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Bunke, M, Dick, JTA, Hatcher, MJ et al. (1 more author) (2019) Parasites influence cannibalistic and predatory interactions within and between native and invasive amphipods. Diseases of Aquatic Organisms, 136 (1). pp. 79-86. ISSN 0177-5103

https://doi.org/10.3354/dao03415

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Parasites influence cannibalistic and predatory interactions within and between native and invasive amphipods

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Running page head: Parasites influence Intraguild Predation and Cannibalism

Abstract

In Northern Ireland UK, the native amphipod Gammarus duebeni celticus and the invasive amphipod Gammarus pulex coexist in some places, whilst in others the native has been replaced by the invader. This study explores the role of parasites in mediating interactions between native and invasive amphipod species. These amphipods demonstrate mutual intraguild predation (predation between animals that also compete for prey). Intraguild predation (IGP) and cannibalism can be important factors in structuring populations and communities. We investigated the effect that parasitism has on rates of IGP between G. d. celticus and G. pulex and on cannibalism within each species by comparing functional responses (FRs, the relationship between the use of a prey resource and its availability). We found that infection with the microsporidian parasite Pleistophora mulleri caused an increase in IGP and cannibalism by G. d. celticus. Infected G. d. celticus showed increased attack rates and reduced prey handling times. In contrast, infection with the acanthocephalan parasite Echinorhyncus truttae did not alter IGP or cannibalism by G. pulex. A prey preference experiment revealed that both amphipods were more likely to feed on heterospecific rather than conspecific prey, and this was also corroborated by the fact that overall IGP FRs were observed to be higher than cannibalism FRs. This is likely to be selectively advantageous as feeding on heterospecific prey removes possible competitors without the risk of consuming juvenile kin or the risk of acquiring parasites that comes with consuming infected conspecifics. Infection of the native G.d. celticus with P. mulleri enhances IGP of the invasive G. pulex, which we infer is likely to facilitate the coexistence of the two species.

Key words: Acanthocephala, biological invasion, cannibalism, Gammarus pulex, Gammarus duebeni celticus, functional response, intraguild predation, microsporidian

Introduction

Biological invasions are a leading cause of changes in ecological systems. Biological invasions and parasitic diseases are often closely linked (Dunn and Hatcher 2016; Hatcher et al 2019). Parasites can alter the outcome of biological invasions through effects on host mortality (density-mediated effects) and also by mediating native-invader interactions through trait-mediated effects such as changes in host behaviour (Petersen, 1990; Hatcher and Dunn, 2011; Dunn et al., 2012; Hatcher et al., 2019). Friesen et al. (2018) for example found that an infection with the trematode parasite Maritrema poulini may mediate the competition between the two isopod species Austridotea annectens and Austridotea lacustris, as behavioural changes of infected hosts affected the habitat choice of the host’s competitors. Similarly, the outcome of competitive interaction between the native mosquito Ochlerotatus triseriatus and the invasive mosquito Aedes albopictus in North America is modified by the gregarine parasite Ascogregarina taiwanensis, with infected invasive individuals having a lower effect on the abundance of the native (Aliabadi and Juliano, 2002). Parasites have also been found to affect predator prey interactions. For example, individuals of the invasive amphipod Gammarus pulex infected by the acanthocephalan parasite Echinorhynchus truttae showed a 30% increase in prey consumption of the isopod Asellus aquacticus (Dick et al., 2010).

In Europe, the native amphipod fauna is threatened by several invasive alien amphipod species (Grabowski et al., 2007). In Northern Ireland, G. pulex Linnaeus, 1758 transplanted from England have invaded a number of habitats where the native Gammarus duebeni celticus Stock and Pinkster, 1970 occurs (Strange and Glass, 1979). Intraguild predation (IGP), the predation between individuals of the same trophic guild which removes a potential competitor (Polis et al. 1989; Holt and Polis 1997), has been observed between the two species (Dick, 1992). These species are also known to be cannibalistic (Dick et al. 1993). The effects of IGP and cannibalism on the population dynamics of the species are predicted to be more complex than those of ordinary predator prey interactions, because such predation also removes potential competitors (Polis et al. 1989). Previous studies have found G. pulex frequently preys upon G. d. celticus and these higher levels of IGP are related to the widespread replacement of the native amphipod (Dick, 1996; Dick et al. 1999; MacNeil et al.,2001).

