen, K. T., Larsen, M. H., Iversen, N. K. and Mouritsen, K. N. 2008. The influence of trematodes on the macroalgae consumption by the common periwinkle *Littorina littorea*. – J. Mar. Biol. Assoc. UK 88: 1481–1485.

Crane, A. L., Fritts, A. K., Mathis, A., Lisek, J. C. and Barnhart, M. C. 2011. Do gill parasites influence the foraging and anti-predator behaviour of rainbow darters, *Etheostoma caeruleum*? – Anim. Behav. 82: 817–823.

Cunningham, E. J., Tierney, J. F. and Huntingford, F. A. 1994. Effects of the cestode *Schistocephalus solidus* on food intake and foraging decisions in the three-spined stickleback *Gasterosteus aculeatus*. – Ethology 97: 65–75.

Davis, A. K. and Prouty, C. 2019. The sicker the better: nematode-infected passalus beetles provide enhanced ecosystem services. – Biol. Lett. 15: 20180842.

de Bekker, C., Will, I., Das, B. and Adams, R. M. 2018. The ants (Hymenoptera: Formicidae) and their parasites: effects of parasitic manipulations and host responses on ant behavioral ecology. – Myrmecol. News 28: 1–24.

Dianne, L., Perrot-Minnot, M.-J., Bauer, A., Gaillard, M., Léger, E. and Rigaud, T. 2011. Protection first then facilitation: a manipulative parasite modulates the vulnerability to predation of its intermediate host according to its own developmental stage. – Evolution 65: 2692–2698.

Dianne, L., Perrot-Minnot, M. J., Bauer, A., Guvenatam, A. and Rigaud, T. 2014. Parasite-induced alteration of plastic response to predation threat: increased refuge use but lower food intake in *Gammarus pulex* infected with the acanothocephalan *Pomphorhynchus laevis*. – Int. J. Parasitol. 44: 211–216.

Dickersin, K. 2005. Publication bias: recognizing the problem, understanding its origins and scope, and preventing harm. – In: Rothstein, H. R., Sutton, A. J., Borenstein, M., (eds), Publication bias in meta-analysis - Prevention, assessment and adjustments. John Wiley & Sons, pp. 11–33.

Duval, S. and Tweedie, R. 2000. Trim and fill: a simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. – Biometrics 56: 455–463.

Ebert, D., Carius, H. J., Little, T. and Decaestecker, E. 2004. The evolution of virulence when parasites cause host castration and gigantism. – Am. Nat. 164: 19–32.

Egger, M., Smith, G. D., Schneider, M. and Minder, C. 1997. Bias in meta-analysis detected by a simple, graphical test. – BMJ 315: 629–634.

Fielding, N. J., MacNeil, C., Dick, J. T. A., Elwood, R. W., Riddell, G. E. and Dunn, A. M. 2003. Effects of the acanthocephalan parasite *Echinorhynchus truttae* on the feeding ecology of *Gammarus pulex* (Crustacea: Amphipoda). – J. Zool. 261: 321–325.

Franceschi, N., Bauer, A., Bollache, L. and Rigaud, T. 2008. The effects of parasite age and intensity on variability in acanthocephalan-induced behavioural manipulation. – Int. J. Parasitol. 38: 1161–1170.

Friesen, O. C., Goellner, S., Poulin, R. and Lagrue, C. 2020. Parasites shape community structure and dynamics in freshwater crustaceans. – Parasitology 147: 182–193.

Goater, C. P. and Ward, P. I. 1992. Negative effects of *Rhabdias bufonis* (Nematoda) on the growth and survival of toads (*Bufo bufo*). – Oecologia 89: 161–165.

Haddaway, N. R., Wilcox, R. H., Heptonstall, R. E., Griffiths, H. M., Mortimer, R. J., Christmas, M. and Dunn, A. M. 2012. Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. – PLoS One 7: e32229.

Harrison, F. 2011. Getting started with meta-analysis. – Methods Ecol. Evol. 2: 1–10.

Hasik, A. Z., de Angeli Dutra, D., Doherty, J. F., Duffy, M. A., Poulin, R. and Siepielski, A. M. 2023. Resetting our expectations for parasites and their effects on species interactions: a meta-analysis. – Ecol. Lett. 26: 184–199.

Hatcher, M. J., Dick, J. T. A. and Dunn, A. M. 2012. Diverse effects of parasites in ecosystems: linking interdependent processes. – Front. Ecol. Environ. 10: 186–194.

Hedges, L. V., Gurevitch, J. and Curtis, P. S. 1999. The meta-analysis of response ratios in experimental ecology. – Ecology 80: 1150–1156.

Herrel, A. and Gibb, A. C. 2006. Ontogeny of performance in vertebrates. – Physiol. Biochem. Zool. 79: 1–6.

