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Myxomatosis: passive immunity in the offspring of immune rabbits (*Oryctolagus cuniculus*) infested with fleas (*Spilopsyllus cuniculi* Dale) and exposed to myxoma virus

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SUMMARY

Kittens with maternal antibodies to myxoma virus, the offspring of rabbits which had recovered from myxomatosis, were exposed to fleas contaminated with myxoma virus and/or contact with infected rabbits from birth. All kittens died or became infected before 8 weeks of age. When compared with adult animals similarly infected the kittens showed no advantage in terms of survival time or recovery rate attributable to maternal antibodies. Flea transmission of virus was found more effective than contact transmissions.

INTRODUCTION

Fenner, Marshall & Woodroofe (1953) found that the titre of complement fixing antibody in the serum of animals which had recovered from myxomatosis fell to a relatively low plateau during the first 6 months after recovery. Neutralizing antibody, however, remained at a high level for periods exceeding 20 months after recovery. Passive immunity to myxomatosis was demonstrated by Fenner & Marshall (1954) in animals following inoculation of antiserum and in the offspring of does immune to myxoma virus. They showed that in kittens older than 7 weeks maternal antibodies, both complement fixing and neutralizing, had fallen to a low titre. It was suggested that because myxomatosis in Australia generally occurs in the summer and rabbits breed during the autumn, winter and spring, maternal antibodies would have little effect on the epidemiology of myxomatosis. Since neutralizing antibody titres remain high for long periods there seems little strength in this suggestion. In parts of Britain where the breeding season overlaps with summer epizootics of myxomatosis, it was suggested that a reduced case mortality could result from maternally transmitted antibodies. This protection would have to be conferred on rabbits 8 weeks old or less, before antibody titres in kittens have fallen. Epizootics of myxomatosis in Australia have been largely confined to the summer because the principal vectors have been rabbit-biting mosquitoes (Fenner & Ratcliffe, 1965) which occur in large enough numbers to cause epizootics during the summer. Despite the long periods during which maternal antibody titres remain high in serum it was decided to examine the epidemiological consequences of passive immunity under Australian conditions. This seemed necessary because of

reports of winter epizootics by Dunsmore, Williams & Price (1971) and Williams, Fullager, Davey & Kogon (1972) and also because of the introduction of the European rabbit flea into Australia (Sobey & Conolly, 1971) with the consequent possibility of virus being spread throughout the year including the breeding season. The main question is whether passive immunity up to 8 weeks is of any consequence to the population.

MATERIALS AND METHODS

Viruses

Three strains of myxoma virus cloned in our laboratory were used: Lausanne (Lu), a field strain (FS/98) collected from the Canowindra district of N.S.W. in 1967, and standard laboratory strain (S.S.).

Rabbits

Domestic rabbits from a randomly bred colony maintained in this laboratory not exposed to myxomatosis and designated 'unselected' (U) together with domestic rabbits selected for genetic resistance (Sobey, 1969) and designated 'selected' (S) were used. The recovered does were all from the selected stock which had been exposed to and recovered from standard laboratory strain (SS) or FS/98 strain of myxoma virus.

Floor pens

Flea-proof pens were constructed within a 3×6 m. room, out of 1 m. high galvanized-iron sheet metal. In the first pen experiment, one pen 3×5 m. was built, but in all other pen experiments two smaller pens $1{\cdot}5 \times 5$ m. were used. Each pen was supplied with five wooden nest boxes 30 cm. high, 30 cm. wide and 50 cm. long, together with two wooden boards, 1 m. $\times$ 0·5 m., leaned against the wall at an angle to act as cover areas. The floor of each pen was completely covered with straw to a depth of 10 cm. Fouled areas, generally one corner, were cleaned out twice a week. Pellets were fed from an automatic hopper and water supplied from an automatic nipple.

Fleas

The flea population of the floor pen was started with laboratory-bred fleas (Sobey, Menzies & Conolly, 1974). A daily estimate of the flea load on each rabbit was made by one observer. To make fleas infective 0·5 g. of scarified back scrapings (Sobey, Conolly & Adams, 1967) was added to 3 ml. Hanks' lactalbumin growth medium with 0·5% horse serum, sonicated for about 1 min. and the supernatant pipetted free of the larger debris: this concentrated virus suspension was mixed with fleas in a glass container in the ratio of 1 ml. virus extract to 5000 fleas. As soon as mixing was complete the fleas were transferred to sheets of filter paper in an enamelled tray with 250 cm. sides and allowed to dry at room temperature for about 1 hr. Fleas were then aspirated into small plastic bottles in the numbers required.