G. pulex and G. duebeni celticus host a range of parasites (Dunn and Dick, 1998) including Microsporaa and Acanthocephala. The native species G. d. celticus is the specific host to the microsporidian parasite Pleistophora mulleri, which infects the abdominal muscle resulting in reduced activity (MacNeil et al. 2003c). This parasite is transmitted orally with a transmission rate of 23% (MacNeil et al. 2003d). P mulleri prevalence varies in the field and can reach 45% (Fielding et al. 2005). P. mulleri causes its infected host to be more cannibalistic towards conspecific juveniles (Bunke et al. 2015). The current study explores the effect of P. mulleri on IGP behaviour of its host, G. duebeni celticus, and compares the impact of infection on cannibalistic behaviour and IGP behaviours between G. duebeni celticus and the invasive species G. pulex.

The invasive G. pulex is host to the acanthocephalan parasite E. truttae, which has a complex life cycle in which G. pulex is the intermediate host whilst the brown trout Salmo trutta is the definitive host. Prevalence varies in the field and can reach 70% (MacNeil et al. 2003b). This parasite manipulates the antipredator behaviour of its intermediate amphipod host, causing increased motility and decreased photophobic behaviour. A previous study also revealed changes in the predatory behaviour of E. truttae infected G. pulex; infected individuals showed increased predation rates on the waterlouse, Asellus aquaticus, likely reflecting the increased metabolic demands of infection and altered behaviour (Dick et al 2010). However, the effect of this parasite on IGP and cannibalism has not been previously studied.

This study measures the influence of two parasites on predatory and cannibalistic interactions between native and invasive amphipods by measuring predatory functional responses. Predatory functional responses (FRs) describe the relationship between the use of a prey resource and its availability (Holling, 1959). Comparative FR provides a way to make comparisons of feeding rates not only between species but also in different contexts (Dick et al. 2010). The use of a FR analysis also enables the derivation of the a and h parameters, which provide information on the predator prey interaction. The a parameter is a scaling parameter which is associated with the attack rate of the predator on its prey and is known to define the initial slope of the functional response curve (Paterson et al. 2015). The h parameter stands for the handling time of the prey by the predator and limits the maximum number of prey consumed over time (Paterson et al. 2015). Comparative FRs have been used to investigate the impact of possible invaders on native prey species. For example, the invasive amphipod Dikerogammarus villosus has been found to have a significantly higher FR than the native amphipods G. pulex, Gammarus roeseli and Gammarus duebeni when feeding on A. aquaticus(Bollache et al. 2008). Here we investigate the effect of parasitism on cannibalistic and intraguild predation interactions of native and invasive amphipods. To our knowledge this is the first study using the comparative FR approach to investigate the impact of parasitism on cannibalism and IGP.

Materials and Methods

Gammarus duebeni celticus were collected by kick sampling from Downhill River, County Antrim, Northern Ireland (55.166674 N, 6.8201185 W). Gammarus pulex were collected by kick net from the river Lagan system at Shaw’s Bridge (54.548509 N, 5.9526063 W). The native and invasive amphipod do not often coexist as the invader displaces the native. Hence animals were collected from similar small rivers (cobble substrate, moderate flow) 60km apart and allowed to acclimatise for 7 days in the lab before use in experiments.

On arrival at the lab, juvenile and adult individuals were separated and placed in separate tanks with plentiful food and shelter (fish food pellets and leaf material) to miminize the risk of cannibalism. Infection status was determined by visual examination under a dissecting microscope. Infection with Pleistophora mulleri was determined by the presence/absence of spore masses visible through the exoskeleton of G. d. celticus (MacNeil, Dick, Hatcher, Fielding, et al., 2003). Parasitized individuals all had visible infections in one to two segments. Infection of G. pulex with Echinorhynchus truttae was determined by the presence of a visible orange cyst (MacNeil, Fielding, Hume and Dick, 2003). Infected and uninfected individuals were maintained in separate tanks by species. Animals were kept in tanks with substrate, leaf material, fish food pellets and aerated river water from their source at 13°C at a 12h:12h light:dark regime. Adults were sexed based on the presence of copulatory papillae using a light microscope (Gledhill et al., 1993). Only adult males were used as predators in the experiments because the predatory ability of females is affected by other factors such as the presence of offspring in their brood pouch. Before the start of the experiment the adult male individuals were kept individually and starved for 48h (Laverty et al., 2015).