Higgins, J. P. T., Thompson, S. G., Deeks, J. J. and Altman, D. G. 2003. Measuring inconsistency in meta-analyses. – BMJ 327: 557–560.

Horký, P., Douda, K., Maciak, M., Závorka, L. and Slavík, O. 2014. Parasite-induced alterations of host behaviour in a riverine fish: the effects of glochidia on host dispersal. – Freshwater Biol. 59: 1452–1461.

IntHout, J., Ioannidis, J. P., Rovers, M. M. and Goeman, J. J. 2016. Plea for routinely presenting prediction intervals in meta-analysis. – BMJ Open 6: e010247.
Jeschke, J. M., Kopp, M. and Tollrian, R. 2002. Predator functional responses: discriminating between handling and digesting prey. – Ecol. Monogr. 72: 95–112.
Khaldi, S., Gargala, G., Le Goff, L., Parey, S., Francois, A., Fioramonti, J., Ballet, J.-J., Dupont, J.-P., Ducrotté, P. and Favennec, L. 2009. *Cryptosporidium parvum* isolate-dependent postinfectious jejunal hypersensitivity and mast cell accumulation in an immunocompetent rat model. – Infect. Immun. 77: 5163–5169.
Khan, R. N., Spiers, J. A. and Pung, O. J. 2003. Effects of the trematode *Microphallus turgidus* on locomotion and prey capture in the grass shrimp *Palaemonetes pugio*. – J. Helminthol. 77: 327–330.
Kunz, A. K. and Pung, O. J. 2004. Effects of *Microphallus turgidus* (Trematoda: Microphallidae) on the predation, behavior, and swimming stamina of the grass shrimp *Palaemonetes pugio*. – J. Parasitol. 90: 441–445.
Kyriazakis, I., Tolkamp, B. J. and Hutchings, M. R. 1998. Towards a functional explanation for the occurrence of anorexia during parasitic infections. – Anim. Behav. 56: 265–274.
Labaude, S., Rigaud, T. and Cézilly, F. 2017. Additive effects of temperature and infection with an acanthocephalan parasite on the shredding activity of *Gammarus fossarum* (Crustacea: Amphipoda): the importance of aggregative behavior. – Global Change Biol. 23: 1415–1424.
Lafferty, K. D., Allesina, S., Arim, M., Briggs, C. J., De Leo, G., Dobson, A. P., Dunne, J. A., Johnson, P. T. J., Kuris, A. M., Marcogliese, D. J., Martinez, N. D., Memmott, J., Marquet, P. A., McLaughlin, J. P., Mordecai, E. A., Pascual, M., Poulin, R. and Thieltges, D. W. 2008. Parasites in food webs: the ultimate missing links. – Ecol. Lett. 11: 533–546.
Lagrue, C., Heaphy, K., Presswell, B. and Poulin, R. 2016. Strong association between parasitism and phenotypic variation in a supralittoral amphipod. – Mar. Ecol. Prog. Ser. 553: 111–123.
Lajeunesse, M. J. 2015. Bias and correction for the log response ratio in ecological meta-analysis. – Ecology 96: 2056–2063.
Larsen, M. H. and Mouritsen, K. N. 2009. Increasing temperature counteracts the impact of parasitism on periwinkle consumption. – Mar. Ecol. Prog. Ser. 383: 141–149.
Laverty, C., Brenner, D., McIlwaine, C., Lennon, J. J., Dick, J. T. A., Lucy, F. E. and Christian, K. A. 2017. Temperature rise and parasitic infection interact to increase the impact of an invasive species. – Int. J. Parasitol. 47: 291–296.
Leaphart, J. C. and Zelmer, D. A. 2017. Wrecking the curve: altered functional response of *Tetragoneuria* (Odonata: Corduliidae) naiads infected with metacercariae of *Haematoloechus floedae*. – J. Parasitol. 103: 147–151.
Lettini, S. E. and Sukhdeo, M. V. 2010. The energetic cost of parasitism in isopods. – Ecoscience 17: 1–8.
Lochmiller, R. L. and Deerenberg, C. 2000. Tradeoffs in evolutionary immunology: just what is the cost of immunity? – Oikos 88: 87–98.
Marcogliese, D. J. 2004. Parasites: small players with crucial roles in the ecological theatre. – EcoHealth 1: 151–164.
Marks, J. C. and Lowe, R. L. 1989. The independent and interactive effects of snail grazing and nutrient enrichment on structuring periphyton communities. – Hydrobiologia 185: 9–17.
Martín-Hernández, R., Botías, C., Barrios, L., Martínez-Salvador, A., Meana, A., Mayack, C. and Higes, M. 2011. Comparison of the energetic stress associated with experimental *Nosema ceranae* and *Nosema apis* infection of honeybees (*Apis mellifera*). – Parasitol. Res. 109: 605–612.
McElroy, E. J. and De Buron, I. 2014. Host performance as a target of manipulation by parasites: a meta-analysis. – J. Parasitol. 100: 399–410.
Mercer, J. G., Mitchell, P. I., Moar, K. M., Bissett, A., Geissler, S., Bruce, K. and Chappell, L. H. 2000. Anorexia in rats infected with the nematode, *Nippostrongylus brasiliensis*: experimental manipulations. – Parasitology 120: 641–647.
Michonneau, F., Brown, J. W. and Winter, D. J. 2016. Rotl: an R package to interact with the open tree of life data. – Methods Ecol. Evol. 7: 1476–1481.
Mills, N. 2009. Parasitoids. – In: Encyclopedia of insects. Academic Press, pp. 748–751.
Minchella, D. J. and Scott, M. E. 1991. Parasitism: a cryptic determinant of animal community structure. – Trends Ecol. Evol. 6: 250–254.
Moher, D., Liberati, A., Tetzlaff, J. and Altman, D. G. 2010. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. – Int. J. Surg. 8: 336–341.
Moran, N. P., Sánchez-Tójar, A., Schielzeth, H. and Reinhold, K. 2021. Poor nutritional condition promotes high-risk behaviours: a systematic review and meta-analysis. – Biol. Rev. 96: 269–288.
Morton, J. P. 2018. Infection by *Parorchis acanthus* (Trematoda) decreases grazing by the keystone gastropod, *Littoraria irrorata*. – PeerJ 6: e4544.
Morton, D. N. and Lafferty, K. D. 2022. Parasites in kelp-forest food webs increase food-chain length, complexity, and specialization, but reduce connectance. – Ecol. Monogr. 92: e1506.
Mrugała, A., Wolinska, J. and Jeschke, J. M. 2023. Data from: A meta-analysis of how parasites affect host consumption rates. – Dryad Digital Repository, https://doi.org/10.5061/dryad.jsxksn0fw.
Nakagawa, S. and Santos, E. S. A. 2012. Methodological issues and advances in biological meta-analysis. – Evol. Ecol. 26: 1253–1274.
Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. – Methods Ecol. Evol. 4: 133–142.
Nakagawa, S., Poulin, R., Mengersen, K., Reinhold, K., Engqvist, L., Lagisz, M. and Senior, A. M. 2015. Meta-analysis of variation: ecological and evolutionary applications and beyond. – Methods Ecol. Evol. 6: 143–152.
Nakagawa, S., Lagisz, M., O'dea, R. E., Rutkowska, J., Yang, Y., Noble, D. W. and Senior, A. M. 2021. The orchard plot: cultivating a forest plot for use in ecology, evolution and beyond. – Res. Synth. Methods 12: 4–12.
Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M. E. and The Scarabaeinae Research Network. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. – Biol. Conserv. 141: 1461–1474.
Noble, D. W., Lagisz, M., O'dea, R. E. and Nakagawa, S. 2017. Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. – Mol. Ecol. 26: 2410–2425.
O'Shaughnessy, K. A., Harding, J. M. and Burge, E. J. 2014. Ecological effects of the invasive parasite *Loxothylacus panopaei* on the flatback mud crab *Eurypanopeus depressus* with implications for estuarine communities. – Bull. Mar. Sci. 90: 611–621.
Paradis, E. and Schliep, K. 2019. Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. – Bioinformatics 35: 526–528.

