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Author: Boag, Brian

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OBSERVATIONS ON THE SEASONAL INCIDENCE OF MYXOMATOSIS AND ITS INTERACTIONS WITH HELMINTH PARASITES IN THE EUROPEAN RABBIT (*ORYCTOLAGUS CUNICULUS*)

Brian Boag
6 Park Road, Invergowrie, Dundee, Scotland DD2 5AH

ABSTRACT: European rabbits (*Oryctolagus cuniculus*) were collected monthly over a 10-yr period and the incidence of myxomatosis and the size of helminth populations were recorded. Myxomatosis occurred annually, always as an epidemic in the latter half of the year and was associated with both an increase in the percentage of animals infected and the size of the infections of the nematodes *Trichostrongylus retortaeformis* and *Passalurus ambiguus* and the cestode *Mosgovoyia pectinata*. It is suggested that myxomatosis had the effect of reducing the rabbits' overall immune response to infection and that due to the regular annual occurrence of myxomatosis, the resulting increase in the size of helminth infections must be considered an integral part of the population dynamics of these parasites.

Key words: Myxomatosis, rabbit, *Oryctolagus cuniculus*, helminth–virus interaction, helminth parasites, nematodes, cestodes, *Trichostrongylus retortaeformis*.

INTRODUCTION

The seasonal fluctuations of the viral disease, myxomatosis, in European rabbits (*Oryctolagus cuniculus*) has received little attention but recent work by Ross and Tittensor (1986) have indicated that a definite seasonal cycle could be detected from reports received from 96 sites in England and Wales. They suggested that the larger significant increase in the incidence which occurred in the autumn/early winter and the second lesser increase which occurred in the spring reflected the activity between rabbits which allowed the transfer of the rabbit flea (*Spilopsyllus cuniculi*) to take place. The seasonal fluctuations in helminth parasites have been studied in New Zealand (Bull, 1964), Australia (Mykytowycz, 1956; Dunsmore, 1966a, b, c) and Great Britain (Boag, 1972, 1985) and have shown similar trends in all three countries although the season when numbers peak vary between species of helminths. The influence of the rabbits' immune response in controlling the numbers of mature *Trichostrongylus retortaeformis* was demonstrated by Michel (1952a, b, 1955) while Mykytowycz (1959) showed experimentally that myxomatosis lowered the rabbits' resistance to *Graphidium strigosum* and significantly increased adult nematode numbers. Boag (1985) also recorded significantly elevated numbers of *T. retortaeformis* and *Passalurus ambiguus* in rabbits from Scotland.

The present paper reports the annual prevalence of myxomatosis in a population of rabbits on a farm in eastern Scotland and the interaction of this viral disease with concurrent infections of both nematodes and cestodes.

MATERIALS AND METHODS

With the exception of November 1978 and April 1979 an average of at least five rabbits were shot monthly between January 1977 and December 1986 from an area of approximately 400 ha on a farm in eastern Scotland (Ordnance Survey grid reference NO 280340). All rabbits were returned to the laboratory where they were weighed, sexed and examined around the anus, ears, eyes and mouth and any rabbits found with the characteristic swellings and pustular lesions were classified as having myxomatosis. The very few rabbits which could be identified as recovering (lesions had healed and body condition was good) were placed in the infected cohort. The abdominal cavity was opened and the alimentary tract removed and separated into the three regions (stomach, small intestine and large intestine) before being opened and the contents sieved through a 100 mesh (125 μm) sieve. The residues were collected and stored in 5% formalin. All helminths were counted if total numbers were <20 while a sample aliquot was counted when helminth numbers were >20.

TABLE 1. Prevalence, intensity and abundance of helminths recorded between January 1977 and December 1986.

