*J. Hyg., Camb.* (1979), **83**, 285
*Printed in Great Britain*



# Myxomatosis: the release and spread of the European rabbit flea *Spilopsyllus cuniculi* (Dale) in the Central District of Victoria

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(*Received* 3 *November* 1978)

SUMMARY

The European rabbit flea was first released in Victoria in August 1969 at Werribee. Releases were made on five different land forms. At one site the first flea was recovered 2 weeks after release. Fleas were recovered between 4 and 6 weeks after release at the other sites. Differences in establishment and spread on the different land forms were due to physically restricted movement of some rabbit populations. By June 1971 80% of rabbits were infested but an occasional young uninfested rabbit was still found in August 1978. Infestation numbers were higher than in the Mallee region especially on pregnant does.

## INTRODUCTION

Observations on the establishment and distribution of the European rabbit flea *Spilopsyllus cuniculi* (Dale) in the semi-arid region of north-western Victoria have been reported previously (Shepherd & Edmonds, 1976). The first Victorian releases of *S. cuniculi* were made in August 1969 on the Melbourne and Metropolitan Board of Works Farm at Werribee. The work was initially designed to obtain information on the effects of transporting *S. cuniculi* under various conditions, and on the release of fleas, in an area which was relatively secure from human interference and within easy travelling distance of the Institute.

As most rabbits live in warrens along channel banks and road margins, and around the perimeters of paddocks rather than in warrens in paddocks, it was expected that spread of the fleas would occur along the channels and fencelines rather than across paddocks. The initial trials were based on this expectation. As the fleas spread observations were extended to cover all the farm (approximately 12000 ha), and then to adjacent farm lands.

The spread and numbers of fleas per rabbit were monitored at regular intervals until an apparently stable host–parasite relationship was reached. This paper reports the initial occurrence and spread of the fleas on different land forms ranging from irrigated pastures to dry non-irrigated basalt country and the development of the host–parasite relationship as flea numbers increased over a 5-year period. The data are contrasted with data from the semi-arid areas of north-western Victoria (Shepherd & Edmonds, 1976).

