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Aspiculuris tetraptera in wild *Mus musculus*. Age resistance and acquired immunity.

JERZY, M. BEHNKE*

Department of Zoology, Bedford College, University of London, London

ABSTRACT

Wild house mice, naturally infected with *Aspiculuris tetraptera* were segregated according to their weight into six age groups. The prevalence of infection and the mean worm burden of these mice were studied in the different age groups. The overall prevalence of infection was high (57% or more) in all the groups except the youngest. Mice acquired larvae soon after weaning; the highest larval burdens were reached in juvenile mice and the highest mature worm burdens, a group later, in mature mice. Older mice had fewer larvae and fewer mature worms. The mature worm burdens decreased but relatively slower than the larval burdens. It is suggested that either innate or acquired resistance could account for these observations.

The occurrence of age resistance in laboratory host-parasite model systems is well documented in the literature (Africa, 1931; Ackert, Edgar and Frick, 1939; Mathies, 1959a; Stahl, 1961; Gray, 1972). There are, however, relatively few reports of age resistance in surveys of parasites of wild host species.

The laboratory mouse *Mus musculus* is known to exhibit marked age resistance when infected with the oxyurid parasite *Aspiculuris tetraptera* (Mathies, 1959a; Stahl, 1961). It is also known that this parasite elicits an immune response which, in some strains of laboratory mice, eliminates most primary infection worms before patency and prevents the establishment of larvae from subsequent reinfections (Behnke, 1975b). This immunity, however, does not prevent the few remaining worms (i.e. worms which have not been eliminated in the primary immune response) from surviving to patency (Behnke, 1974: Ph.D. Thesis of London University).

In a study of the prevalence of *A. tetraptera* in a wild house mouse population, it was shown that more male mice were infected than females and the frequency distribution studies suggested that this was because, initially, fewer larvae became established in female mice and subsequently a greater proportion of established larvae was eliminated from female mice before patency (Behnke, 1975a). The material collected during this study was also used to examine the level and the prevalence of infection with *A. tetraptera* in mice of different ages.

MATERIALS AND METHODS

The methods used to trap mice, treatment of captured animals, and the procedures used at autopsy have already been described (Behnke, 1975a).

The allocation of mice to different age groups

The method used to estimate the age of mice was similar to that used by Whitaker (1970), but instead of subdividing the population into Whitaker's four categories, mice were arranged into six different age groups.

*Present address: Zoology Department, Nottingham University, School of Biological Sciences, University Park, Nottingham NG7 2RD.

Although the choice of the weight categories was not based on exact details of the relationship between age and weight in wild house mice, five-week-old mice would be expected to weigh 13 or more grams and growth would be expected to slow down after maturity at about five weeks (Barnett *et al.*, 1975).

Pregnant female mice were not included in this study. The remaining 93 male and female mice were arranged into six categories corresponding to:

Group W (Weanlings)	—	under 5 gms
Group Y (Young)	—	6–9 gms
Group J (Juvenile)	—	10–13 gms
Group M (Mature)	—	14–17 gms
Group A (Adult)	—	18–21 gms
Group O (Old)	—	over 21 gms

Since the purpose of the project was to examine the relationship between age and level of infection with *Aspiculuris tetraptera*, the following assumptions were made: (1) The six groups represented mice of different ages; (2) the lightest mice were the youngest and the heaviest (non-pregnant) mice were the oldest.

With the exception of group W (group W—six mice), the results were based on an examination of 13 or more mice per group. The sex of the host is known to influence parasitic infections and therefore the data for both sexes has also been included in the analysis.

RESULTS

Overall, the group with the fewest infected mice was group W in which all of the mice were weanlings. Only two of the six mice were infected with larvae (1 and 9 larvae respectively). The overall prevalence of infection in the remaining categories was high, 57·1% or more in all groups (Table 1). The prevalence of larvae was highest in groups J and M, which corresponded to mice only just sexually mature.