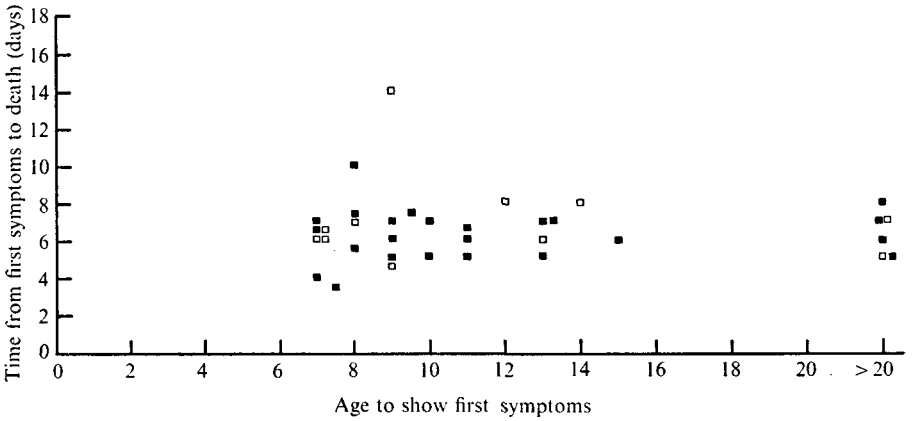

Fig. 1. The survival times to the Lausanne strain of virus, given as the time from first visible symptom to death, of caged animals infected at different ages. ■, The offspring of immune selected does (with maternal antibodies) and, □, the offspring of susceptible (unchallenged) selected does (without maternal antibodies), each infected via ten infective fleas.

Circulating antibodies

Blood samples were collected on filter paper strips as described by Sobey, Conolly & Adams (1970) and the antibody to the 'd' soluble antigen (Williams, Dunsmore & Sobey, 1973) measured.

RESULTS

To estimate the protection given to rabbits 6 weeks of age or older by maternal antibodies the survival times of rabbits born to selected recovered dams were compared with those born to selected unchallenged dams. The recovered dams ranged between 8 and 24 months post-recovery. Caged rabbits of both types varying in age from 6 weeks to adult were each given ten fleas made infective with Lu virus and their survival times estimated from the time they first showed a visible sign of the disease to death. The survival times which were 6·3 days for offspring of recorded dams and 7·1 for offspring of unchallenged dams are illustrated in Fig. 1. No survival advantage was conferred on the offspring of dams which had previously recovered from myxomatosis suggesting that at these ages maternal antibodies had little or no influence on the course of the disease caused by Lu strain virus initiated via fleas.

To study the effects of maternal antibodies during the period from birth to 7 weeks of age rabbits were bred in floor pens in an environment containing fleas and virus. It was hoped to obtain information on the age at which kittens became infected and when they did become infected, whether maternal antibodies would extend their survival times. Non-immune does could not have been used to produce control kittens in the floor pen because they would almost certainly have contracted myxomatosis before littering and either died, or survived and produced kittens with maternal antibodies. Instead, kittens of recovered does were compared