Predatory Functional response experiments

The FR experiments were carried out in clear circular plastic arenas with a circumference of 8 cm. These pots were filled with 200ml water. For IGP FR experiments the water was made up in equal parts from the Gammarus pulex and the Gammarus duebeni celticus field sites. For the cannibalism FR experiments the experimental arena contained water from the source field site of the amphipod. For the intraguild predation (IGP) FR experiments single adult males were offered juveniles of the other species at a different densities (2, 4, 6, 8, 10, 15, 20, 30 and 40) with three replicates at each density. For the cannibalism FR experiments single adult male individuals were offered juveniles of their own species at a number of densities (2, 4, 6, 8, 10, 15 and 20) with three replicates for each density. We only needed seven densities for cannibalism instead of the nine that were used for IGP FR experiments, because the number of prey consumed plateaued at a lower density for the cannibalism experiment than the IGP experiment. During both types of FR experiments the prey individuals were placed into the experimental arena 30 minutes prior to the start of the experiment to allow them to acclimatise. Then a single adult male predator was placed into the arena and left for 40h. After 40h the predator was removed and the number of remaining prey individuals were counted.

All statistical analyses for the FR experiments were undertaken in R version 3.3.3 (R Core Team 2017). The type of predatory functional response (the relationship between proportional mortality of prey and prey density) occurring was analysed using the 'frair_test' function of the frair package in R (Pritchard, 2016) for each of the treatments. Subsequently the predatory functional responses were modelled using the Rogers'-random predator equation (eq 4.1.) this was appropriate in this situation because the FRs were type two and prey was not replaced during the cause of the experiment. (Juliano, 2001).

$$(N = N_o(1-e^{a(Nh-PT)})) \qquad \text{eq 4.1}$$

where N is the number of prey eaten, N_o is the initial prey density, a is the attack constant, h is the handling time and T is the total time available for predation.

The equation assumes non-replacement of prey in order to obtain estimates of the saturation parameter h and the scaling parameter a for each of the treatments. FRs were modelled using the R package frair (Pritchard, 2016) which utilizes maximum likelihood estimation within the bbmle package (Bolker, 2014). The FR curves were bootstrapped and plotted with CIs in order to visualise the variability. To visualise the uncertainty around the fitted functional responses, bootstrapping was used to construct empirical 95% confidence intervals (Barrios-O'Neill et al., 2014).

The a and h parameters were compared between the predator groups and infection status using function frair_compare to explicitly model differences in the parameter estimates for each experimental treatment (function frair_compare; Juliano, 2001; Pritchard et al., 2017; Taylor and Dunn, 2016) . It provides a coefficient that can be interpreted within a regression modelling framework. The mean number of juveniles killed was examined with respect to the infection status of the predator, the prey type (conspecific versus hetero-specific) and juvenile density using generalized linear models (GLMs) with quasi-poison error distribution, to account for overdispersion, that were simplified via a step-deletion process.

Prey preference

To explore whether adult males were more likely to to prey on juveniles of the competing species, or to cannibalise conspecific juveniles, two size-matched juveniles, one juvenile of each species, were placed into a small plastic pot (8cm diameter) containing 200ml water (100ml from each amphipod source). After 30 minutes an adult individual (either Gammarus pulex or Gammrus duebeni celticus) was placed into the experimental arena and left there until one juvenile was consumed. Only visually uninfected adult males were used in this experiment. The remaining juvenile was then checked under a dissection microscope to determine its species identification. This was done based on the shapes of the eyes. While *G. pulex's* eyes are round in shape, the eyes of G. d. celticus are more kidney shaped (Gledhill et al. 1993). The results of 30 replicates for each species were analysed using a chi-squared test.

Results

All FR experiments were observed to be Type-II FRs, with logistic regression first order coefficients, which were significantly negative. This can be seen in Figure 1 in which lines are fitted to average data points at each density (Table 1). A Type II FR is characterised by an increase in the consumption of prey by the predator as the density increases. However, this rate of predation levels off at a plateau even as the prey density further increases (Holling, 1959).