Species	Prevalence (%)	Intensity (±standard error)	Abundance (± standard error
Graphidium strigosum	38	28.0 (2.4)	11.0 (10.0)
Trichostrongylus retortaeformis	79	647.0 (31.0)	514.0 (26.0)
Nematodirus battus	<1	68.0 (0)	0.05 (0)
Passalurus ambiguus	12	1,938.0 (622.0)	189.0 (16.0)
Mosgovoyia pectinata	29	5.7 (0.4)	1.6 (0.1)
Cittotaenia denticulata	15	2.4 (0.2)	0.40 (0.02)
Coenurus pisiformis	2.3	2.8 (0.6)	0.10 (<0.01)
Cysticercus serialis	<1	21.0 (15.0)	0.03 (<0.01)
Fasciola hepatica	<1	1.0 (0)	0.01 (0)

Cestodes were fixed using Dammin's procedure (Dammin, 1937) and identified using the key of Arnold (1938). Helminth abundances were transformed by $\log_{10}(N + 1)$ to normalise the overdispersed distribution of the counts (Dunsmore and Dudzinski, 1968) before being statistically analysed using the Statistical Package for Social Scientists (SPSS) program available at the Edinburgh Regional Computing Centre (James Clerk Maxwell Building, Mayfield Road, Edinburgh EH9 3JZ). An analysis of variance was used to determine the level of significance between the populations of helminths in rabbits with and without myxomatosis.

Use of the terms prevalence, intensity and abundance follow the definitions of Margolis et al. (1982). Voucher specimens of the five most common helminth species are deposited in the British Museum of Natural History and assigned registration numbers 1987.12.7.1, 1987.12.7.2, 1987.12.7.3–7, 1987.2691–2700 and 1987.2701–2710. The identifications of *F. hepatica* and *N. battus* were confirmed by R. J. Thomas (Newcastle-upon-Tyne University) and *T. pisiformis* and *T. serialis* by A. Jones (Commonwealth Institute of Parasitology, St. Albans, England).

RESULTS

Nine helminth parasites were recorded from 985 rabbits collected from the study area between 1977 and 1986 (Table 1), but two larval cestodes (*Taenia pisiformis, Taenia serialis*), and trematode (*Fasciola hepatica*) and one nematode (*Nematodirus battus*) were found in <10% of the rabbits and were not included in the subsequent analyses in the present paper. Myxomatosis was recorded regularly in the second half of each year between 1977 and 1986 (Fig. 1). The mean duration of any single outbreak in the study area was 3.8 mo. Between August and December the percentage of all rabbits collected which has myxomatosis was >20%, with the peak occurring at 37% in December. Although the distribution of the rabbits varied within the study area (Boag, 1986, 1987) there was no evidence to suggest myxomatosis did not affect all rabbits equally.

The population dynamics of the parasites in rabbits varied between species (Fig. 2). The intensity of *G. strigosum* populations was highest between January and April and lowest during August and September. There was no statistically significant difference in the intensity of *G. strigosum* infections between June and January in rabbits with and without myxomatosis (Table 2). The prevalence of *G. strigosum* in rabbits with and without myxomatosis also was very similar; 42% and 37%, respectively (Table 2).

The epidemiological pattern of *T. retortaeformis* was markedly different to that of *G. strigosum* with its populations tending to be greater in the autumn. The intensity of *T. retortaeformis* infections was significantly greater in rabbits with myxomatosis for most of the months between June and January (Fig. 2); the mean number of nematodes in rabbits with and without myxomatosis was 1,094 and 566, respectively. *Trichostrongylus retortaeformis* also was more prevalent in rabbits

