

Parasite co-infection and interaction as drivers of host heterogeneity

I.M. Cattadori ^{a,b,*}, B. Boag ^a, P.J. Hudson ^b

^a Division of Animal Production and Public Health, Faculty of Veterinary Medicine, The University of Glasgow, Glasgow G61 1QH, UK

^b Center for Infectious Disease Dynamics, 208 Mueller Laboratory, The Pennsylvania State University, University Park, PA 16802, USA

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Abstract

We examined the hypothesis that the interaction between concomitant infecting parasites modifies host susceptibility, parasite intensity and the pattern of parasite distribution within the host population. We used a 26 year time series of three common parasites in a natural population of rabbits: two gastrointestinal nematodes (*Trichostrongylus retortaeformis* and *Graphidium strigosum*) and the immunosuppressive myxoma virus. The frequency distribution of nematodes in the host population and the relationship between host age and nematode intensity were explored in rabbits with either single or dual nematode infections and rabbits infected with the nematodes and myxoma virus. The aggregation of *T. retortaeformis* and *G. strigosum* among the rabbits varied with the nature of the co-infection both in male and female hosts. The two nematodes exhibited different age–intensity profiles: *G. strigosum* intensity increased exponentially with host age while *T. retortaeformis* intensity exhibited a convex shape. The presence of a secondary infection did not change the age–intensity profile for *G. strigosum* but for *T. retortaeformis* co-infection (either both nematodes or myxoma–nematodes) resulted in significantly greater intensities in adult hosts. Results suggest that multi-species infections contributed to aggregation of parasites in the host population and to seasonal variation in intensity, but also enhanced differences in parasitism between sexes. This effect was apparent for *T. retortaeformis*, which appears to elicit a strong acquired immune response but not for *G. strigosum* which does not produce any evident immune reaction. We concluded that concomitant infections mediated by host immunity are important in modifying host susceptibility and influencing heterogeneity amongst individual hosts.

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1. Introduction

Species interactions, either through direct interaction or mediated through an indirect mechanism, are fundamentally important processes in shaping community structure and generating biodiversity (Bonsall and Hassell, 1997). In the parasite communities of animal populations, direct interactions occur when parasites compete for the same resource, either space or food, while indirect interactions occur, for example, when the host's immune response to one parasite affects the host's ability to control a second

parasite species. Specifically, one parasite can enhance the immune response to a second through cross-immunity (negative interaction), or alternatively cause immuno-suppression (positive interaction) (Behnke et al., 2001; Cox, 2001). In the latter case, the extreme scenario is seen when a second parasite subverts the immune response leading to reduced resistance and increased susceptibility to the first parasite (Graham et al., 2007). This interaction can be illustrated by the co-infection of a host with a virus and a helminth. Viruses usually cause acute, highly inflammatory infections that promote a response mediated by cellular mechanisms, while helminth infections promote chronic but less harmful responses and stimulate a humoral reaction mediated by antibodies and other molecules (Quinnell and Keymer, 1990; Abbas et al., 1996; Cox, 2001). The mechanism of regulation of the virus and the helminth often activates different effectors that can be mutually

* Corresponding author. Address: Division of Animal Production and Public Health, Faculty of Veterinary Medicine, The University of Glasgow, Glasgow G61 1QH, UK. Tel.: +44 141 330 6942; fax: +44 141 942 7215.

E-mail address: i.cattadori@vet.gla.ac.uk (I.M. Cattadori).

inhibitory (Jankovic et al., 2001; Neurath et al., 2002). As a consequence of this, host susceptibility to the helminth infection is likely to change and potentially affect worm intensities and transmission rates, and have important non-linear effects on host-parasite interaction and parasite dynamics (Graham et al., 2007; Hudson et al., in press). An alternative indirect route of interaction may also occur when a parasite secretes compounds that influence another parasite species or may induce physiological changes in the host that alter the survival of the second species but this route seems relatively uncommon in natural systems (Behnke et al., 2001; Cox, 2001).

One inference from these observations is that immune-mediated species interactions can drive variation in susceptibility and infectiousness between individual hosts and consequently shape the parasite community of a host population (Hershow et al., 1997; Nacher et al., 2002; Elliott et al., 2004; Andreansky et al., 2005; Graham et al., 2005; Thorburn et al., 2006; Cattadori et al., 2007). For example, if variation in susceptibility is influenced not only by past and current exposure to the focal parasite but also to the presence and history of infection of the second species, this will increase variation in intensity between hosts and the overall pattern of parasite distribution in the whole host population (Boag et al., 2001).

