



Contents lists available at ScienceDirect

## International Journal for Parasitology

journal homepage: [www.elsevier.com/locate/ijpara](http://www.elsevier.com/locate/ijpara)

## The reliability of observational approaches for detecting interspecific parasite interactions: comparison with experimental results

Andy Fenton<sup>a,\*</sup>, Sarah C.L. Knowles<sup>b</sup>, Owen L. Petchey<sup>c</sup>, Amy B. Pedersen<sup>d</sup>

<sup>a</sup> Institute of Integrative Biology, University of Liverpool, Biosciences Building, Crown Street, Liverpool L69 7ZB, UK

<sup>b</sup> Department of Infectious Disease Epidemiology, Imperial College London, St. Mary's Campus, Norfolk Place, London W2 1PG, UK

<sup>c</sup> Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

<sup>d</sup> Institute of Evolutionary Biology and Centre for Immunity, Infection and Evolution (CIIE), School of Biological Sciences, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK

## ARTICLE INFO

## Article history:

Received 7 December 2013

Received in revised form 27 February 2014

Accepted 2 March 2014

Available online xxx

## Keywords:

Coinfection

Helminths

Polyparasitism

Cross-sectional and longitudinal analyses

Field study

Experimental perturbation

Small mammals

## ABSTRACT

Interactions among coinfecting parasites have the potential to alter host susceptibility to infection, the progression of disease and the efficacy of disease control measures. It is therefore essential to be able to accurately infer the occurrence and direction of such interactions from parasitological data. Due to logistical constraints, perturbation experiments are rarely undertaken to directly detect interactions, therefore a variety of approaches are commonly used to infer them from patterns of parasite association in observational data. However, the reliability of these various approaches is not known. We assess the ability of a range of standard analytical approaches to detect known interactions between infections of nematodes and intestinal coccidia (*Eimeria*) in natural small-mammal populations, as revealed by experimental perturbations. We show that correlation-based approaches are highly unreliable, often predicting strong and highly significant associations between nematodes and *Eimeria* in the opposite direction to the underlying interaction. The most reliable methods involved longitudinal analyses, in which the nematode infection status of individuals at one month is related to the infection status by *Eimeria* the next month. Even then, however, we suggest these approaches are only viable for certain types of infections and datasets. Overall we suggest that, in the absence of experimental approaches, careful consideration be given to the choice of statistical approach when attempting to infer interspecific interactions from observational data.

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### 1. Introduction

Interspecific parasite interactions are a major research focus in disease ecology. Most hosts, including humans in communities around the globe, are coinfecting by many parasite species (Petney and Andrews, 1998; Cox, 2001). Numerous laboratory studies (Behnke et al., 1978; Christensen et al., 1987; Adams et al., 1989; Frontera et al., 2005) have shown coinfecting parasites can interact strongly, either positively or negatively (Griffiths et al., 2011), with important implications for disease progression, transmission and control. In particular, if strong interactions are present then targeted treatment may result in potentially unwanted responses in other, non-target parasite species (Lello et al., 2004; Pedersen and Fenton, 2007; Knowles et al., 2013; Pedersen and Antonovics, 2013). Clearly it is essential to know the occurrence

and direction of such interactions in order to predict disease dynamics and the likely impact of control efforts.

Given the evidence for parasite interactions in the laboratory, there is great interest in evaluating their occurrence in nature. As is well known in community ecology, experimental perturbation (e.g., measuring responses to the removal or addition of other species) is the most reliable way to detect natural interspecific interactions (Bender et al., 1984). Unfortunately, such experiments are rarely undertaken on parasite communities (but see Ferrari et al., 2009; Knowles et al., 2013; Pedersen and Antonovics, 2013). Hence, our knowledge of the natural occurrence and significance of parasite interactions is based primarily on observational studies, with various papers reporting clear evidence of strong interspecific parasite interactions, in both animal and human populations (Lello et al., 2004, 2013; Telfer et al., 2010; Shrestha et al., 2013). However, other studies have found little evidence for interactions in natural populations, concluding they are insignificant in shaping parasite communities (Haukisalmi and Henttonen, 1993; Poulin,

\* Corresponding author. Tel.: +44 151 7954473; fax: +44 151 7954408.

E-mail address: [A.fenton@liverpool.ac.uk](mailto:A.fenton@liverpool.ac.uk) (A. Fenton).

<http://dx.doi.org/10.1016/j.ijpara.2014.03.001>

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Please cite this article in press as: Fenton, A., et al. The reliability of observational approaches for detecting interspecific parasite interactions: comparison with experimental results. Int. J. Parasitol. (2014), <http://dx.doi.org/10.1016/j.ijpara.2014.03.001>

1996; Behnke et al., 2005; Behnke, 2008). There is therefore great variation among studies from natural populations, and a disconnection between these observational results and the consistent interactions reported from laboratory experiments.