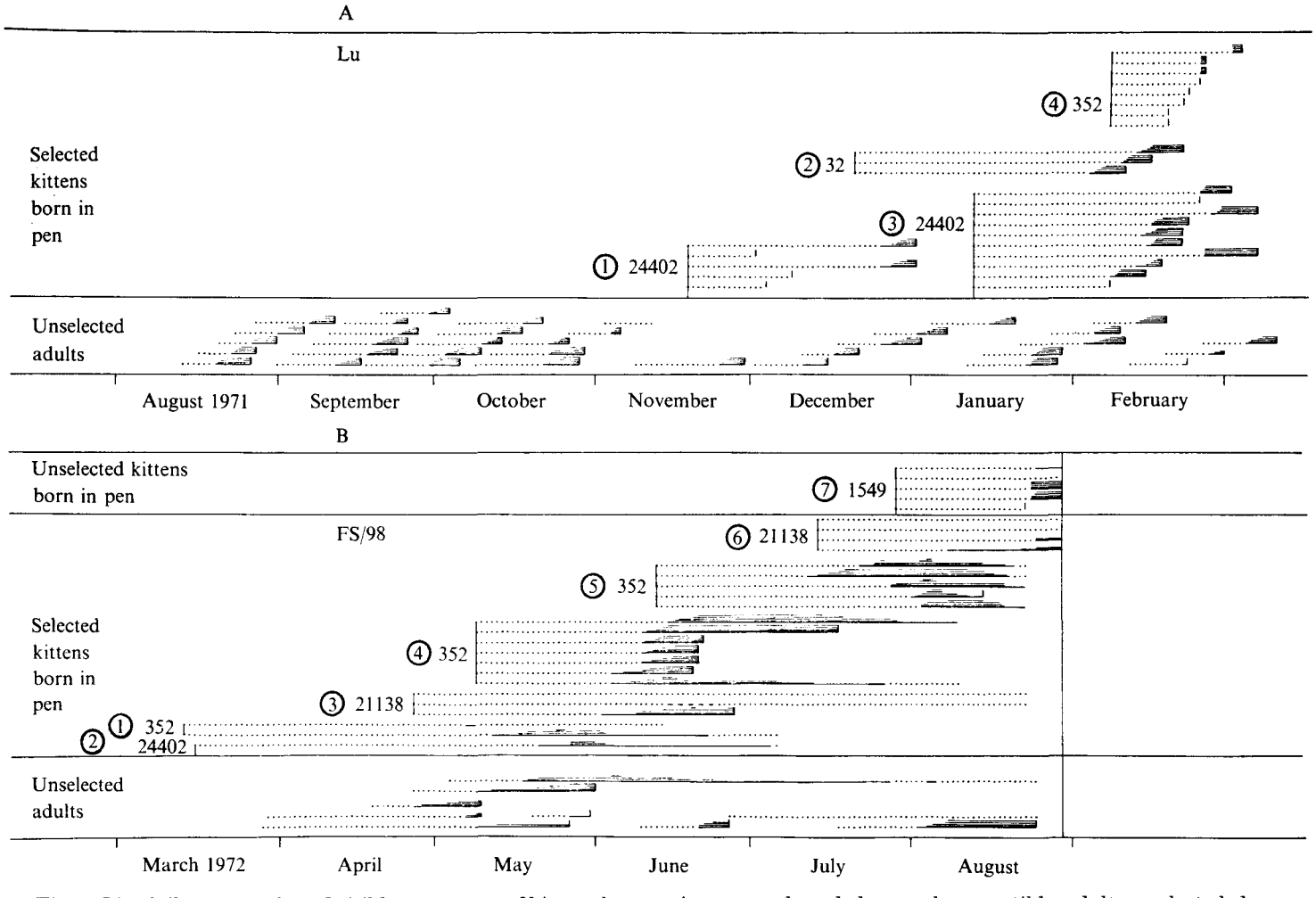

Fig. 2. The daily progression of visible symptoms of kittens born to immune selected does and susceptible adult unselected does housed in a floor-pen in the presence of fleas and (A) virulent Lausanne strain of virus, Lu; (B) a field strain of virus, FS/98. ●, No visible symptoms; —, just visible eye lesion; ═, eye quarter shut; ≡, eye half shut; ≣, eye three-quarters shut, ▤, eye fully shut; †, death.

with adult offspring from recovered does on the assumption that the survival times of such offspring would no longer be affected by maternal antibodies.

In the present work it has been assumed that the offspring of any doe which had recovered from myxomatosis would receive a high level of neutralizing maternal antibodies from their dam. In the floor pens described above where fleas and virus were a constant part of the environment, recovered animals were observed on occasions to become re-infected and exhibited localized skin lesions at the ear base and a dramatically elevated titre of anti-d antibodies. Thus the parent animals in the floor pens had antibody titres sufficiently high to prevent re-infection or were re-infected with a resulting boost to their antibody. It was assumed that animals much more than 7 weeks old would no longer be protected, hence adults, whatever their dam, were not protected.