One signal that indicates that a helminth is regulated by an acquired immune response is a convex age–intensity relationship, a profile sometimes referred to as a Type III response (Hudson and Dobson, 1995; Hudson et al., 2006). This age–intensity curve is well illustrated by models that describe the development of acquired immunity as a response to the accumulated exposure to the parasite's infective stages (Woolhouse, 1992, 1998). However, the convex profile can also be generated by other host-parasite processes, such as parasite-induced host mortality, age related effects or frailty in the data, and disentangling their role can be challenging (Hudson and Dobson, 1995; Cattadori et al., 2005). Nevertheless, the evidence of a shift in the peak intensity of infection with host age, as a function of changes in the force of infection, the rate at which susceptible hosts acquire infection (McCallum, 2000), or an increase in parasite intensity in breeding females, the periparturient rise in nematode burdens, provides good support for the hypothesis that parasites are immuno-regulated (Soulsby, 1965; Woolhouse, 1998; Cattadori et al., 2005; Cornell et al., unpublished data). If a host is infected with two parasites, the first species immune-regulated and the second that reduces resistance to the first, then we expect that the age–intensity profile of the first will be modified (Cattadori et al., 2007). If the first parasite is not regulated by immune mechanisms, then there will be no apparent changes in the age–intensity profile, assuming all other factors remain constant.

In this paper we investigate the hypothesis that concomitant infections of indirectly competing species that are regulated by host immunity will generate variation in resistance between hosts leading to an increased mean

intensity of infection but reduced variance within the co-infected groups; over the whole host population this will promote increased variance. To address this hypothesis we examined time series data from a free-living population of European rabbits (*Oryctolagus cuniculus*) and the most common parasites of this lagomorph, two gastrointestinal nematodes, *Trichostrongylus retortaeformis* and *Graphidium strigosum*, and the poxvirus myxoma, that causes myxomatosis. We selected these parasites because they differ in their age–intensity relationships. *Trichostrongylus retortaeformis* causes a Type III convex age–intensity profile and previous studies have suggested that this is generated by an acquired immune response (Michel, 1952a,b; Cattadori et al., 2005, 2007; Cornell et al., unpublished data). In contrast, *G. strigosum* exhibits a Type I profile where intensity increases constantly with host age and does not show any clear sign of acquired immunity (Supplementary Figs. S3 and S4). Myxoma has a strong immunosuppressive effect, so we expected it to reduce the immune regulation of other parasites (McFadden et al., 1995; Nash et al., 1999; Zuniga, 2002; Seet et al., 2003). In our case, we predicted that rabbits co-infected with myxoma would have greater intensities of the nematode *T. retortaeformis* but no such effects would be observed in hosts with *G. strigosum*. We examined both the frequency distribution and the host age–intensity relationship for each nematode in rabbits with single and dual nematode infections and rabbits co-infected with myxoma and the nematodes, with respect to sex and breeding status.

2. Materials and methods

2.1. The parasite–host system

Parasite and host data were obtained from a population of European rabbits sampled with a .22 rifle by walking transects across an area of 400 ha in central Scotland, every month from 1977 to 2002 (Boag et al., 2001). Wild rabbits represent a pest in the UK and no special permission is required to harvest this lagomorph, other than the permission of the landowner. From each rabbit, we recorded the intensity of two nematodes, *T. retortaeformis* and *G. strigosum*, and the presence of myxoma virus from characteristic internal and external lesions (Boag, 1988; Best and Kerr, 2000; Boag et al., 2001). We also quantified the intensity of three less common gastrointestinal helminths and the prevalence of the hepatic protozoan *Eimeria stiedai*, but rabbits co-infected with these parasites were excluded from the current study. In this paper, and to be consistent with epidemiological terminology, we define intensity as the total number of worms in a host, intensity is zero when a host has no nematodes; this contrasts with the definition suggested by Bush et al. (1997). Rabbit sex, mass, body size and reproductive status were recorded and the age structure of the sampled population was reconstructed using body mass as a proxy for age. The age classification was initially based on myxoma-free individuals and rabbits

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