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REPORT

The role of host sex in parasite dynamics: field experiments on the yellow-necked mouse *Apodemus flavicollis*

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Abstract

We investigated the role of host sex in parasite transmission and questioned: 'Is host sex important in influencing the dynamics of infection in free living animal populations?' We experimentally reduced the helminth community of either males or females in a yellow-necked mice (*Apodemus flavicollis*) population using an anthelmintic, in replicated trapping areas, and subsequently monitored the prevalence and intensity of macroparasites in the untreated sex. We focussed on the dominant parasite *Heligmosomoides polygyrus* and found that reducing parasites in males caused a consistent reduction of parasitic intensity in females, estimated through faecal egg counts, but the removal of parasites in females had no significant influence on the parasites in males. This finding suggests that males are responsible for driving the parasite infection in the host population and females may play a relatively trivial role. The possible mechanisms promoting such patterns are discussed.

Keywords

Gastrointestinal nematodes, macroparasite dynamics, sex-biased parasitism.

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INTRODUCTION

The predisposition of macroparasites to aggregate within their host populations is generated by the presence of one or more heterogeneities in the transmission or establishment process (Wilson *et al.* 2002). Exhaustive empirical studies have shown that heterogeneities in parasite infection arise as a consequence of individual differences in exposure and susceptibility to infection (Keymer & Anderson 1979; Hudson & Dobson 1995; Shaw & Dobson 1995; Poulin 1996a). While the importance of the two mechanisms in the generation of aggregation appears to vary from one host species to the next (Gregory & Woolhouse 1993), there is evidence from mammal species that susceptibility is the dominant process and that variation between individuals is associated with sex, age and body size and also individual behaviour and diet (Poulin 1996a; Schalk & Forbes 1997; Wilson *et al.* 2002).

Recently, a number of comparative studies have investigated sex-biased parasitism and reached the conclusion that within vertebrate hosts, males tend to have significantly higher parasite prevalence and intensity than females (Poulin 1996a; Schalk & Forbes 1997; McCurdy *et al.* 1998; Moore & Wilson 2002). Furthermore, experimental manipulations have shown that male-biased infection was greater when hosts were artificially infected with standard numbers of infective stages than in naturally infected hosts (Schalk & Forbes 1997). While this evidence is not conclusive for all groups of hosts and parasites, the direction is consistent: males harbour higher levels of infection than females. However, these findings provide no insight into the consequences of this disparity on the dynamics of the infection.

One implication of sex-biased parasitism in vertebrate hosts is that heavily infected males may drive the parasite dynamics although successful transmission will depend on other mechanisms, such as the behaviour of susceptible hosts and the spatial distribution of infective stages. Counter to this hypothesis, some authors have suggested that as the sex bias observed is often relatively small (usually <5%) this is unlikely to have a high effect on parasite dynamics (Wilson *et al.* 2002). Either way, disentangling which functional group is important in driving the infection process could be crucial to our understanding of how parasites flow through a host population.

In this study we investigated the role of host sex in parasite transmission and questioned: 'Is host sex important in influencing the dynamics of infection in free living animal populations?' We experimentally reduced the helminth community to either males or females of

yellow-necked mice (*Apodemus flavicollis*) using an anthelmintic, in replicated trapping areas, and subsequently monitored the prevalence and intensity of macroparasites in the untreated sex. We focussed our attention on the trichostrongylid nematode *Heligmosomoides polygyrus*, a species that exhibits a direct life cycle and that is known to infect a large number of microtine and murine rodents (Lewis 1987; Gregory 1992). In the sibling host species, *A. sylvaticus*, infections are generally sex biased with females carrying 5% fewer parasites than males (Gregory & Montgomery 1992; Gregory 1992). The route of infection is either through ingestion of larvae with contaminated food or through the grooming of fur contaminated with infective stages (Hernandez & Sukhdeo 1995). The yellow-necked mice–*H. polygyrus* system represents an ideal system to investigate heterogeneities in host parasites dynamics, partly because previous studies have examined this relationship in detail (e.g. Keymer & Hiorns 1986; Gregory & Montgomery 1992; Gregory 1992) and also because prevalence of *H. polygyrus* is reasonably high and mice can be regularly trapped and sampled.

METHODS

Study area and rodent monitoring

The yellow-necked mouse is a widely distributed rodent in the woodlands of the Italian Alps, and was the most abundant small mammal species in the study area: Malga Campo (Trentino). We undertook a long-term study of the yellow-necked mouse population and estimated mean local density of 2.8 mice per hectare (±0.5SE) during the year of this study (2001).