In an experiment with Lu virus four does and one buck, all of which had recovered from an infection of myxomatosis during selection for genetic resistance, were introduced into a 3×5 m. floor pen. These rabbits were infested at the outset with a total of 1000 fleas. In order to maintain a high rate of infection unselected and susceptible doe rabbits were introduced into the pen initially at the rate of two a week and later one a week. The first three unselected does were infected with Lu virus by intradermal injections at the ear base. None of these rabbits lived long enough to breed, and showed symptoms of myxomatosis on average 10 days after entering the pen. The results of the experiment are illustrated in Fig. 2A. Kittens which died within 3 days of birth are not shown. From the beginning of the experiment in the middle of August 1971 until the end of October 1971, no litters were born. During late October and early November 1971 an unidentified disease affected the whole rabbit colony and a number of animals died in the pen without obviously contracting myxomatosis. The virus was re-introduced by the intradermal injection of the surviving unselected rabbit about the middle of November, at which time the first litter of kittens were born, litter 1. Three of these kittens died without symptoms and the cause of death was unknown; as some 20-week-old rabbits had died in the pen just before the birth of this litter without showing symptoms, death due to myxomatosis is in doubt. The remaining two kittens did not show symptoms until they were 5–6 weeks old. The kittens in litter 2 showed symptoms between 6 and 8 weeks and those in litter 3 between 4 and 6 weeks of age. In litter 4, three kittens died without showing symptoms and the remaining three showed symptoms between 2 and 3 weeks and were all dead before 4 weeks of age. Taking the 14 kittens that certainly died of myxomatosis we find an average time to visible symptoms of 38·2 days; the remaining 7 lived for 20 days. The comparable figures for the introduced adults is a lapse of 10·0 days between introduction and visible symptoms. During the first week after the birth of litter 4 several kittens from other litters had severe myxomatosis, two unselected adults died after having had an unusually high load of fleas and the dam of litter 4 also had an abnormal post-partum infestation. This was the only litter to be born in the presence of a high number of fleas. The times between first appearance of symptoms and death for the kittens born in the pen in 1971 and 1972 are shown in Fig. 3. Also shown are the times between first appearance of symptoms and death

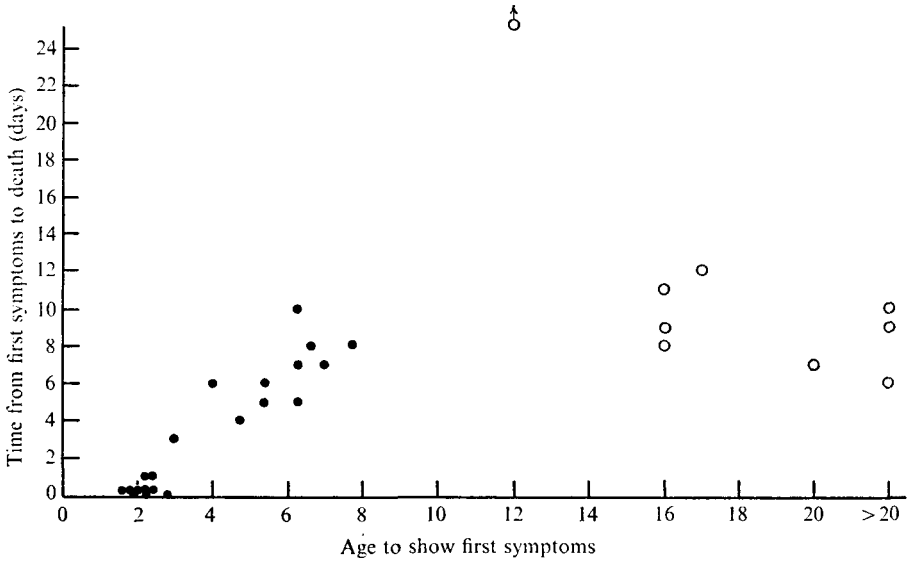

Fig. 3. The survival times, given as the time from first visible symptoms to death, of animals which became infected in the floor-pen at different ages; ●, Animals born in the pen to immune selected does; ○, the offspring of immune selected does introduced into the pen at ages in excess of 8 weeks.