The analysis of IGP FRs showed that overall there was no significant difference between IGP predation by uninfected Gammarus pulex and Gammarus duebni celticus (GLM, $X^2_{1,52}$=0.396, p=0.652; Figure 1c). In G. pulex there was no significant effect of infection with the parasite Echinorhynchus truttae on the FR (GLM, $X^2_{1,52}$=3.237, p=0.160; Figure 1a). In contrast, G. d. celticus infected individuals were observed to have a higher IGP FR than uninfected individuals (GLM, $X^2_{1,100}$ =33.189, p=0.018; Figure 1b). A comparison of the a and h parameters for infected and uninfected G. d. celticus individuals showed that infected individuals had a higher value for the a parameter while having a lower value for the saturation parameter h (Table 1). A higher a parameter indicates that the rate at which the predator encounters and attacks a prey item is higher, meaning that the predator attacks prey more frequently. A lower value of h indicates that the predator will spent less time processing a prey item.

In G. pulex, cannibalism was not affected by infection with the parasite E. truttae (GLM, $X^2_{1,40}$=0.225, p=0.663; Figure 3a). In contrast, infection with Pleistophora mulleri caused a significant increase in the cannibalism FR in G. d. celticus (GLM $X^2_{1,40}$=3.329, p=0.032; Figure 3b). Although the bootstrapping polygon shows some overlap, the GLM analysis confirms a significant difference in the FR (Alexander et al., 2012). A direct comparison of the cannibalism FR between G. d. celticus and G. pulex found no significant difference between the two species (GLM $X^2,_{1,40}$=3.329, p=0.082; Figure 3c), indicating that G. pulex and G. d. celticus have similar rates of cannibalism when feeding on conspecific juveniles.

The IGP FR for uninfected individuals of both G. pulex and G. d. celticus was higher than the cannibalism FR observed for each species (G. pulex, GLM, $X^2_{1,45}$=11.968, p=0.006; G d. celticus, GLM, $X^2_{1,98}$=34.52, p<0.001; Figure 2). The comparison of the h and a parameters showed that h parameters were significantly higher in cannibalism than in IGP for both G. pulex (frair_compare, p<0.001) and G. d. celticus (frair_compare, p=0.002). In contrast, a difference in the a parameter was not observed (frair_compare, p=0.316). In G. duebeni celtius it was observed that the IGP FR was significantly higher than the cannibalism FR for individuals infected with the parasite P. mulleri (GLM, $X^2_{1,46}$=71.969, p<0.001). A comparison showed that while the a parameter did not differ between the two groups (frair_compare, p=0.767), the h parameter was significantly lower in IGP than in cannibalism interactions (frair_compare, p<0.001).

When presented with prey items of both species, both G. pulex and G. d. celticus more frequently fed on prey of the other species over conspecific juveniles ($X^2{}_1$=32.26, p<0.001; figure 4), with 87% of individuals adults feeding on heterospecific juveniles. The number was the same for adults of both species.

Discussion

Infection with the microsporidian parasite Pleistophora mulleri caused an increase in IGP and cannibalism by the native amphipod G. d. celticus, driven by increased attack rates and reduced prey handling times. In contrast, infection with the acanthocephalan parasite Echinorhynchus truttae did not alter IGP and cannibalism by the invasive amphipod G. pulex. The comparative FR experiment showed that IGP between G. pulex and G. duebeni celticus can have a potential destabilizing impact on the prey population with the FR relationship reflecting a constant predation pressure even at low prey densities which could drive the decline of the population (Williams and Martinez, 2004; Rindone and Eggleston, 2011).

In Northern Ireland the invasive amphipod Gammarus pulex has displaced the native Gammarus duebeni celticus from a large number of sites (Dick and Platvoet 1996; Dick et al. 1999; MacNeil et al. 2001). However, our data do not support the hypothesis that differential IGP of juveniles underlies the exclusion of the native species, as we found no significant difference between the IGP by G. pulex and G. d. celticus of juveniles of the competing species In contrast, Dick et al (1996) found that G. pulex was the stronger IGP predator when predation of adults (singletons and pairs) was compared, suggesting a role for adult IGP in species replacement. Taken together, these studies indicate that the success of IGP is dependent on the size of prey, with our results indicating that both species are equally capable IGP predators of juveniles of the competing species.