Parker, T. H., Forstmeier, W., Koricheva, J., Fidler, F., Hadfield, J. D., Chee, Y. E., Kelly, C. D., Gurevitch, J. and Nakagawa, S. 2016. Transparency in ecology and evolution: real problems, real solutions. – Trends Ecol. Evol. 31: 711–719.

Pérez-Miguel, M., Drake, P. and Cuesta, J. A. 2017. Experimental predatory behavior of the stone crab *Eriphia verrucosa* (Forskål, 1775) (Decapoda, Brachyura, Eriphiidae). – Nauplius 25: 1–11.

Pirhonen, J., Schreck, C. B., Reno, P. W. and Ögüt, H. 2003. Effect of fasting on feed intake, growth and mortality of chinook salmon, *Oncorhynchus tshawytscha*, during an induced *Aeromonas salmonicida* epizootic. – Aquaculture 216: 31–38.

Poulin, R. 1999. The functional importance of parasites in animal communities: many roles at many levels? – Int. J. Parasitol. 29: 903–914.

Poulin, R. and Thomas, F. 1999. Phenotypic variability induced by parasites: extent and evolutionary implications. – Parasitol. Today 15: 28–32.

Poulin, R. and Maure, F. 2015. Host manipulation by parasites: a look back before moving forward. – Trends Parasitol. 31: 563–570.