of rabbits aged between 9 and 27 weeks introduced into the pens, the offspring of selected recovered dams. None of the kittens born in the pen survived the disease and there was a clear trend for their survival time to increase with increasing age, the inverse to the fall off of maternal antibodies. The three kittens from litter 4 which died without showing any symptoms possibly died from myxomatosis. This is supported by the finding of Williams *et al.* (1973) that 2 out of 11 wild rabbit kittens from recovered dams injected with Lu virus at 3 weeks of age died without showing symptoms. Similar observations were reported by Fenner & Marshall (1954). One of the offspring from selected recovered dams introduced into the pen survived for 3 months (Fig. 3) and must be regarded as a recovery. However, the other animals in this group died with survival times differing little from those of the older kittens born in the pen. The slight but consistent fall in the survival time with increased age beyond 16 weeks is in agreement with the age effect described by Sobey, Conolly, Haycock & Edmonds (1970) for another virulent strain of virus, standard laboratory strain.

Attenuated field strain FS/98

Four does and one buck, all of which had recovered from myxomatosis during selection for genetic resistance to myxomatosis, were introduced into a $1{\cdot}5 \times 5$ m. floor pen. Of two litters born in March 1972 (litters 1 and 2) all but three of the kittens were removed before the introduction of virus. Two unselected female rabbits were introduced into the pen and left for 3 weeks before the introduction of FS/98 to ensure that no residual Lu remained from the previous experiment. FS/98 was introduced about the middle of April via an unselected female rabbit

Table 1. *The survival rates to FS/98 virus in selected and unselected domestic rabbits of differing ages infected by different routes and housed in floor pens or cages, showing the alleviating effect of floor pen conditions on the disease*

	Source of rabbits					
	Unchallenged unselected domestic			Offspring of recovered selected domestic		
Mode of infection	Age (weeks)	Survival rate	Survived (%)	Age (weeks)	Survival rate	Survived (%)
Fleas or contact infection in floor pens	— — 7–20	— — 5/11	— — 45	3–4 5–6 7–30	2/8 8/10 17/17	25 80 100 (56)
I.D. in cages	10–30	1/27	4	10–60	68/107	64
I.D. in floor pens	—	—	—	10–23	4/4	100

injected intradermally in the ear base with about 10 L.F.U. of virus. After a further 3 weeks this donor rabbit and one of the other two unselected rabbits, both of which had contracted myxomatosis, were destroyed to avoid overcrowding. The results are shown in Fig. 2B. All of the kittens except two in litter 3 showed clear symptoms of the disease. Two kittens in litter 6 and one in litter 7 showed symptoms 2 or 3 days after being caged at the termination of the experiment. Of the two kittens from litter 3 which failed to show eye symptoms, one showed some small lumps in the ears at 4 weeks of age but no eye lesions and the other showed no visible symptoms at all. At the conclusion of the experiment these two animals were bled and both were found to have circulating anti-d antibodies. One of the unselected female rabbits put into the pen failed to show any visible symptoms after 8 weeks in the pen and also had circulating anti-d antibodies at the conclusion of the experiment. This rabbit produced litter 7 in the pen, consisting of five kittens, of which two died of myxomatosis in the pen, two died of myxomatosis shortly after the termination of the experiment and one died without symptoms (it is not known whether these kittens were born before or after the dam became infected). The presence of circulating antibodies to viral soluble antigens in the blood of these three symptomless rabbits indicates they must have supported some viral multiplication and thus have been subclinically infected. The 20 kittens born into an environment of FS/98 averaged 35·6 days to show visible symptoms and introduced adults (4 only) averaged 13 days between introduction and first symptoms.

The survival rate to this attenuated strain in selected rabbits in the floor pen was high, deaths only occurring in rabbits less than 7 weeks of age (Table 1). Clearly rabbits less than 7 weeks of age (offspring of immune dams) were at a disadvantage when compared with rabbits older than 7 weeks. These data also illustrate that rabbits infected in pens suffer a milder disease than rabbits in cages.