We found no evidence that infection by the acanthocephalan parasite Echinorhynchus truttae affected the FR of G. pulex feeding on G. d. celticus juveniles. This result is surprising as, in field enclosure experiments, MacNeil et al (2003b) found that survival of adult G. duebeni was higher in the presence of E. truttae infected G. pulex than in the presence of uninfected G. pulex. They also observed that an infection with E. truttae caused G. pulex to have a lower ability to prey on G. d. celticus females, which are carried in precopulatory pairs. However, MacNeil's experiments used adults of both species. It is likely that the burden of infection reduces the ability of the host to predate large adult prey, but may not affect the ability to predate smaller juvenile prey as used in our experiment. In keeping with this suggestion, E truttae infected G pulex have a higher FR than do uninfected individuals when feeding on the smaller species Asellus aquaticus (Dick et al. 2010). In combination, these results suggest that infection with E. truttae may compromise the ability of G. pulex to predate adult native G. d. celticus, but not smaller juvenile of this competing species.

The observation that G. d. celticus infected with Pleistophora mulleri had a higher FR feeding on G. pulexcould reflect the fact that an infection with the parasite puts a burden on its host driving a higher need for consumption (Fielding et al. 2003). It also matches the finding of Bunke et al. (2015), who found that an infection with the parasite makes the species more cannibalistic when feeding on conspecific juveniles.

For both G. pulex and G. d. celticus, the FRs feeding on heterospecific juveniles (IGP) were higher than the FRs feeding on conspecific juveniles (cannibalism). This makes sense for a number of reasons. The first is that IGP removes a possible competitor without the risk of consuming kin as could be the case during cannibalism. Secondly, cannibalism carries a higher risk than intraguild predation of acquiring an infection with a parasite through consumption (Pfennig et al. 1998; MacNeil et al. 2003d) as many parasites, including P. mulleri are host specific. Hence, selection will favour amphipods that show preference for IGP over cannibalism as this will reduce the risk of parasite acquisition. This notion is further supported by the observation of higher rates of IGP than of cannibalism in G. duebeni celticus that were infected with P. mulleri, as well as by the prey preference experiment which revealed that individuals of both species preferred to prey on juveniles of the other species rather than conspecific juveniles.

Taken together, the findings from our study show that parasitism can potentially have a strong influence not only on the dynamics of its host population but could also potentially indirectly affect the population of species with which its host interacts through competition and IGP. In such situation parasitism has the potential to cause a reversal of dominance relationships between species making its host the superior predator. Theoretical models predict that such trait- mediated effects of parasites can allow species to co-exist in situations in which one species might have otherwise excluded the other from the ecosystem (Hatcher et al. 2008). Our results suggest that parasitism mediates the outcome of amphipod species interactions and might be able to reverse them, thereby increasing the likelihood of native/invader coexistence.

Acknowledgements

This work was funded by NERC studentship 200565413 All authors conceived and designed the experiment, MB collected and analysed the data. MB &AD wrote the manuscript. All authors critically revised the manuscript. We thank Dan Warren for statistical advice.

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Table 1. Parameter estimates and significance levels from first-order logistic regression analysis of the proportion of prey killed against initial prey density, with functional response parameters. Estimates extracted from Rogers' random predator equation fitted to data in the frair package. p – value referring to the significance value of to the first order term, a - attack coefficient, h – handling time, SE – standard error

Predator	Prey	First order term	p	a	SE	h	SE
G. pulex uninfected	IGP	-0.057	<0.001	1.189	0.211	0.093	0.013
	Canni	-0.159	<0.001	1.838	0.777	0.321	0.053
G. pulex infected	IGP	-0.042	<0.001	0.964	0.231	0.121	0.022
	canni	-0.057	0.037	0.620	0.210	0.149	0.064
G. duebeni uninfected	IGP	-0.047	<0.001	1.123	0.195	0.078	0.012
	Canni	-0.110	<0.001	0.773	0.357	0.385	0.097
G. duebeni infected	IGP	-0.059	<0.001	1.499	0.209	0.056	0.007
	Canni	-0.120	<0.001	1.752	0.826	0.320	0.057