TABLE 1
The prevalence of *Aspiculuris tetraptera* in male and female mice from the six age groups

Group	W	Y	J	M	A	O
Number of mice	6	14	20	12	26	13
Percentage of mice infected	33·0	57·1	85·0	91·7	76·9	92·3
Number of females infected	0	5/9	10/12	6/7	5/8	8/9
Number of males infected	2/3	3/5	7/8	5/5	15/18	4/4
Percentage of females infected	0	55·6	83·3	85·7	62·5	88·8
Percentage of males infected	66·7	60·0	87·5	100·0	83·3	100·0
Percentage of mice infected with larvae	33·0	57·1	85·0	66·7	34·6	61·5
Percentage of females infected with larvae	0	55·6	83·3	71·4	50·0	55·5
Percentage of males infected with larvae	66·7	60·0	87·5	60·0	27·8	50·0
Percentage of mice infected with mature worms	0	0	40·0	91·7	69·2	69·2
Percentage of females infected with mature worms	0	0	25·0	85·7	50·0	77·8
Percentage of males infected with mature worms	0	0	62·5	100·0	77·8	50·0

The highest mean worm recovery (MWR) was recorded in groups J and M and this pattern was consistent in all the MWR analyses undertaken (e.g. MWR in male and female mice, overall MWR, larval MWR, and mature worm MWR) (Figs. 1 and 2). The