Intensive live trapping of yellow-necked mice was carried out in a mixed broadleaf woodland of mainly mature stands of beech with scattered alder and pine and sparse understorey and little ground flora (Dolomitic Alps, 650–950 m a.s.l., 1652050E 5073750E). A set of nine trapping grids (each consisting of 49 traps, 7 × 7 at 15 m intertrap interval, covering an area of 0.81 ha) was established using multicapture live traps (Ugglan Type 2; Graham, Sweden). The woodland area was selected as representative of the yellow-necked mouse habitat, and the replicated trapping grids were positioned in woodlands with similar vegetation composition and structure. To minimize possible movement of individuals between grids, each grid was more than 500 m from the neighbouring grid with natural or artificial barriers (rock falls, roads, etc.) between them.

Live trapping was undertaken for two nights, every other week for a total of 14 994 trap nights from February to mid-September. Traps were baited with a standardized amount of seeds (a mix of maize, oat, wheat, rice, millet, linseed, rape, vetch; Zanandrea Sementi, Italy), and with potatoes as a source of water and hay for bedding. Special care was taken not to overfeed or to attract transient individuals. Each mouse trapped was individually tagged with a subcutaneous passive induced transponder (Trovan ID 100; Ghislandi and Ghislandi, Italy). Faeces samples were collected from each trap (no faeces were gathered when traps contained more than one individual) during each trapping session. We also recorded details on body condition, mass and breeding status. We classified juveniles as individuals with a body mass below 15 g and a pelage that indicated the post-juvenile moult had occurred (Gurnell & Flowerdew 1990). Adults were classified as individuals in breeding condition (descended testes for males and perforated vagina or pregnant for females; Gurnell & Flowerdew 1990), while subadults were classified as not in breeding condition with a mass >15 g and with adult pelage.

Parasite manipulation

The yellow-necked mouse population was monitored every 2 weeks from February to March, and from the first week of April until the middle of September, we selectively treated adult and subadult individuals with the anthelmintic Ivermectin (Ivomec®, Merial, Merck Sharp & Dohme, Harlem, Netherlands) by injecting a subcutaneous dose of 10 mg kg^{-1} (Wahid *et al.* 1989). We did not treat the juveniles below 15 g as they were not yet infected. Of nine trapping grids, we randomly selected three and treated all females caught. In a second random group of three trapping grids we treated only males and the three remaining grids were used as controls where no individuals were treated. We assumed that the drug efficacy lasted 11–15 days (Wahid *et al.* 1989) and as the prepatency period of *H. polygyrus* from egg to egg was 13–15 days long (Keymer 1985), each individual was treated once a month. *Heligmosomoides polygyrus* egg production follows a 24-h cycle fluctuation (Brown *et al.* 1994b) and to avoid a possible temporal effect in faeces collection we randomized the order of collection of faeces samples between the trapping grids and the grids themselves.

Bank vole *Clethrionomys glareolus* was the second most abundant small rodent in the study area, and to circumvent any confounding effect caused by interspecies transmission of gastrointestinal parasites (Mèszàros 1978; Lewis 1987), all bank voles trapped were treated with anthelmintic for the entire experiment.

Parasite identification and count

While we monitored the community of gastrointestinal parasites in the faeces (detailed parasite list in Rosso *et al.*

2002), we concentrated our attention on the helminth *H. polygyrus*. This helminth is one of the most common parasites of the genus *Apodemus* and has a relevant impact of host population (Scott 1987). Moreover this parasite has been extensively used as a laboratory model. Nevertheless, we checked the entire community of gastrointestinal parasites for any unusual patterns and found that the helminths community our mice population was characterized by a relatively low prevalence and intensity of infection (Rosso *et al.* 2002).

Faeces collected from each individual were stored at 4°C overnight in Petri dishes on damp blotting paper to standardize the humidity content. Each sample was then weighed and a flotation technique performed to assess the presence of *H. polygyrus* eggs to provide prevalence estimates (Sloss & Kemp 1978). To quantify the amount of parasite's eggs per gram of faeces (EPG), we used the McMaster technique on faecal samples more than 0.4 g in weight (Keymer & Hiorns 1986). One gram of faeces was diluted in 10 ml of flotation solution that allowed a minimum resolution of 33 *H. polygyrus* EPG. For both techniques, samples were inspected under microscope magnification of 100× and we classified every *Heligmosomoides* spp. egg as *H. polygyrus* because this is the only species of this genus found in *A. flavicollis* in our study areas (Rosso *et al.* 2002).