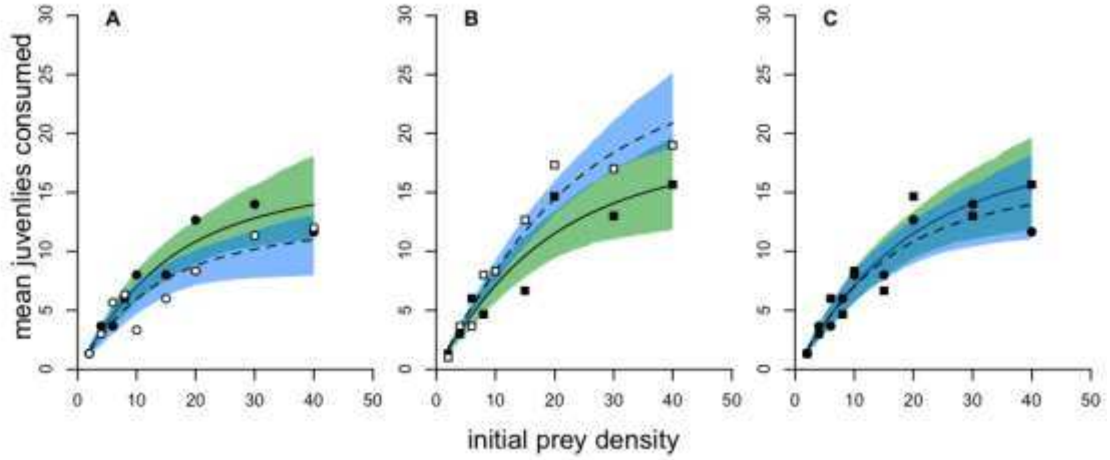

Figure 1. Comparative FR curves for IGP between G. pulex and G. d. celticus. Circles represent G. pulex, squares represent G. d. celticus. In A and B Full shapes and lines represent uninfected individuals and empty shapes and dotted lines represent individuals infected with E. truttae and P. mulleri respectively. The direct species comparison uses data from uninfected individuals only (full lines G. pulex, dotted lined G. d. celticus) A) Comparison of FRs between uninfected and infected G. pulex feeding on G. d. celticus juveniles. B) Comparison of FRs between uninfected and infected G. d. celticus feeding on G pulex juveniles C) Comparison of FRs between uninfected G. pulex and G. d. celticus feeding on heterospecific juveniles. The coloured areas are the

bootstrapping polygons. In A and B green represents the uninfected individuals and blue the infected individuals. The third colour in the figure is caused by an overlap of the polygons. In C green is the polygon for G.d.celticus and blue for G. pulex. The third colour in the figure is caused by an overlap of the polygons

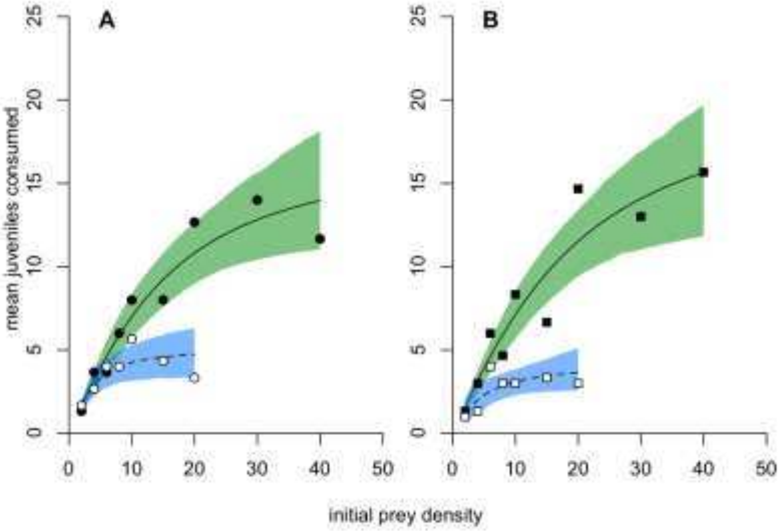

Figure 2. Comparison of FR between IGP and cannibalism in A) G. pulex B) G. d. celticus. Full shapes represent IGP and empty shapes represent cannibalism datapoints.. Shaded areas are the bootstrapping polygons. Green represents IGP and blue represents cannibalism. Only data points from uninfected individuals are used for the figures.