One kitten from litter 3 (Fig. 2B) and one unselected adult rabbit remained

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Table 2. *The proportion of fleas combed from three rabbits at different times after infection that produced lesions when individually fed on the marked backs of unselected rabbits*

Day sampled	Proportion of flea bites giving lesions — Donor rabbit no. 1	Donor rabbit no. 2	Donor rabbit no. 3
7	0/16	—	0/15
8	3/9	2/8	2/18
9	—	0/18	4/14
10	3/11	0/19	2/20
11	—	0/10	0/4
Tested after 8 days refrigeration			
9	—	1/18	4/18
10	—	—	1/18

—, No fleas recovered for testing.

without symptoms but were found to have circulating anti-d at the conclusion of the experiment. Another kitten from litter 3 was observed to have some small lumps in the ears at 7 weeks of age but showed no other symptoms and was also found to have circulating anti-d at the end of the experiment. Clearly subclinical myxomatosis can occur – at least with attenuated field strains of the virus.

Flea distribution

With one exception, when 20 fleas were seen on a kitten at a time of exceptionally high flea numbers in the pen, infestations of more than 10 fleas per kitten were not observed after 10–14 days of age when the kittens began moving about the pen. Those kittens observed with a few fleas before infection appeared to lose these at the onset of visible symptoms, the fleas returning only as the symptoms regressed or, on a few occasions, just before death due to myxomatosis. Only those kittens recovering from FS/98 and over 10 weeks of age were found with more than 20 fleas and the infestation rate was lower than that of 20-week-old unselected rabbits in the pen at the same time.

All of the unselected adult rabbits introduced into the floor pens were does and after death their uteri were examined for embryos. Of 17 does examined, 5 were found to be between 10 and 14 days pregnant as judged by the size of the fetuses. Of the 5 rabbits which were pregnant, 4 had retained their fleas until death. The retention of fleas by does in such early stages of pregnancy in spite of severe virus infections was interesting and unexpected.

Data presented by Lockley (1954) suggest that flea transmission is density-dependent. Further evidence to support this suggestion is presented in Table 2. Fleas were combed from rabbits at different times after infection and the number of lesions resulting from feeding individual fleas on marked areas of an unselected rabbit back were compared with the number of fleas fed. At no time were more than about one third of the fleas infective. Of the fleas from one donor rabbit combed during the time it was most infectious only 2 out of 55 bites produced lesions.

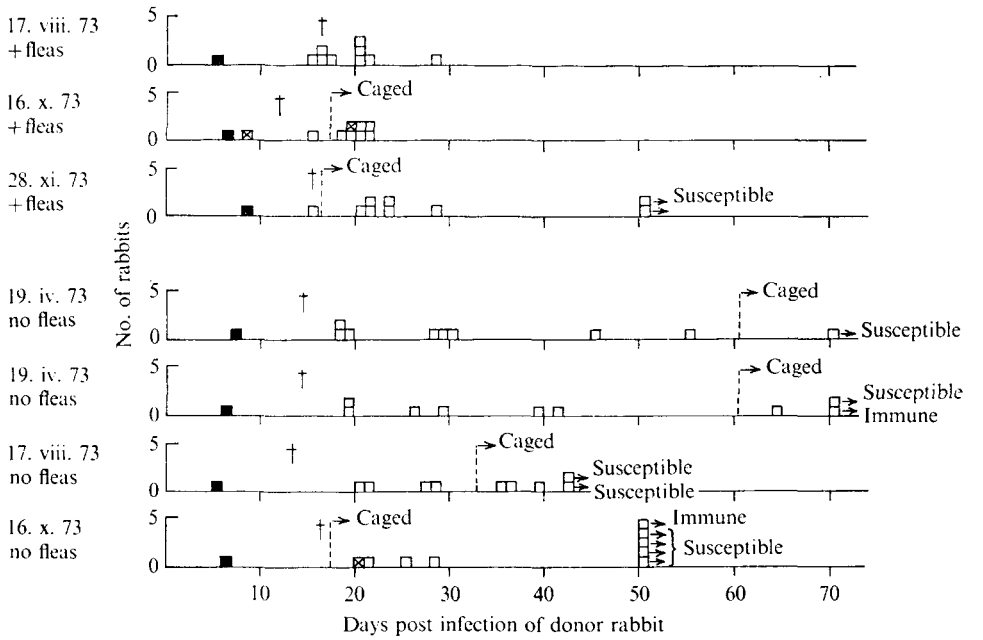

Fig. 4. Showing that the virus spread more quickly and fewer animals escaped infection in the floor-pen in the presence than in the absence of fleas. The donor rabbit in each group was infected on day zero; ■ shows when it first showed eye symptoms, + shows when it died, □ shows when the other nine animals in each group first showed eye symptoms, and ⊠ indicates an animal died of causes other than myxomatosis.