0022-1724/79/0129-1978 $01.00 

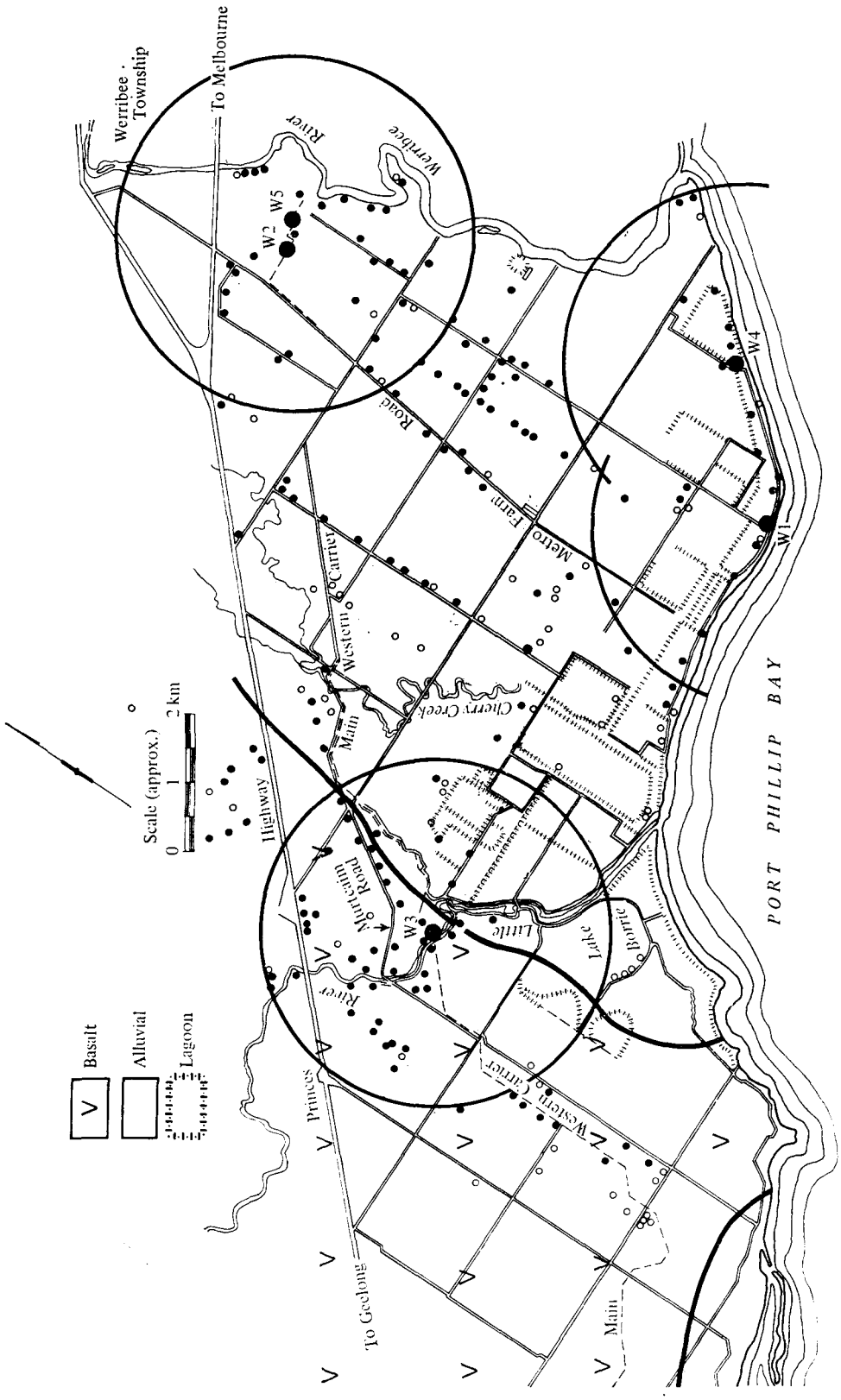


Fig. 1. Rabbits with and without fleas collected within and beyond 2·4 km of release sites, W1–W5, between September 1969 and June 1971 on the Melbourne Metropolitan Board of Works Farm, Werribee. Each circle represents one to five rabbits collected in the area. ●, Rabbits carrying fleas; ○, rabbits not carrying fleas.

https://doi.org/10.1017/S0022172400026085 Published online by Cambridge University Press

## MATERIALS AND METHODS

### *Description of study area*

Releases were made at five environmentally distinct sites (Fig. 1). These sites have been described previously (Shepherd & Edmonds, 1973). Briefly they were: W1, saltbush covered coastal dunes; W2, dryland pasture with warrens in sugar-gum plantations; W3, dryland pasture on basalt with warrens in drain and river banks; W4, dense tea-tree; W5, irrigated paddock.

### Spilopsyllus cuniculi

All fleas released were bred by Dr W. R. Sobey, Division of Animal Genetics, C.S.I.R.O., Sydney (Sobey, Menzies & Conolly, 1974). Active warrens were seeded by releasing fleas from vials into each warren. The times of releases and number of *S. cuniculi* released are shown in Table 1.

Table 1. *The numbers of* S. cuniculi *released at five sites on the Melbourne and Metropolitan Board of Works Farm, Werribee, August* 1969

| Area | No. of active warrens seeded | No. of *S. cuniculi* released |
|---|---|---|
| W1 | 1 | 200 |
| W2 | 5 | 200 |
| W3 | 2 | 200 |
| W4 | 2 | 200 |
| W5 | 2 | 200 |

### *Sampling and counting*

Each site was sampled regularly, by trapping rabbits using C.S.I.R.O.-designed spring traps, 'gin' traps, by netting with a gill net along a fence line, by using a spotlight and hand nets to catch them alive, or by spotlighting and shooting at night (Shepherd, Nolan & Edmonds, 1978). Trapping and netting were used until the fleas spread more than about 1 km from each site. After that all samples taken were shot samples, usually at 6 monthly intervals during each spring and autumn.

Rabbits captured alive were sexed and their ages estimated. They were examined for fleas and other ectoparasites (Shepherd & Edmonds, 1973), tagged and released. Shot rabbits were examined in a vehicle set up as a mobile laboratory. Data collected included number of fleas present, their position on the rabbit, the sex and the breeding status of the rabbit, its approximate age, and its weight. An eye was taken (usually the right eye) and stored in 10% formalin. The rabbit was later aged by the dried eye lens technique of Myers & Gilbert (1968). A blood sample was taken and tested for the presence of antibody to myxoma virus (Mansi, 1957; Sobey, Conolly & Adams, 1966).