One explanation for this variability is that parasite interactions are indeed highly variable and context-dependent. This would be an important result, telling us that parasite interactions are only significant under certain conditions (e.g., dependent on timings of coinfection, or infection burdens; Fenton, 2013) or within certain subsets of the host population (e.g., immuno-compromised hosts, or varying with sex or age etc.); if so, and we can identify the conditions or individuals in which interactions are strongest, this may improve our ability to predict the implications of those interactions and target treatment appropriately. A second explanation is that there is genuine variation in the importance of parasite interactions between different study systems, such as the types of parasite communities considered. However, assessing these possibilities is confounded by the fact that different studies often use different statistical approaches to infer interactions, and so it is not clear whether the reported differences are due to differences in biology of the systems or differences in the techniques used. Clearly, if different studies use different methods that themselves vary in reliability then we may be getting an inaccurate picture of the extent of parasite interactions in natural populations. Before we can fully evaluate the occurrence of these interactions, we need to establish the reliability of the various techniques used to infer their presence, ideally within a single study system.

Observational approaches have been suggested to have limited ability to infer interspecific interactions in general (Schluter, 1984). We have previously assessed this theoretically for parasite interactions (Fenton et al., 2010), showing that some commonly-used approaches are limited in their ability to detect genuine interactions. However, that analysis was purely theoretical and ignored many of the complexities of natural systems that could prevent, or even enhance, the performance of different statistical tests. There is a clear need to test the reliability of these various approaches on genuine parasite infection data from natural systems; to do so requires independent measures of the occurrence

of interspecific parasite interactions within a given system, against which the different analytical approaches can be compared. We have previously carried out perturbation experiments using targeted drug treatments on two different natural rodent parasite communities, and have found clear evidence of interspecific parasite interactions in both systems (Knowles et al., 2013; Pedersen and Antonovics, 2013). These provide an ideal opportunity to test the inferences made using standard analytical techniques applied to observational (unmanipulated) data from the same populations. We show that many of the standard approaches are unable to detect the experimentally-demonstrated interactions, and often report associations in the opposite direction to those found experimentally. Overall, we urge caution for the interpretation of observational data when inferring the occurrence of interspecific interactions, suggesting it is only feasible for certain types of analysis applied to certain datasets, and highlight the importance of using perturbation approaches where possible to measure the strength and occurrence of parasite interactions in wild animal and human systems.

## 2. Materials and methods

### 2.1. Summary of interspecific interactions determined via experimental perturbations

We previously conducted experimental manipulations of the natural parasite communities of two small mammal species: wood mice, (*Apodemus sylvaticus*) in the UK (Knowles et al., 2013) and a mixed population of white footed mice (*Peromyscus leucopus*), and deer mice (*Peromyscus maniculatus*) in the USA (Pedersen and Antonovics, 2013). Specific details of each study are given in the relevant papers and information about the data structure, parasite diversity and infection prevalences are given in Table 1. Both studies adopted similar longitudinal designs, whereby permanent sampling grids were regularly trapped (fortnightly in the *Peromyscus* study or monthly in the *Apodemus* study). All individuals caught were given a unique identification tag and biometric data (size,

**Table 1**  
Summary of observational data available for the *Peromyscus* and *Apodemus* analyses in this study.

	<i>Peromyscus</i>	<i>Apodemus</i>
Sample size (experimental data)	270 individuals (453 captures)	146 individuals (312 captures)
Sample size (observational data)	235 individuals (363 captures)	362 individuals (653 captures)
<i>Mean nematode</i>		
Prevalence	35.5%	57.4%
Abundance in EPG (range)	68.86 (0–9087)	41.15 (0–1023)
Intensity in EPG (range)	193.8 (3.23–9087)	72.04 (0.91–1023)
Dominant species (prevalence)	<i>Aspiculurus americana</i> (15.4%) <i>Capillaria americana</i> (15.7%)	<i>Heligosomoides polygyrus</i> (52%) <i>Syphacia stroma</i> (8.2%) <i>Aonchotheca murissylvatici</i> (1.4%) <i>Aspiculuris sp</i> (0.8%)
<i>Mean Eimeria</i>		
Prevalence	64.7%	49.0%
Abundance <sup>a</sup> in EPG (range)	1847 (0–61350)	2402 (0–181000)
Intensity <sup>a</sup> in EPG (range)	2853 (2.66–61350)	4918 (1.25–181000)
Dominant species (prevalence)	<i>Eimeria delicata</i> (9.1%) <i>Eimeria arizoniensis</i> A (57.0%) <i>Eimeria arizoniensis</i> B (30.9%)	<i>Eimeria hugaryensis</i> (27.6%) <i>Eimeria apionodes</i> (14.2%) <i>Eimeria uptoni</i> (2.4%)
Covariates (levels) <sup>b</sup>	Species ( <i>leucopus</i> , <i>maniculatus</i> ) Sex (Male, Female) Age (Adult, Sub-adult, Juvenile) Year (2001, 2002, 2003 <sup>c</sup> , 2004) Trap session (1, 2, 3, 4)	Grid (A <sup>c</sup> , B <sup>c</sup> , C <sup>c</sup> , D <sup>c</sup> , E <sup>c</sup> , F) Sex (Male, Female) Age (Adult, Sub-adult, Juvenile) Year (2009, 2010 <sup>c</sup> ) Trap month (8 levels, May–Dec)

<sup>a</sup> Abundance refers to data including uninfected hosts; intensity refers to data from infected hosts only.

<sup>b</sup> All covariates were coded as factors.

<sup>c</sup> Indicates the year and/or grids from which the experimental data were taken.

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