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Eaten alive: cannibalism is enhanced by parasites

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Summary

Cannibalism is ubiquitous in nature and especially pervasive in consumers with stage-specific resource utilisation in resource-limited environments. Cannibalism is thus influential in the structure and functioning of biological communities. Parasites are also pervasive in nature and, we hypothesise, might affect cannibalism since infection can alter host foraging behaviour. We investigated the effects of a common parasite, the microsporidian *Pleistophora mulleri*, on the cannibalism rate of its host, the freshwater amphipod *Gammarus duebeni celticus*. Parasitic infection increased the rate of cannibalism by adults towards uninfected juvenile conspecifics, as measured by adult functional responses, that is, the rate of resource uptake as a function of resource density. This may reflect the increased metabolic requirements of the host as driven by the parasite. Further, when presented with a choice, uninfected adults preferred to cannibalise uninfected rather than infected juvenile conspecifics, likely reflecting selection pressure to avoid the risk of parasite acquisition. In contrast, infected adults were indiscriminate with respect to infection status of their victims, likely due to metabolic costs of infection and the lack of risk as the cannibals were already infected. Thus parasitism, by enhancing cannibalism rates, may have previously unrecognised effects on stage structure and population dynamics for cannibalistic species, and may also act as a selective pressure leading to changes in resource use.
1. Introduction

Cannibalism has been recorded in more than 3000 species [1–4] and may be influential at the levels of individuals, populations and communities. It is especially common in stage-structured populations where generations overlap in time and space [2,5]. Direct individual benefits of cannibalism include increased growth and survival [3], whilst indirect positive effects include the elimination of competitors [6]. Cannibalism may also enhance population persistence when resources are limited; for example, cannibalism may function as a “lifeboat mechanism” whereby cannibalistic adults have access to resources and energy accrued by the cannibalised juveniles [7]. There are, however, a number of costs associated with cannibalism, including the acquisition of parasites via consumption of infected conspecifics [8].

Parasitism is also pervasive in nature [9] and influences a number of intra- and interspecific interactions, including competition and predation, through both density- and trait-mediated effects [9–11]. In particular, parasites can modify the rate of predatory interactions [12,13] as well as alter the vulnerability of infected hosts to predation [9,14]. Parasitism, we propose, may therefore also be an important determinant in cannibalistic interactions with implications for population structure and community dynamics. This may be evidenced through changes in host behaviour as a result of metabolic costs [12], parasite manipulation to increase transmission likelihood [15–17] or can reflect selection on hosts to avoid costs of infection [17].

The microsporidian parasite *Pleistophora mulleri* is specific to the amphipod *Gammarus duebeni celticus*. It has a prevalence of up to 90%, and can alter predation hierarchies among species [13] with both parasitized and unparasitized occurring in close proximity to one another [18]. There is a large body of evidence that indicates *G. duebeni celticus* commonly engages in cannibalism in the field [19]. In addition, the only known route for the transmission of the microsporidian is cannibalism, providing further evidence of field cannibalism [20]. Therefore, as the parasite is transmitted orally, with an efficiency rate of 23% [20] and, as cannibalism in this species is common, it imparts a risk of infection of *P. mulleri* [20]. As such, parasite mediation of cannibalism may occur with important implications for host populations. We therefore investigated whether the cannibalistic rate and preferences of *G. duebeni celticus* are affected by infection with *P. mulleri*.

We used a ‘functional response’ approach (FR; resource uptake as a function of resource density), which can inform on consumer impacts on resource populations [21]. First, we investigated the impact of parasitism on cannibalistic propensity by deriving FRs for individuals with and without the parasite. Second, we used an intra-specific prey choice
experiment to test whether infected and uninfected *G. d. celticus* showed any preferences with respect to the infection status of juvenile conspecific victims.

2. Methods

Adult male and juvenile *Gammarus duebeni celticus* were collected from Downhill River, County Antrim, Northern Ireland (55.166674N, 6.8201185W) in November 2010 and April 2011. No permissions are required for this sampling activity. Males were selected for experiments due to the wide variation in female cannibalism that can occur due to factors relating to egg and embryo brooding [22]. Parasite status was determined by the presence/absence of *Pleistophora mulleri* spore mass visible through the exoskeleton (status confirmed by later dissection) and parasitised individuals all had visible infection of 1-2 segments [23]. Animals were separated according to infection status and maintained in aquaria with water and leaf material from their source at 12˚C and a 12h light : 12h dark cycle.

For functional response (FR) experiments, we selected similar sized infected and uninfected adult male *G. d. celticus* (body mass (mg) ± SE, infected 52.57 ± 1.49, uninfected 50.90 ± 1.23; 2-sample t-test, t=0.86, p>0.05). We presented single infected and uninfected males (starved for 48h) with uninfected juveniles (4-6mm body length) at seven juvenile densities (2, 4, 6, 8, 10, 15, 20; n=3 per density) in plastic dishes (8cm diameter) containing 200ml of aerated water from the amphipod source river. The densities of juvenile prey used were informed by previous functional response studies on gammarids in combination with known densities from the wild that are hyper-variable and can reach several thousand per square metre [24]. Controls were three replicates of each juvenile density without adults. Replicates were initiated at 17.00h and prey consumption was examined after 40h.