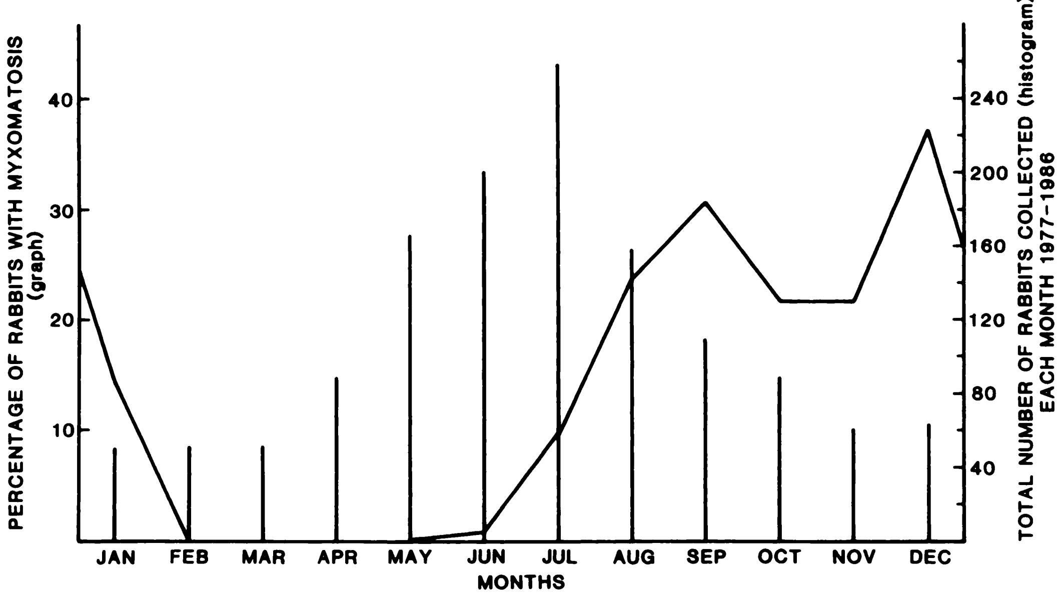

FIGURE 1. A total number of rabbits collected each month 1977 to 1986 and the average percentage of rabbits with myxomatosis.

with myxomatosis (96%) compared with those without myxomatosis (81%) (Table 2).

The seasonal fluctuations in the intensity of *P. ambiguus* indicated a peak in mid-winter especially in rabbits infected with the myxomatosis. The mean number of nematodes recovered between June and January was 5,029 versus 1,570 in rabbits without myxomatosis. The prevalence of *P. ambiguus* in rabbits with myxomatosis also was greater (16%) than in rabbits without the virus (10%).

Mosgovoyia pectinata was recovered from 29% of the rabbits (Table 1). The prevalence in rabbits infected with the myxoma virus between June and January was 46% compared with 26% in uninfected rabbits (Table 2). The intensity of infection was significantly greater in December and January in rabbits with myxomatosis than in those without the virus.

The population dynamics of *Cittotaenia denticulata* showed a peak in intensity of infection between May and July, months when few rabbits were infected with the myxoma virus. There were significant differences in the intensity or prevalence of *C. denticulata* in rabbits with and without myxomatosis.

TABLE 2. Prevalence (%) and intensity of helminth populations in rabbits with and without myxomatosis (excluding data from rabbits collected during February, March, April and May).

Species	Rabbits with myxomatosis (n = 158)		Rabbits with no myxomatosis (n = 827)		
	Prevalence	Intensity	Prevalence	Intensity	P =[a]
Graphidium strigosum	42	15	37	19	0.86
Trichostrongylus retortaeformis	96	1,094	81	566	0.001
Passalurus ambiguus	16	5,029	10	1,570	0.15
Mosgovoyia pectinata	46	8	26	6	0.03
Cittotaenia denticulata	18	2	18	2	0.67

[a] Value of P based on ANOVA between intensities of helminths in rabbits infected with myxomatosis versus uninfected rabbits.