Rabbit counts, initially fortnightly then monthly, were made along a 12 km transect to monitor rabbit numbers.

## RESULTS AND DISCUSSION

### *Initial spread from release sites*

The distribution of fleas from the coastal dune site W1 (Fig. 1) was observed by trapping with C.S.I.R.O. designed cages, gin traps, and later by netting. The first flea was found close to the release warren 6 weeks after the release. The same rabbit was recaptured a week later and carried two fleas. The next sighting of fleas was on a kitten 3 months after release, again close to the release warren. During the following 3 months every rabbit caught within 0·2 km of the release carried fleas. By April 1970 fleas had spread up to 0·8 km along the coast and inland although only 50 % of the rabbits shot within 0·4 km carried fleas and the most heavily infested rabbit carried 32 fleas only.

One year after the release nearly all rabbits (10/13) collected within 0·4 km of the release site carried fleas, while only 8 out of 26 rabbits collected outside that area carried fleas. During the following non-breeding season again only about 50 % of rabbits were found to carry fleas although they could be found on rabbits from W1 to W4.

The spread of fleas from site W2 was observed by netting (Shepherd & Williams, 1976) along an east–west fence line for a distance of 400 m. The first rabbit (a buck) carrying fleas was collected 40 m from the release site 4 weeks after the flea release. Eight weeks after the release rabbits carrying fleas were collected up to 60 m from the release site and 8 rabbits out of 15 collected carried fleas. Six of these rabbits carried less than five fleas, one carried ten and one pregnant doe, collected 40 m from the release site, carried about 50.

Twelve weeks after the release rabbits up to 300 m from the release site were found carrying fleas. Eighteen out of 32 rabbits carried fleas but no rabbit carried more than ten and most carried less than five fleas. After 16 weeks the fleas had spread beyond the netted area. Within the netted area, i.e. within 400 m of the release site, 75 % of rabbits collected carried fleas.

The area was examined again 9 months after the release. Fifteen per cent of the rabbits (5 out of 33) did not carry fleas, i.e. after one breeding season some rabbits in an area over which the fleas had spread 5 months before were uninfested.

The spread of fleas along the Little River from W3 was followed by netting along the fence line beside the river and by shooting rabbits in the paddock. No netting was carried out after July 1970 when fleas had spread up to 450 m along the Little River in a north-easterly direction and 75 % of the rabbits carried fleas with a heaviest infestation of 27 fleas on a pregnant doe.

The fleas had crossed the Little River, probably by movement of rabbits across a road bridge, by April 1970 when 25 % of rabbits in the 68 ha paddock on the southern bank were infested compared with 45 % of rabbits shot at random in the 97 ha release paddock. In June 1971 32 of the 42 rabbits caught within a 3·2 km radius of the release site carried fleas and the fleas had spread across the Princes Highway to the west.

C.S.I.R.O. traps placed within 0·2 km of the release point were used at the 6 ha site W4. The first flea was collected from a sub-adult doe 6 weeks after the release.

Twenty-five per cent of rabbits trapped during October 1969 carried fleas.

By December 50% of rabbits carried fleas. The cages were then moved to cover 0·4 km from the release point. By July 1970 all rabbits collected were infested and the fleas had spread to the coast. In June 1971, 19 of the 20 rabbits shot within 2·4 km of the release site carried fleas.

At W5 the first fleas found were five on a kitten caught at the release site 2 weeks after release. One week later a buck carrying one flea was caught. The infestation percentage reached 25% during November–December, 100% by June 1970, and by August 1970, 1 year after release, fleas had reached the Werribee River 1 km from the release point. Spread along the southern bank of the river was observed but the first infested rabbits on the northern bank were not collected until June 1971.

The differences in initial rate of spread from the sites were probably due to some rabbit populations having physically restricted freedom of movement. Spread was slowest inland from W1 where lagoons tend to confine the rabbits to the coastal strip. The fleas apparently infested the rabbit populations at W4 the most quickly but this population is also restricted by lagoons.

Maximum distance of spread during the first year was 1·7 km from the release points.