Statistical analysis

To investigate if prevalence of *H. polygyrus* in yellow-necked mice was significantly affected by host characteristics and environmental variables, a generalized linear mixed model (GLMM; Genstat 3.2, 5th edition, Lawes Agricultural Trust, Rothamsted Experimental Station) with binomial errors was performed. Prevalence was used as the response variable and a series of fixed explanatory variables and their interactions (i.e. anthelmintic treatment, host sex, breeding status, grid and period of trapping) were selected to identify the model that best explained the variance observed. This procedure was repeated using GLMM with interactive reweighed linear model (IRREML; with negative binomial errors) based on EPG as response and host population, and environmental characteristics as explanatory components.

To overcome autocorrelations in the multiple trapping data points and therefore non-independence of data, the transponder code, which represented each animal's unique identity tag, was entered into GLMM models as a random effect. The variance explained by each explanatory factor and its significance were calculated using stepwise backwards deletion and Wald test (Crawley 2002).

An *a posteriori* multiple comparison Tukey test was carried out between treatment groups to identify which sex-treated component caused the pattern observed.

RESULTS

Rodents monitoring

A total of 143 yellow-necked mice (73 males and 70 females) were trapped between February and September (equal to 403 captures) and 46% of these individuals were trapped only once. There were no significant differences in the total number of individuals trapped or the sex ratio between the three treatment types (for all: $P > 0.05$). No significant temporal variation in sex ratio was observed during the experiment ($P > 0.05$).

We collected a total of 319 faeces samples of which 315 samples (83.5% of these samples were from multicaptured individuals) were analysed using the flotation technique and 243 samples (87.2% of these were multicaptured individuals) were selected for the McMaster analysis. While we were aware that a percentage of these samples (16.5% for flotation and 12.8% for McMaster) were from individuals trapped once, we added these cases together with the control groups as no significant differences in parasite prevalence and EPG were observed between these transient individuals and the control individuals (for all: $P > 0.05$).

Parasite manipulation

Prior to anthelmintic treatment, host sex did not differ between grids including parasite prevalence and EPG intensity (for all: $P > 0.05$).

Following the selective treatment of either males or females, no significant temporal changes were observed in parasite prevalence and EPG intensity in the control areas ($P > 0.05$), in contrast *H. polygyrus* prevalence showed a significantly different response between the two treated sexes. In trapping grids where females had been manipulated parasite prevalence was 73% in untreated males and 10% in the treated females, while in trapping grids where males had been manipulated prevalence was 25% in untreated females and 6.7% in treated males. In the control grids, prevalence was 60.5% in males and 58.3% in females (Fig. 1). The interaction between sex and treatment significantly contributed to the variation in *H. polygyrus* prevalence in the host population (GLMM: sex treatment, $\chi^2 = 8.24$, d.f. $= 2$, $P = 0.016$) but sex or treatment alone did not significantly explain this variation ($P > 0.05$). The *a posteriori* pairwise comparison between treatment groups revealed a significant decrease in prevalence in females where males were treated compared with females in control grids ($P < 0.038$; Table 1).

In the grids where females were treated, the geometric mean of the *H. polygyrus* EPG was 28.9 (±3.1 SE) in males and 0.5 (±1.0 SE) in females, while in grids where males were treated EPG geometric mean was 1.3 (±1.2 SE) in females and 0.0 (±1.0 SE) in males (Fig. 2). In the control

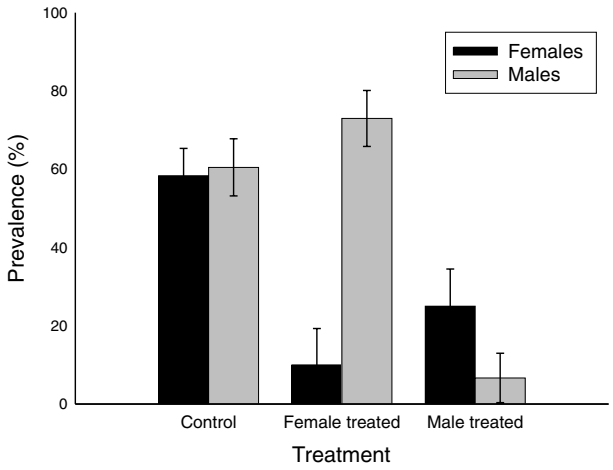

Figure 1 Prevalence of *Heligmosomoides polygyrus* by sex and treatment.