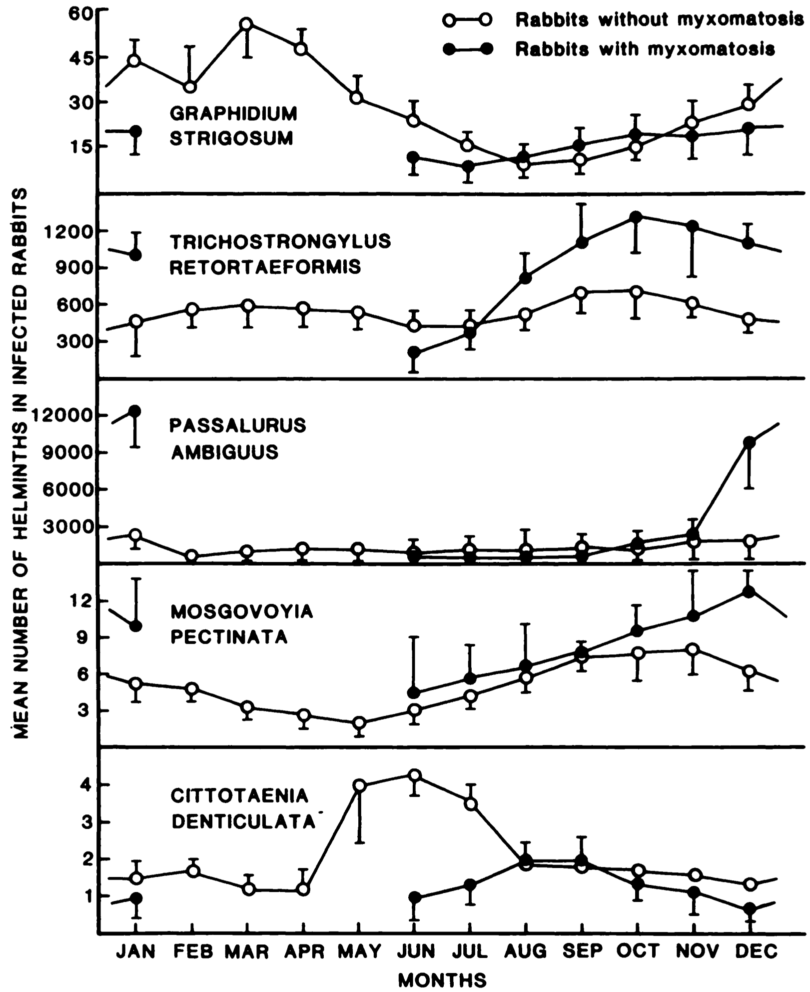

FIGURE 2. The population dynamics of helminth parasites of rabbits with and without myxomatosis.

An analysis of the results also indicated that the sex ratio of the rabbits was close to unity (female to male ratio 1:1.1) and that sex had no effect on the prevalence of the helminths or of myxomatosis. The age of the rabbits were not determined in this study and consequently its effect on the prevalence of myxomatosis or of the helminths cannot be determined.

DISCUSSION

The marked seasonal incidence in myxomatosis in the autumn and early winter recorded at the study site each year between 1977 and 1986 was similar to the major wave of infection reported by Ross and Tittensor (1986), but there was no evidence of the equivalent smaller spring wave of infection. Mortality and mortality rate resulting from myxomatosis in the rabbit population was difficult to estimate for a number of reasons, especially the alteration in their behaviour which allowed them to be more easily caught. A certain number of the infected rabbits also were known to recover. However, results of this study indicated that in the infected rabbits the populations of *T. retortaeformis*, *P. ambiguus* and *M. pectinata* were greatly increased compared with the uninfected rabbits. The reason why the rabbits with myxomatosis had increased helminth infections is not understood, but it may have been that high helminth abundances caused the rabbits to be more susceptible to myxomatosis. However, it is more probable that the viral infection left the rabbit in an immunosuppressed state in terms of both nematode and cestode infections. Mykytowycz (1959) found that a large proportion of the naturally acquired *G. strigosum* in rabbits were in an arrested state, but once the rabbits had been artificially infected with myxomatosis these arrested nematode larvae resumed development and molted to adults. This is supported in the present study, because the greatest differences between rabbits with and without myxomatosis occurred in November and December and not earlier in the year when the rabbits had less time to acquire and develop immunity to high abundances of helminths. The reason why the abundances of both *G. strigosum* and *C. denticulata* were similar in myxomatosis infected and uninfected rabbits may be explained by the fact that both these species have peak infections in spring and early summer when very few rabbits have myxomatosis.

The regular occurrence of myxomatosis in the latter part of each year and its significant interaction with both nematode and cestode infections indicate that the phenomenon of increased nematode abundance should be considered an integral part of the population dynamics of these parasites. It has been demonstrated also that *G. strigosum* and *T. retortaeformis* can have an adverse effect on the growth rate and body weight and fecundity of rabbits (Bull, 1964; Dunsmore, 1980). Thus, it may be concluded that the increased helminth abundances could exacerbate the effects of myxomatosis and reduce the chances of recovery of the infected rabbits, especially since myxomatosis usually occurs in the autumn when rabbits are storing fat prior to the onset of winter.

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