The Princes Highway did not restrict spread nor did the Little River. However the Werribee River, about 30 m wide when in full flow and not dry at any time, apparently blocked flea spread for several months. Fleas were probably carried across the river during the summer when the river falls to 3 m wide and 10 m deep opposite the W2–W5 paddocks.

### *Infestation numbers and rate of spread*

From October 1969 on, fleas were found in every collection made within 0·4 km of the release sites although the numbers of fleas remained low and spread from the sites was initially slow. The data on rabbits collected within and beyond 0·4 km of the release sites until June 1971 are shown in Table 2 and the most distant flea collections from release sites in Fig. 1.

The infestation of rabbits collected within 0·4 km of the release sites increased until 75% of those collected during the summer of 1969–70 carried fleas. However the numbers of fleas carried remained low and the percentage of infested rabbits dropped sharply in the April 1970 collection. Both the percentage infested and the numbers of fleas carried rose during the following breeding season. By June 1971 almost all rabbits were infested and the mean number of fleas per rabbit was about 50. There is no evidence that does were more quickly infested than bucks although the does usually carried more fleas than the bucks.

All rabbits collected within 0·4 km of the release sites after June 1971 carried fleas and these rabbits are not shown separately in data from subsequent collections (Table 3).

Data from rabbits collected beyond 0·4 km from the release sites between September 1969 and June 1971 (Table 2 and Fig. 1) show the comparatively slow spread of the fleas and the comparatively low peak numbers with breeding until

Table 2. *Occurrence of* S. cuniculi *at Werribee release sites, and dispersal from the sites, from September* 1969 *until June* 1971, *shown as number of rabbits, including kittens, sub-adults and adults infested, number collected and mean number of fleas per infested rabbit. Unsexed rabbits are not included*

| Collection months | Within 0·4 km of site | | | | Beyond 0·4 km from site | | | |
|---|---|---|---|---|---|---|---|---|
| | Male rabbits | | Female rabbits | | Male rabbits | | Female rabbits | |
| September 1969 | 3/11 | 2·3 | — | — | — | — | — | — |
| October | 6/13 | 1·0 | 6/16 | 2·0* | — | — | 0/2 | — |
| November | 5/15 | 1·9 | 8/14 | 3·0* | — | — | 1/3 | 1·0* |
| December | 14/24 | 2·0 | 2/10 | 1·0*† | — | — | 1/2 | 1·0* |
| January 1970 | 20/23 | 6·0 | 5/5 | 15·4* | — | — | 1/3 | 1·0* |
| February | 9/12 | 3·7 | 6/8 | 6·1* | 2/2 | 1·0 | 0/1 | — |
| April | 7/30 | 4·3 | 8/21 | 4·5* | 0/5 | — | 4/4 | 2·8 |
| June | 23/27 | 11·0 | 7/8 | 19·6* | 4/5 | 2·8 | 2/3 | 3·5* |
| July | 22/25 | 12·0 | 12/13 | 24·0* | 7/51 | 11·0 | 6/13 | 17·2* |
| August | — | — | 1/1 | 10·0 | 9/67 | 8·0 | 8/39 | 8·6* |
| September | — | — | — | — | 9/51 | 6·4 | 5/25 | 31·6* |
| October | 4/4 | 14·3 | 4/4 | 30·5* | 7/54 | 11·0 | 4/24 | 13·5* |
| November | 1/1 | 113·0 | — | — | — | — | 1/1 | 35·0* |
| December | — | — | 2/2 | 18·5* | 0/18 | — | 7/21 | 18·6* |
| February 1971 | 6/6 | 14·7 | 2/5 | 30·5* | 22/44 | 14·8 | 2/10 | 20·4* |
| June | 7/7 | 54·4 | 6/7 | 49·1* | 54/63 | 37·4 | 25/32 | 100·0* |

* Some pregnant does included in the collection.
† Some lactating non-pregnant does included in this collection.