Flea transmission

To assess the importance of fleas in the transmission of virus, a series of experiments was run in 1972 and 1973 in the floor pens with and without the presence of fleas. In each experiment ten selected female rabbits 9–27 weeks old were penned together and one, the donor, was injected intradermally in the ear base with Lu virus. In those experiments 'with fleas' each doe was initially infested with 100 fleas. The first experiment with fleas and the first three without fleas were allowed to run until all the animals had died, or to about 50–60 days after the infection of the donor; surviving animals were then bled and tested for susceptibility by the I.D. injection of S.S. virus in the ear base. These experiments were time-consuming and subsequent experiments were modified to allow greater use of the two available floor pens by caging the animals 24 hr after the donor rabbit died. The times for each rabbit to show visible eye symptoms relative to the day of injection of the donor rabbit are given in Fig. 4. It is clear that the virus spread more quickly in the presence of fleas and fewer animals escaped infection. (4/25 with fleas and 24/33 without fleas failed to become infected within about 18 days of the donor rabbit being challenged $\chi^2_{(1)} = 18{\cdot}3$, $P < 0{\cdot}001$.) Two animals from pens without fleas showed no visible symptoms but were found to have circulating anti-d antibodies and to be immune to challenge with S.S. virus. The dam of one of these animals had never been exposed to myxomatosis and the

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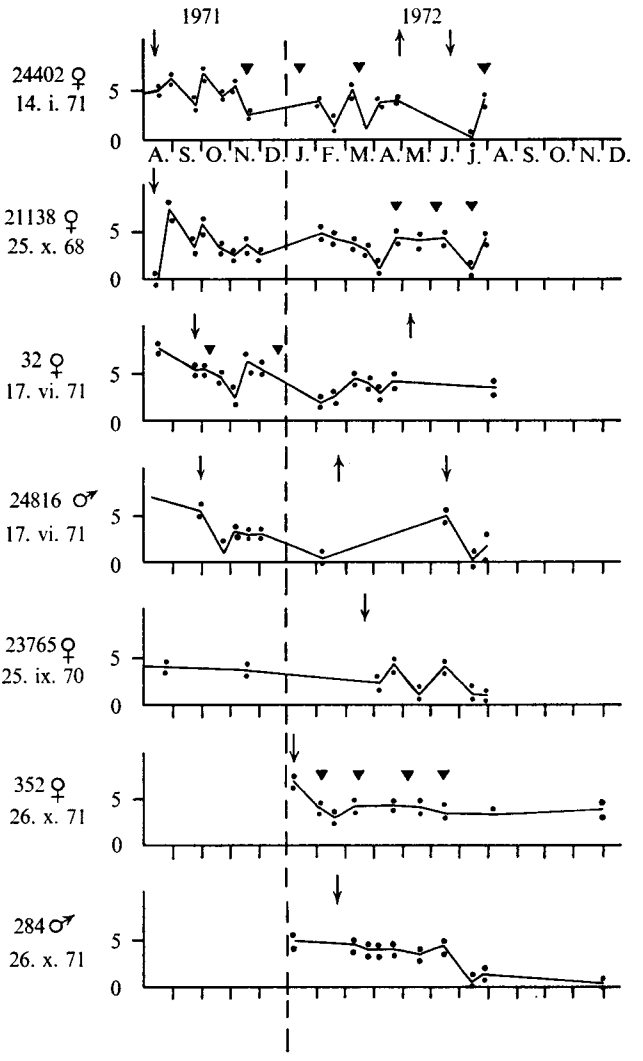

Fig. 5. Variations in the levels of anti-d antibody with time of rabbits which had recovered from myxomatosis and were exposed to fleas and virus in the floor-pen; ↓ into floor-pen, ↑ out of floor-pen, and ▼ littered.

other animals were 12 weeks old when the donor became infectious; thus it seems unlikely that their lack of symptoms and recovery from infection was related to maternal antibodies.