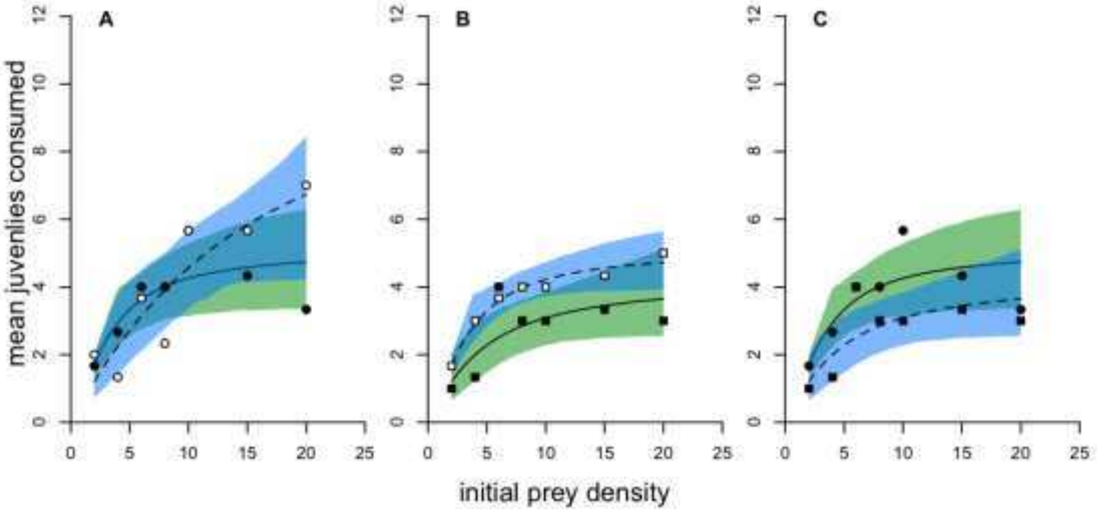

Figure 3. Comparison of cannibalism FR curves. A) comparison of uninfected G. pulex (vs individuals infected with E. truttae blue B) comparison of G. duebeni celticus uninfected vs infected with P. mulleri C) comparison of cannibalistic FR between G. pulex and G. duebeni celticus using data from uninfected individuals only.

In A and B full shapes represent uninfected individuals, open shapes represent infected individuals. The coloured areas are the bootstrapping polygons. B green represents the uninfected individuals and blue the infected individuals. The third colour in the figure is caused by an overlap of the polygons. In C, circles represent G. pulex, squares represent G d. celticus. Green is the polygon for G. pulex and blue for G d. celticus. The third colour in the figure is caused by an overlap of the polygons.

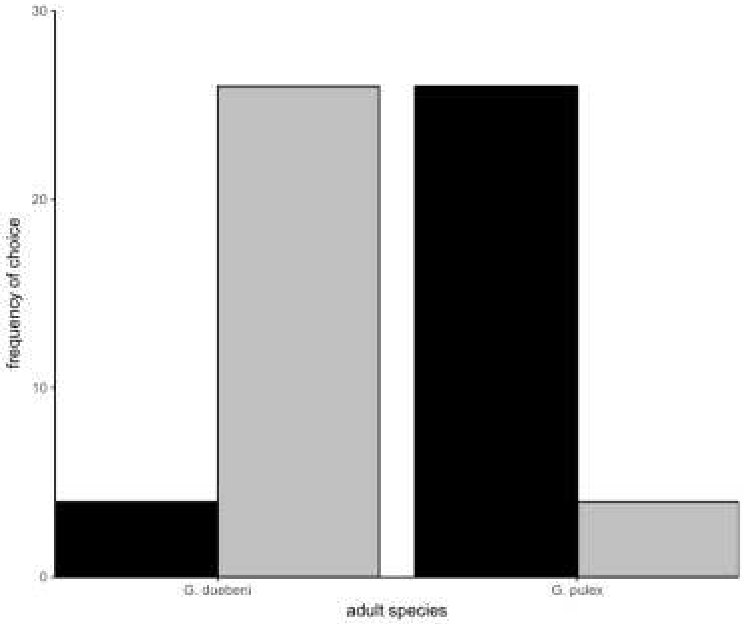

Figure 4. The frequency of consumption of conspecific versus herterospecific juveniles by uninfected adults of G. pulex and G. d. celticus. Black bars represent G. d. celticus juveniles and grey bars represent G. pulex juveniles