Table 3. *Occurrence of* S. cuniculi *at Werribee from July* 1971 *until August* 1978 *shown as number of rabbits infested/number collected and mean number of fleas per infested rabbit. Collections of* 20 *or more rabbits only are shown*

| Collection months | Male rabbits | | Female rabbits | |
|---|---|---|---|---|
| October 1971 | 9/9 | 12·1 | 16/17* | 57·7 |
| December 1971 | 30/44 | 18·1 | 39/50* | 19·5 |
| May 1972 | 65/76 | 18·9 | 31/40* | 23·0 |
| January 1973 | 4/7 | 11·5 | 12/13* | 23·4 |
| February 1973 | 24/24 | 18·2 | 25/27 | 25·8 |
| March 1973 | 21/23 | 10·2 | 13/15* | 17·9 |
| July 1973 | 11/11 | 34·0 | 14/14* | 35·7 |
| September 1973 | 76/77 | 51·0 | 92/93* | 129·9 |
| January 1974 | 43/43 | 26·9 | 36/37* | 19·6 |
| February 1974 | 66/66 | 11·9 | 65/67* | 15·9 |
| March 1974 | 8/10 | 12·4 | 12/12 | 10·2 |
| May 1974 | 12/12 | 57·7 | 8/8* | 34·1 |
| September 1974 | 61/62 | 36·8 | 77/79* | 80·3 |
| April 1975 | 66/66 | 42·8 | 42/42* | 67·6 |
| October 1975 | 71/71 | 62·0 | 50/50* | 210·9 |
| July 1976 | 63/63 | 29·4 | 39/39* | 60·1 |
| August 1978 | 50/51 | 39·5 | 38/39* | 98·9 |

* Sample includes pregnant does.

https://doi.org/10.1017/S0022172400026085 Published online by Cambridge University Press

the June 1971 collection when about 80 % of the rabbits collected were infested and the does carried high numbers of fleas with a mean of 100 compared with a mean of 37 on bucks.

There is some evidence in these data that initially the does were preferentially infested. In the autumn–winter collections of 1970, 20 out of 59 does were infested compared with 20 out of 128 bucks.

The data collected between July 1971 and August 1978 (Table 3) show that almost all rabbits in the experimental area were infested after the breeding season of 1972 although young rabbits without fleas were collected occasionally until the collections ended in August 1978.

The erratic nature of infestation during the first years of establishment is shown in Table 4. Although the pattern of heaviest infestations during the rabbit breeding season was well established by October 1971 even by September 1973 there were still many rabbits carrying few fleas and the October 1975 collection was the first to show the pattern expected if the host–parasite relationship is stabilizing. It must be emphasized that this apparent stabilization took 5 years to achieve even in a rabbit population living under apparently close to ideal pasture conditions and capable of breeding for most of the year.

The differential infestation of bucks and does during the main breeding season was first apparent during 1971 but the slower increase in numbers on bucks than on does was not clearly evident until October 1975 when 64 % of does carried more than 200 fleas and only 12 % carried less than 50 whereas no bucks carried more than 200 and 50 % carried less than 20.

The 1974 summer collection showed a marked return towards equality in infestation rates between bucks and does after the heavier infestation of does during the preceding breeding season. No major summer collections were made during 1975 and 1976 and we do not know whether the return towards equality was similar as the host–parasite relationship stabilized. However the data for July 1976 and August 1978 when the rabbits were breeding freely suggest that the infestation rates on bucks and does may have been similar before breeding began.

We were not able to make regular monthly collections at Werribee as we did in the Mallee (Shepherd & Edmonds, 1976) and we were not able to follow changes in infestation in detail. We also could not show the temporary increase in flea numbers on bucks which occurred in the Mallee in 1976 when the host–parasite relationship probably stabilized (Shepherd & Edmonds, unpublished data) and which occurs normally in the United Kingdom (Mead-Briggs, Vaughan & Rennison, 1975).

We can however compare the rates of spread and infestation numbers with those found elsewhere. The initial rate of spread among the non-restricted rabbit population was slightly faster than we found in the Mallee, probably because of the extended breeding season and the availability of young rabbits forced out of the social system despite the low pressure for food. The initial rate was however slower than that found by Sobey & Conolly (1971) in western New South Wales where 70 % of rabbits in a 140 ha paddock were infested 4 months after flea release. They also found that all rabbits were infested within 1 year. Williams &