Pyron, M. and Brown, K. M. 2015. Introduction to mollusca and the class Gastropoda. – In: Thorp and Covich's freshwater invertebrates. Academic Press, pp. 383–421.

Reisinger, L. S. and Lodge, D. M. 2016. Parasites alter freshwater communities in mesocosms by modifying invasive crayfish behavior. – Ecology 97: 1497–1506.

Rosenthal, R. 1979. The file drawer problem and tolerance for null results. – Psychol. Bull. 86: 638.

Sadd, B. M. and Schmid-Hempel, P. 2009. Perspective: principles of ecological immunology. – Evol. Appl. 2: 113–121.

Sánchez, M. I., Paredes, I., Lebouvier, M. and Green, A. J. 2016. Functional role of native and invasive filter-feeders, and the effect of parasites: learning from hypersaline ecosystems. – PLoS One 11: e0161478.

Sánchez-Tójar, A., Moran, N. P., O'Dea, R. E., Reinhold, K. and Nakagawa, S. 2020. Illustrating the importance of meta-analysing variances alongside means in ecology and evolution. – J. Evol. Biol. 33: 1216–1223.

Sargent, L. W., Baldridge, A. K., Vega-Ross, M., Towle, K. M. and Lodge, D. M. 2014. A trematode parasite alters growth, feeding behavior, and demographic success of invasive rusty crayfish (*Orconectes rusticus*). – Oecologia 175: 947–958.

Schwarzer, G. 2007. meta: an R package for meta-analysis. – R News 7: 40–45.

Senior, A. M., Grueber, C. E., Kamiya, T., Lagisz, M., O'Dwyer, K., Santos, E. S. and Nakagawa, S. 2016. Heterogeneity in ecological and evolutionary meta-analyses: its magnitude and implications. – Ecology 97: 3293–3299.

Shea, J. F. 2005. The effect of *Hymenolepis diminuta* (Cestoda) cysticercoids on the weight change, frass production, and food intake of the intermediate host, *Tenebrio molitor* (Coleoptera). – Parasitol. Res. 98: 1–4.

Sterne, J. A. and Egger, M. 2001. Funnel plots for detecting bias in meta-analysis: guidelines on choice of axis. – J. Clin. Epidemiol. 54: 1046–1055.

Thomas, F., Schmidt-Rhaesa, A., Martin, G., Manu, C., Durand, P. and Renaud, F. 2002. Do hairworms (Nematomorpha) manipulate the water seeking behaviour of their terrestrial hosts?. – J. Evol. Biol. 15: 356–361.

Thompson, S. G. and Higgins, J. P. 2002. How should meta-regression analyses be undertaken and interpreted?. – Stat. Med. 21: 1559–1573.

Thünken, T., Baldauf, S. A., Bersau, N., Frommen, J. G. and Bakker, T. C. 2019. Parasite-induced colour alteration of intermediate hosts increases ingestion by suitable final host species. – Behaviour 156: 1329–1348.

Tompkins, D. M., Greenman, J. V. and Hudson, P. J. 2001. Differential impact of a shared nematode parasite on two gamebird hosts: implications for apparent competition. – Parasitology 122: 187–193.

Toscano, B., Newsome, B. and Griffen, B. 2014. Parasite modification of predator functional response. – Oecologia 175: 345–352.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. – J. Stat. Softw. 36: 1–48.

Vivas Muñoz, J. C., Staaks, G. and Knopf, K. 2017. The eye fluke *Tylodelphys clavata* affects prey detection and intraspecific competition of European perch (*Perca fluviatilis*). – Parasitol. Res. 116: 2561–2567.

Vivas Muñoz, J. C., Hilt, S., Horák, P. and Knopf, K. 2018. Impact of trematode infections on periphyton grazing rates of freshwater snails. – Parasitol. Res. 117: 3547–3555.

Vivas Muñoz, J. C., Bierbach, D. and Knopf, K. 2019. Eye fluke (*Tylodelphys clavata*) infection impairs visual ability and hampers foraging success in European perch. – Parasitol. Res. 118: 2531–2541.

Wood, C. L., Byers, J. E., Cottingham, K. L., Altman, I., Donahue, M. J. and Blakeslee, A. M. H. 2007. Parasites alter community structure. – Proc. Natl Acad. Sci. USA 104: 9335–9339.

Yin, F., Gong, H., Ke, Q. and Li, A. 2015. Stress, antioxidant defence and mucosal immune responses of the large yellow croaker *Pseudosciaena crocea* challenged with *Cryptocaryon irritans*. – Fish Shellfish Immun. 47: 344–351.

Yin, F., Liu, W., Bao, P. and Tang, B. 2018. Food intake, survival, and immunity of *Nibea albiflora* to *Cryptocaryon irritans* infection. – Parasitol. Res. 117: 2379–2384.