Manipulation of host-resource dynamics impacts transmission of trophic parasites

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A B S T R A C T

Many complex life cycle parasites rely on predator–prey interactions for transmission, whereby definitive hosts become infected via the consumption of an infected intermediate host. As such, these trophic parasites are embedded in the larger community food web. We postulated that exposure to infection and, hence, parasite transmission are inherently linked to host foraging ecology, and that perturbation of the host-resource dynamic will impact parasite transmission dynamics. We employed a field manipulation experiment in which natural populations of the eastern chipmunk (*Tamias striatus*) were provisioned with a readily available food resource in clumped or uniform spatial distributions. Using replicated longitudinal capture-mark-recapture techniques, replicated supplemented and unsupplemented control sites were monitored before and after treatment for changes in infection levels with three gastro-intestinal helminth parasites. We predicted that definitive hosts subject to food supplementation would experience lower rates of exposure to infective intermediate hosts, presumably because they shifted their diet away from the intermediate host towards the more readily available resource (sunflower seeds). As predicted, prevalence of infection by the trophically transmitted parasite decreased in response to supplemental food treatment, but no such change in infection prevalence was detected for the two directly transmitted parasites in the system. The fact that food supplementation only had an impact on the transmission of the trophically transmitted parasite, and not the directly transmitted parasites, supports our hypothesis that host foraging ecology directly affects exposure to parasites that rely on the ingestion of intermediate hosts for transmission. We concluded that the relative availability of different food resources has important consequences for the transmission of parasites and, more specifically, parasites that are embedded in the food web. The broader implications of these findings for food web dynamics and disease ecology are discussed.

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1. Introduction

Parasites constitute an enormous amount of biomass in the ecosystem, so it should not be surprising that they are embedded in larger food webs, even linking different trophic levels through chains of multi-host species (Lafferty et al., 2006; Rosa et al., 2011). Several studies have demonstrated that incorporating parasites into food webs can inform, strengthen and, in some instances, stabilise food web structure and dynamics (Marcogliese and Cone, 1997; Hall et al., 2007; Johnson et al., 2010; Dunne et al., 2013; Thompson et al., 2013). The inclusion of parasites in food webs has been shown to increase the number of species in a food web

by as much as two to four times, extending the length and connectedness of food chains (Marcogliese and Cone, 1997; Marcogliese, 2005; Dobson et al., 2006; Hudson et al., 2006; Lafferty et al., 2008). In particular, the presence of trophically transmitted parasites can serve as indicators of long-term feeding habits, which can be used to track and construct pathways within food webs (Marcogliese and Cone, 1997; Marcogliese, 2002; Marcogliese et al., 2003; Valtonen et al., 2010). Conversely, food webs and the trophic interactions therein can shed light on the role of predator–prey linkages in determining exposure to infection of susceptible hosts (Marcogliese, 2002). Here, we ask: how do trophic interactions among consumers and their resources influence parasite transmission dynamics and infection prevalence? The classical question of 'who eats whom' can therefore inform the question 'who infects whom'. Moreover, our study examines how the relative contribution of a particular food item to host diet can potentially impact rates of parasite transmission.

Parasites with complex life cycles provide an ideal system for investigating how consumer-resource dynamics influence disease risk and prevalence. Many complex life cycle parasites rely on predator–prey interactions for transmission where definitive hosts become infected via the consumption of an infected intermediate host. Hence, parasite transmission and specifically exposure to infection are directly linked to host foraging ecology, defined broadly here to encompass the behavioural processes associated with searching, acquiring and consuming a food item among a matrix of alternative food items. The availability of resources and alternative food availability can impact disease risk via the predator–prey interactions that underlie the transmission of trophically transmitted parasites. Studies have demonstrated that rates of predation on focal prey are strongly influenced by relative densities of alternative prey species (Symondson, 2002; Harwood et al., 2004; Koss and Snyder, 2005; Symondson et al., 2006). When the host is a generalist predator, the presence of alternative food sources can result in satiation or switching to a more abundant prey item (Holling, 1961). Transmission to the definitive host will be decreased if the more abundant prey is not an intermediate host for a trophic parasite. Satiation can also occur when total gut content or time available for foraging, prey handling and/or consumption is limited, and time and energy spent on an alternative prey translates into less time and gut space available for eating the focal prey (Abrams and Matsuda, 1996; Harmon and Andow, 2004; Tschanz et al., 2007). In a cafeteria-style experiment, Bellocq and Smith (1994) showed that the deer mouse (*Peromyscus maniculatus*) shifted to alternative prey when the abundance of preferred prey decreased. We propose that since consumers (i.e., definitive hosts) are resource limited, the presence of readily available alternative food items will lead to a change in host feeding behaviour with direct consequence for exposure and transmission of trophically transmitted parasites.