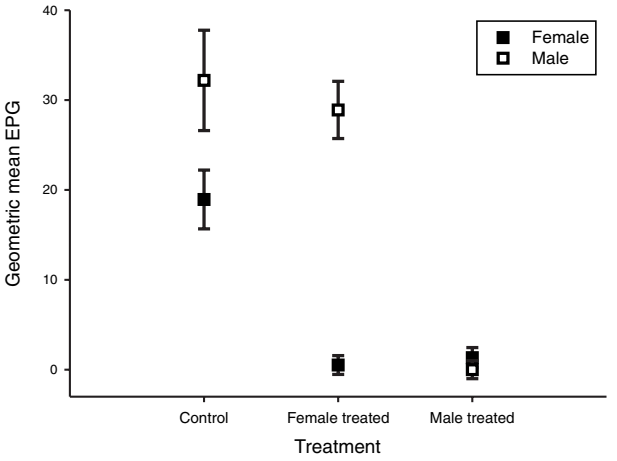

Figure 2 EPG (eggs per gram of faeces) of *Heligmosomoides polygyrus* by sex and treatment.

grids, EPG geometric mean was 18.9 (±3.2 SE) in females and 32.2 (±5.5 SE) in males. Both sex alone and the interaction between sex and treatment significantly contributed to the variation of *H. polygyrus* EPG in the host population (GLMM-IRREML: EPG by sex: $\chi^2 = 5.30$, d.f. = 1, $P = 0.021$; EPG by sex and treatment: $\chi^2 = 6.17$, d.f. = 2, $P = 0.045$); treatment alone did not show any apparent effect ($P > 0.05$). *Heligmosomoides polygyrus* EPG was similar between sexes within control grids. In accordance with the *a posteriori* prevalence analysis, a significant decrease in EPG was found between females where males were treated compared with control females ($P < 0.014$) (Table 1).

Despite the treatment, a low percentage of re-infected positive cases were recorded in the treated individuals (<10%). This is not surprising, as some individuals could have become re-infected before being treated again (see Methods). However, as these mice were treated almost immediately, the effect of these few individuals has been probably negligible on the final result.

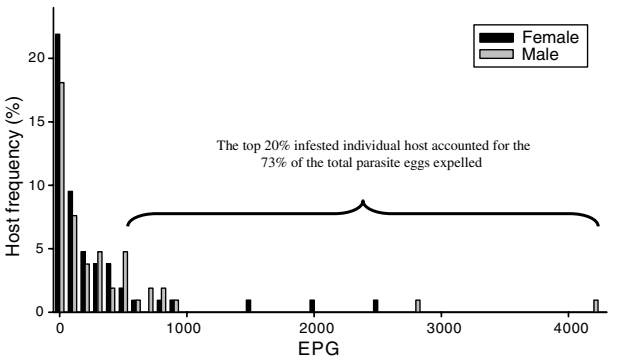

Figure 3 Aggregated distribution of EPG from the control population of males and females *Apodemus flavicollis*.

Groups tested	Differences between effects (±SE)	d.f.	*P*-value
Prevalence			
Female control vs. male control	0.193 (0.578)	166	0.38
Female control vs. female untreated	1.357 (0.749)	166	0.038
Male control vs. male untreated	0.731 (1.404)	166	0.305
Female control vs. female treated	2.448 (1.240)	166	0.026
Male control vs. male treated	2.850 (1.399)	166	0.022
EPG			
Female control vs. male control	0.2149 (1.069)	191	0.42
Female control vs. female untreated	2.794 (1.266)	191	0.014
Male control vs. male untreated	0.825 (2.079)	191	0.346
Female control vs. female treated	4.574 (1.721)	191	0.004
Male control vs. male treated	13.356 (26.805)	191	0.310

Table 1 Pairwise comparison Tukey test between control and treatments by sex analysis based on prevalence and analysis based on eggs per gram of faeces (EPG)

Finally, we investigated the pattern of distribution of EPG in the control group and this did not differ from the negative binomial distribution for both males ($k = 0.156$, $P = 1.00$) and females ($k = 0.131$, $P = 1.00$). We observed that the top 20% of the most infected hosts accounted for 73% of the total *H. polygyrus* eggs expelled and had been collected from males in 62% of cases (Fig. 3).