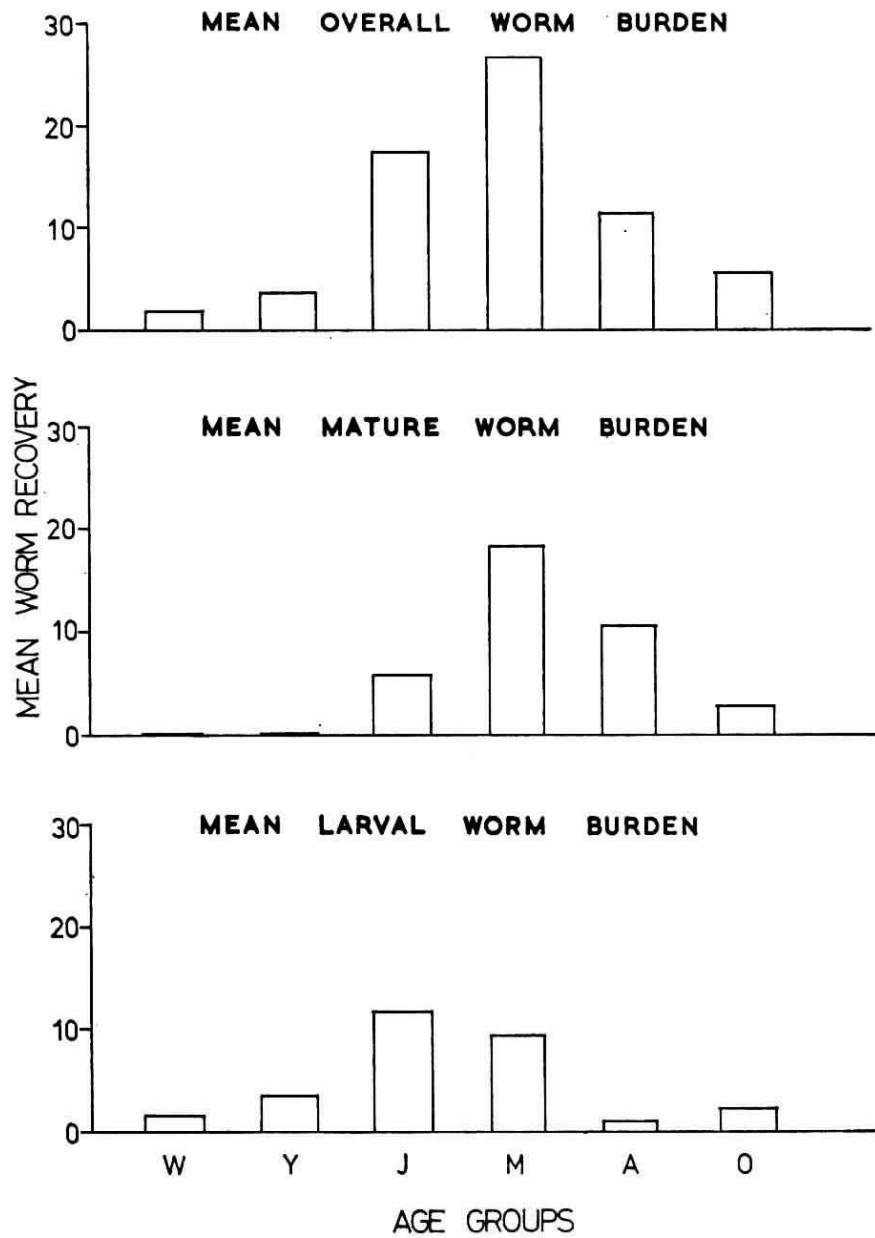


FIG. 1 A comparison of the mean overall, larval and mature worm recovery in mice from six different age groups.

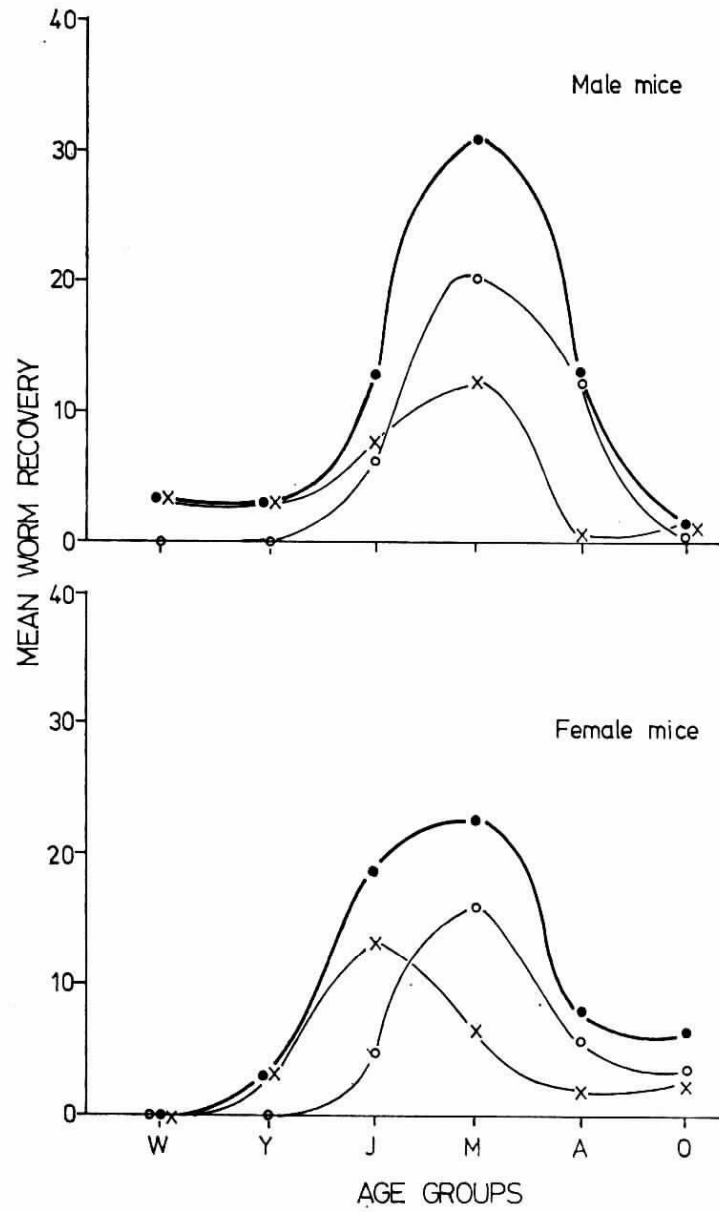


Fig. 2 A comparison of the overall (●—●), larval (x—x), and mature worm (o—o) recovery in male and female mice from six different age groups.

lowest MWR's were found in the youngest and also in the oldest mice. Thus, for example, the overall MWR was 3.4 ± 4.1 in group Y, rose to 26.5 ± 30.5 in group M and declined to 5.1 ± 8.3 in group O. A similar pattern was obtained in all the other groups studied (Figs. 1 and 2). Perhaps the most spectacular was the overall MWR in male mice where group Y had a MWR of 3.0 ± 3.7 , group M a MWR of 31.2 ± 34.2 which then fell to 1.3 ± 0.5 in group O.