Mean number of juveniles killed was examined with respect to adult infection status and juvenile density using generalised linear models (GLMs) with quasi-poisson error distribution in R version 3.0.1 that were simplified via a step-deletion process. We determined FR types using logistic regression of the proportion of prey consumed against initial prey density [25] and modelled FRs using the Rogers random predator equation for a Type II functional response, which accounts for non-replacement of prey as they are consumed [26]. FR data were bootstrapped (n=15) and the parameters attack rate \( a \), handling time \( h \), and maximum feeding rate \( 1/hT \) (\( T=\)experimental time) compared using GLMs.

Preferences of infected and uninfected adults for cannibalism of infected versus uninfected juveniles were investigated by presenting adult males (n=30 uninfected and 30
infected individuals; sizes as above; starved for 72h) with a choice between an infected and uninfected juvenile individual (6mm body length; matched by weight) in plastic dishes (10cm diameter, 150ml volume). Trials began from the addition of the prey and were terminated when a prey item had been selected. Prey choice by the adults with respect to juvenile infection status was determined using Chi-squared tests.

3. Results

Control juvenile *G. d. celticus* survival was high (99.5%), thus experimental deaths were attributed to cannibalism by adults. This was further evidenced through observation and amphipod body parts littering the aquarium floor. Significantly more juveniles were eaten by infected than uninfected adults \((F_{1, 40} = 5.03, p < 0.05); \) Figure 1) and both functional responses were found to follow a Type II curve (Figure 1). Infected adults had significantly greater attack rates \(a\) \((t = 5.87, p < 0.001)\) and significantly lower handling times \(h\) \((t=3.67, p < 0.01)\). This translated into significantly higher maximum feeding rates \((1/hT)\) \((t = 2.71, p < 0.05)\) in comparison to uninfected individuals (Figure 1). Uninfected adults more frequently consumed uninfected than infected juveniles \((\chi^2 = 4.8, \text{d.f.} = 1, p < 0.0285); \) Figure 2), whereas infected adults showed no preference \((\chi^2 = 1.333, \text{d.f.} = 1, p > 0.05); \) Figure 2).

4. Discussion

Although the role of parasitism in interspecific predator-prey interactions has been studied in a number of systems \([12,13]\), the influence of parasites in mediating cannibalism has received far less attention, despite cannibalism and parasitism both being widespread and pervasive in natural communities \([3,9]\). Parasites may affect cannibalism since they have been shown to affect foraging behaviour, both increasing and decreasing host consumption of resources, with potential implications for population dynamics and community structure in such taxa \([12]\).

Here, the functional response (FR) of the amphipod *Gammarus duebeni celticus* infected with the microsporidian parasite *Pleistophora mulleri* towards juvenile (uninfected) conspecific prey was significantly higher in comparison to uninfected adults. Furthermore, infected amphipods had significantly greater attack rates, decreased handling times and hence heightened maximum feeding rates, demonstrating that infected amphipods are more efficient than their uninfected counterparts at cannibalising juveniles. This likely reflects the metabolic burden imposed by the parasite, leading to higher feeding rates \([12]\). That infected
individuals are such efficient foragers is despite the fact that this parasite degrades host tissue and substantially debilitates its host [27].

The preferential consumption of uninfected juveniles by uninfected adults likely reflects selection for avoiding cannibalising infected juveniles and therefore reducing the risk of parasite acquisition [8,28]. On the other hand, infected adults showed no such discrimination. One explanation for this lack of discrimination may be that immune priming or immune up-regulation protects infected individuals from further infection [29]. However, as Terry et al (2003) found no evidence of encapsulation or other immune responses in P. mulleri infected hosts. Rather, we suggest that the lack of discrimination in cannibalism of infected versus uninfected juveniles by infected adults again reflects the metabolic burden of infection whereby parasitised individuals cannot afford to be as selective in what prey they consume. Furthermore, as they are already infected with the parasite, there is no advantage to avoiding infection risk by preferentially consuming uninfected prey.

Overall, we show that infection of G. d. celticus with the parasite P. mulleri altered cannibalism rates and feeding preferences on juvenile conspecific victims. This in turn may increase the rate of juvenile mortality (over and above conventional virulence effects), which could lead to changes in population stage structure and density [5,11,30]. Furthermore, this interplay between cannibalism and parasitism could have powerful impacts on population and community resilience in changing environments, whereby cannibalism becomes an important mechanism in preserving populations [7], although in the wild, population outcomes will also depend on the relative importance of interspecific predation and cannibalism. Cannibalism and intraguild predation co-occur frequently in a broad range of systems [1,5] and the balance of these intra-versus inter-specific interactions is key to species coexistence and replacement patterns [31]. Parasites are also recognized as having important indirect and pervasive effects on communities and ecosystems, often due to their density and trait-mediated indirect effects on species that interact with their hosts [32]. Further exploration of parasite-modified cannibalism thus has potentially to further understand and predict population dynamics and community processes.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

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References


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Figure 1. Functional responses of infected (closed circles, solid line) and uninfected (open circles, dashed line) *G. duebeni celticus* adults towards juvenile conspecific prey. Lines are modelled by the Rogers random predator equation for a Type II response. Data points are mean numbers of juveniles consumed at each density ± SE.

Figure 2. The frequency of consumption of uninfected versus infected juveniles by uninfected and infected adult *G. duebeni celticus*.
Figure 1.

Initial juvenile density

Mean juveniles consumed (±SE)
Figure 2.