DISCUSSION

We experimentally manipulated parasite load with respect to sex in a natural population of yellow-necked mice and found that after reducing the parasite intensity of males we observed a decrease of the intensity of parasites in females. In contrast we did not observe a similar effect on males when females were treated for parasites. This result suggests that males have a dominant role to play in driving the dynamics of parasite transmission in this system while females have a relatively trivial role.

We used faecal analysis to investigate the dynamics of parasite transmission in a host population. While there is evidence that this is a reliable technique (Scott 1988), the slightly different results we found between the flotation and the McMaster method was probably caused by both a different amount of faecal samples available for the two tests and differences in test sensitivity. Ideally total number of parasites per individual would have been recorded but this would have meant killing the mice and leading to immigration of new untreated mice. We also removed parasites with a systemic anthelmintic drug that would have affected the whole community of parasites and their interactions, including ticks (Wahid *et al.* 1989). This may have had an influence on the nature of our results, nevertheless, the difference observed in parasite reduction between the sexes was clear.

So far, heterogeneities in parasite distribution, such as sex-biased parasitism, have been associated with differences in host susceptibility and, accordingly, differences in their parasite load. Little attention has been given to the role of sex bias in parasite transmission; in effect the male bias in parasite rates does not explain the different abilities of sexes in maintaining the infection. In the absence of empirical evidence, some authors have tended to emphasize the role of sex bias while others have dismissed it as unimportant (Poulin 1996a, Wilson *et al.* 2002). Few studies have highlighted the importance of identifying the functional groups responsible for transmission in the population or have been able to disentangle their contribution in the maintenance of parasite populations (Anderson & May 1991; Woolhouse *et al.* 1997; Perkins *et al.* 2003). The experiments undertaken here demonstrate that host sex affects vary not only in the ability to modulate parasite establishment but also in their contribution to parasite transmission dynamics, with males playing a dominant role in successful parasite infection.

These findings lead us to question the mechanisms which could be associated with the role of males in causing differences in subsequent infection levels of females and other males. The experiments do not reveal what the mechanism could be but this could arise as a consequence of differential behaviour between the sexes that would lead to increased exposure of one sex to transmission. For example, transmission can occur through grooming and differences in allogrooming between sexes could result in increased rate of transmission from one sex to the next (see Hernandez & Sukhdeo 1995). Furthermore, infected males have been observed to have larger territories than uninfected males and this could influence contact rates between infected males and susceptible hosts (Brown *et al.* 1994a). In this respect, Ims (1987a) found that while spatial distribution of reproductive female microtine rodents was determined by food availability, the spatial strategy in reproductive males reflected the availability of fertilizable females. Therefore reproductive females show a stronger site-specific organization, which could explain low rate of transmission, whereas home ranges of males tended to extensively overlap at high density and decrease at low densities (Ims 1987b), which could explain the higher rate of transmission.

Another possible mechanism may act through sexual differences in the immunological response of hosts such that worms in males produce fertile eggs at a higher rate than in female hosts. In fact, immunological differences between the sexes may contribute by modulating parasite egg fertility, parasitic worm size, and the rate of development and survival of infective stages with males providing a better environment for parasite growth and reproduction than females (Poulin 1996b; Finkelman *et al.* 1997). However, as Tompkins & Hudson (1999) noted, density dependence in worm size may cause different responses in the development and fecundity of the worms. In this regard, we carried out a gastrointestinal analysis on 111 individuals collected from an area near our study site in the summer of 2001 and found no significant differences in prevalence and mean intensity of infection of *H. polygyrus* between sexes (prevalence 35.2% males vs. 29.8 % females, mean intensity 1.2 males vs. 7.5 females, for all $P > 0.05$, unpublished data).

Interestingly, when we examined the distribution of EPG among sexes we found that 20% of the most infected individuals (represented by 62% of males) accounted for the 73% of the total eggs expelled. This finding is in line with other observations on yellow-necked mice by Perkins *et al.* (2003) that investigated the occurrence of Tick borne encephalitis virus in a population near to our study area. These researchers found that more than 90% of the

potential transmission of Tick borne encephalitis comes from male yellow-necked mice. These heterogeneities can play a very important role in influencing the size of the parasite basic reproduction number (R_0) and have important implications in the selective treatment of individuals in control programmes.

In conclusion, we identified a male bias in parasite transmission and evidence that this had important consequences for parasite dynamics. Not only are there differences in sex susceptibility to parasite infection but also in the sex ability to modulate transmission such that even a relatively small proportion of the host population can be responsible for the majority of the transmission. This finding improves our knowledge on parasite dynamic and may be useful for planning parasite control programmes when the identification of functional groups is practicable.

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