The age of mice acquiring a maximum level of infection with larvae was of particular significance. The maximum value for the larval MWR was found in group J (mean larval recovery 11.5 ± 10.1 ; mean mature worm recovery 5.6 ± 10.2) a group earlier than that for mature worms (group M: mean larval recovery 9.3 ± 18.6 ; mean mature worm recovery 18.1 ± 25.3).

DISCUSSION

The survey results reported in this paper demonstrate that older mice were a less suitable host for *Aspiculuris tetraptera*. This was evident both in the prevalence of infection and the mean worm recovery in different age groups.

It was found that only group W (weanling mice) had a low prevalence of infection. In all the remaining groups it was relatively high, although fewer older mice (groups A and O) were infected with larvae. The MWR data confirmed that the highest worm burdens were associated with the mice in group M, after which the MWR declined to a lower value in group O. The finding that the larval MWR was at its highest in group J and thereafter fell whilst the mature worm MWR rose to a peak in mice of the next age group (group M) before subsequently declining in older mice was particularly significant. Laboratory studies have shown that mice can be infected only after 14 days of age and *A. tetraptera* infections become patent 24 days post infection (Behnke, 1974: Ph.D. Thesis, London University). Therefore sexually immature mice, i.e. groups W and Y would not be expected to harbour mature worms.

At least two possibilities can be proposed to explain this result: (a) older mice acquire fewer larvae because behavioural differences in these mice reduce the extent of exposure to infective eggs of the parasite; (b) all groups of mice are equally exposed to the parasite but endogenous differences within the groups, arising either from physiologically unfavourable changes with age or from varying immunological experience of the parasite, result in different levels of infection in the six age groups. Although at present it is impossible to eliminate the first possibility, this is unlikely to be a major contributing factor and it is suggested that the alternative explanation is more probable.

In the present population 28.7% of males and 31.3% of non-pregnant female mice were infected with 11 or more worms and it was suggested previously (Behnke, 1975a) that there were either exogenous or endogenous factors which enhanced the susceptibility of these mice to infection. Clearly, the influence of these factors on the MWR was most important in mice from groups J and M because the high MWR in these groups were almost entirely the consequence of a few mice with high worm burdens. Thus the apparent rise in the MWR in groups J and M was brought about not by a general increase in the level of infection in these groups, but by the presence of relatively more mice with high worm burdens. The fall in MWR is similarly represented by fewer older mice with high MWR's and is certainly reflected in a very marked decrease in both the incidence and level of infection with larvae.

Recently, it has been shown that laboratory mice develop immunity to *A. tetraptera*, and this is manifest by an expulsion of most primary infection worms and a greater resistance to reinfection (Behnke, 1975b). Acquired resistance could satisfactorily account for the observations made in this study. It is possible therefore that larvae were acquired by young mice until a critical level (a threshold value; Jarrett, Jarrett and Urquhart, 1968; Wakelin, 1973) in group J. The presence of larvae and/or mature worms in these mice conceivably triggered events which ensured that in the older mice the survival of incoming larvae was reduced.

The persistence of mature worms for a long time suggests that these worms were unaffected by the host response, senescence perhaps accounting for their eventual disappearance from the host. The presence of mature worms in old mice, apparently resistant to reinfection, suggests that concomitant immunity may be of importance here in enabling the parasite to survive in the wild. Such an adaptation can be expected to benefit both the host and the parasite; the host is protected from over-infection, and the parasite is ensured survival since the first larvae can expect to reach maturity before subsequent reinfections stimulate sufficient immunity to make further infection impossible.

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