The mode of transmission in the absence of fleas was not determined. The mites *Haemodipsus ventricosus* (Denny) and *Chyletiella parasitivorox* (Megnin) known to be capable of transmitting myxomatosis (Mykytowycz, 1958) were not observed macroscopically and examination of pelts by the method described by Williams (1972) (Rosamond Shepherd, personal communication) showed only *Chyletiella parasitivorox* to be present, and only in very low numbers. Mykytowycz (1958) has shown that transmission can occur by direct contact and in the confined

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conditions of the floor pens there was ample opportunity for this to occur. The survival times of 30 unselected rabbits in the floor pens over a period of seven months failed to show any change in the virulence of the virus.

Antibody fluctuations

The parent rabbits were bled periodically and the anti-d antibody measured. In order to avoid the possibility of unnecessary exposure to accidental infection kittens were not bled during the experiment. The fluctuations in the antibody titres, as illustrated in Fig. 5 indicate that subclinical re-infection or reactivation (Williams *et al.* 1973) occurred periodically. Rises or falls in antibody titres were not correlated with any event such as pregnancy, parturition, flea load or virus availability. Substantial rises were noted in two does at a time when no active virus was present in the pen.

DISCUSSION

The offspring of rabbits which had recovered from myxomatosis and were exposed to infection from birth (via fleas and/or contact) took longer to infect but they neither escaped infection nor showed extended survival times relative to adult animals of similar origin. These results suggest that the spread of virus by fleas and/or contact during the breeding season is unlikely to result in an increased recovery rate due to maternal antibodies.

Rabbits infected with both Lu and field strain underwent a milder disease under floor pen conditions than in cages, due possibly to their being able in the floor pen to shelter from draughts, thus facilitating the maintenance of body temperature. Higher mortality rates would be expected in rabbits of all ages under the cold conditions of the breeding seasons in the field.

Kittens born into an environment of virus and fleas in floor pens averaged 38·2 days for Lu and 35·6 days for FS/98 from birth to when they first showed symptoms of myxomatosis; adult rabbits introduced into the same environment averaged 10 days for Lu and 13 days for FS/98 from the time of introduction to the first signs of myxomatosis. This delay in onset of symptoms could have been due to maternal antibodies the kittens acquired from their dams, or to kittens being unattractive to fleas or both.

During the first week after birth, rabbit kittens are attractive to fleas (Mead-Briggs, 1964) and they may be very heavily infested. Fleas acquired by the doe from outside the nest at this time would be likely to move on to the kittens and thus if the doe were to bring in virus-infected fleas the kittens would be exposed to myxomatosis during this period. After this initial infestation kittens tend to remain free of fleas until they reach about 15 days of age, after which they may pick up a few non-infective, newly emerging fleas from the nest. Under floor-pen conditions no kittens between 1 and 3 weeks of age were observed with fleas. Most kittens in the floor pens became infected or were seen with fleas between the ages of 3 and 6 weeks, although kittens and juveniles were less attractive to fleas than adults. One litter (litter no. 4 in Fig. 2(A)) was born during a period of very high flea infestation and virus availability and three of the eight kittens died by 16 days

of age without symptoms. It is suggested that these kittens died of myxomatosis as a result of infection during the first week after birth by infective fleas brought into the nest by the doe.

Myxomatosis is a highly infectious disease which can be transmitted by direct contact. However, the rate of transmission is enhanced by biting insect vectors. Flea transmission appears to be density-dependent and flea density in rabbit populations is highest during the breeding season (Allan, 1956; Sobey & Conolly, 1971; Williams & Parer, 1971); virus transmission via fleas is thus likely to be most effective at this time. It is suggested that the introduction of virulent virus into the field would achieve the most effective rabbit control if introduced early in the breeding season when the weather is cold, fleas are in abundance and before natural outbreaks of field strains.

We are indebted to Miss Rosamond Shepherd for examining our floor-pen rabbits for the presence of ectoparasites and to Miss Elizabeth Emery and Mrs Gail McFarland for technical assistance and doing all the hard yakka.

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