We examined the link between host foraging ecology and parasite transmission by experimentally manipulating the food supply in natural populations of eastern chipmunks (*Tamias striatus*). Eastern chipmunks are most commonly parasitised by gastro-intestinal helminths with faecal–oral transmission modes, including *Capillaria tamiasstriati* and *Citellinema bifurcatum*. Chipmunks are also infected with a trophically transmitted parasite, *Rictularia halli*, that relies on an insect intermediate host for transmission. The host range for *R. halli* is fairly broad and have been reported in other rodents, including flying squirrels, grey squirrels, voles and white-footed mice (Oswald, 1958).

By providing an abundant supplemental food source, we hypothesised that the transmission of trophically transmitted parasites would decrease due to hosts switching their diet away from invertebrates that serve as intermediate hosts for transmission. Specifically, the hypothesis predicts a decrease in the prevalence of trophically transmitted parasites in response to food supplementation compared with non-supplemented controls. While we predicted a decrease in the level of infection by trophically transmitted parasites, the level of infection by directly transmitted parasites is not expected to change as a result of food supplementation because direct transmission routes do not depend on what food item is consumed.

2. Materials and methods

2.1. Animal trapping

Using replicated longitudinal capture-mark-recapture techniques, we live-captured eastern chipmunks (*T. striatus*) on 12 open trapping grids, consisting of 64 traps in an 8 × 8 array at 12.5 m intervals (100 ha, Ugglan #2 multiple capture traps,

Grahnab, Sweden). All grids were 20 km south of State College, Pennsylvania, USA, in open forested habitat and separated by at least 800 m. We individually marked chipmunks using a passive induced transponder (PIT) tag (EIDAP, Alberta, Canada) and trapped every week from 1 June to 29 August 2009 with two consecutive trap days per trap session, for a total of six trap sessions. A trap day was an 8–10 h period, with traps set in the morning at 0600–0700 and checked and opened at 1200–1600 on the first trap day; and traps set at 0900–1000 and checked at 1600–1900 on the second consecutive trap day. Faecal samples were collected from trap contents and stored at 4 °C in Petri dishes lined with a damp towel (1 ml of water) overnight to standardise humidity. Parasite infection was determined using a modified McMasters egg flotation method (Sloss and Kemp, 1978). All animal handling was approved by the Institutional Animal Care and Use Committee at Pennsylvania State University, USA (IACUC #23268).

2.2. Food supplementation experiment

Experimental manipulations were conducted by supplementing treatment sites with sunflower seeds in either a clumped or uniform distribution. Four experimental sites were provisioned with clumped food resources via feeding stations located at four locations in each site. Feeding stations were filled with 250 g of sunflower seeds (1 kg per grid per week) once per week following the last trapping session of the week (3 days before the beginning of the next trapping session). Stations were spaced evenly across the trapping grid and consisted of an enclosed wooden platform with holes to allow small rodents to enter while excluding birds and other larger consumers. Four additional sites provisioned with uniformly dispersed food resources (broadcast feeding once per week following the last trap day). For this treatment, a total of 1000 g of sunflower seeds were manually spread uniformly across the forest floor while walking along the trapping grid. Finally, we maintained four control sites with no food supplementation. Control and uniform resources treatments were fitted with empty feeding stations. Chipmunks were trapped 6 weeks prior to initiation of treatment; food supplementation commenced on week 7 at both treatment sites and was maintained for the duration (12 weeks) of the experiment.

2.3. Statistical analyses

We compared the prevalence of infection during the period before treatment with the prevalence in response to treatment 4 weeks after commencing food supplementation. The directly transmitted parasites, *C. tamiasstriati* and *C. bifurcatum*, have direct life cycles whereby eggs are shed into the environment with host faeces 1–2 weeks p.i. (Anderson, 2000). By comparison, eggs of the trophically transmitted parasite *R. halli* cannot be detected in the environment until at least 4 weeks p.i. (Oswald, 1958). Hence the response period was set at 4 weeks to ensure detection of parasite eggs from all three nematode species in the study. We considered each trapping grid as a response unit and evaluated the probability of infection using generalised linear mixed regression models (GLMMs) with binomial errors; the prevalence of infection at each trapping site served as the response variable (GLMM, R package lme4; development core team 2013, http://www.r-project.org/). The following explanatory variables were included in the full model: treatment type, response period and their interaction. The trap site was entered into the model as a random factor to account for repeated measures. The site supplementation treatment factor with time period interaction explicitly tested for the effect of the experimental treatment on transmission by comparing the change in parasite prevalence between treatment and control