Table 4. *The numbers of fleas carried by male and female rabbits collected at Werribee*

| Collection month | Sex | No. examined | No. of rabbits shown as a percentage of each group: No. of fleas carried 0 | 1–4 | 5–10 | 11–20 | 21–50 | 51–100 | 101–200 | > 200 |
|---|---|---|---|---|---|---|---|---|---|---|
| June 1971 | Male | 70 | 12·9 | 18·6 | 20·0 | 8·6 | 18·6 | 14·3 | 7·1 | — |
| | Female | 39 | 20·5 | 10·3 | 25·6 | 10·3 | 10·3 | 17·9 | 5·1 | — |
| October and November 1971 | M. | 12 | — | 16·7 | 16·7 | 41·7 | 8·3 | 16·7 | — | — |
| | F. | 20 | 5·0 | 5·0 | 10·0 | 5·0 | 40·0 | 20·0 | 10·0 | 5·0 |
| December 1971 | M. | 44 | 31·8 | 13·6 | 18·2 | 25·0 | 9·1 | 2·3 | — | — |
| | F. | 50 | 22·0 | 18·0 | 22·0 | 22·0 | 10·0 | 2·0 | 2·0 | 2·0 |
| May 1972 | M. | 76 | 14·5 | 26·3 | 15·8 | 22·4 | 13·2 | 7·9 | — | — |
| | F. | 40 | 22·5 | 22·5 | 20·0 | 5·0 | 20·0 | 7·5 | 2·5 | — |
| January and February 1973 | M. | 31 | 6·5 | 16·1 | 22·6 | 22·6 | 32·3 | — | — | — |
| | F. | 40 | 7·5 | 15·0 | 12·5 | 22·5 | 30·0 | 2·5 | 10·0 | — |
| March 1973 | M. | 23 | 8·7 | 30·4 | 47·9 | 4·3 | 4·3 | 4·3 | — | — |
| | F. | 15 | 13·3 | 26·7 | 26·7 | 6·7 | 13·3 | 13·3 | — | — |
| July 1973 | M. | 11 | — | — | 18·2 | 9·1 | 45·5 | 27·3 | — | — |
| | F. | 14 | — | 7·1 | 21·4 | 28·6 | 21·4 | — | 21·4 | — |
| September 1973 | M. | 77 | 1·3 | 2·6 | 10·4 | 18·2 | 31·2 | 29·9 | 3·9 | 2·6 |
| | F. | 93 | 1·1 | 2·2 | 5·4 | 7·5 | 25·8 | 19·4 | 18·3 | 19·4 |
| January and February 1974 | M. | 109 | — | 11·9 | 34·9 | 23·9 | 21·1 | 7·3 | 1·0 | — |
| | F. | 104 | 2·9 | 19·2 | 35·6 | 25·0 | 11·5 | 3·8 | 1·9 | — |
| March 1974 | M. | 10 | 20·0 | 20·0 | 20·0 | 30·0 | 10·0 | — | — | — |
| | F. | 12 | — | 8·3 | 41·7 | 50·0 | — | — | — | — |
| May 1974 | M. | 12 | — | — | 25·0 | 16·7 | 25·0 | 25·0 | — | 8·3 |
| | F. | 8 | — | — | — | 37·5 | 25·0 | 25·0 | 12·5 | — |
| September 1974 | M. | 62 | 1·6 | 4·8 | 16·1 | 22·6 | 27·4 | 24·2 | 3·2 | — |
| | F. | 79 | 2·5 | 6·3 | 17·7 | 18·9 | 16·5 | 17·7 | 16·5 | 3·9 |
| April 1975 | M. | 66 | — | 6·1 | 22·7 | 28·8 | 22·7 | 16·7 | — | 3·0 |
| | F. | 42 | — | 16·7 | 23·8 | 9·5 | 19·0 | 2·4 | 11·9 | 16·7 |
| October 1975 | M. | 71 | — | — | 8·5 | 14·1 | 28·2 | 30·2 | 18·3 | — |
| | F. | 50 | — | — | 2·0 | 2·0 | 8·0 | 10·0 | 14·0 | 64·0 |
| July 1976 | M. | 63 | — | — | 20·6 | 33·3 | 31·8 | 12·7 | 1·2 | — |
| | F. | 39 | — | 2·2 | 17·9 | 10·3 | 20·6 | 30·8 | 17·9 | — |
| August 1978 | M. | 51 | 2·0 | 21·6 | 17·6 | 25·5 | 13·7 | 3·9 | 11·8 | 3·9 |
| | F. | 39 | 2·5 | 25·6 | 10·3 | 7·7 | 12·8 | 10·3 | 10·3 | 20·5 |

Parer (1971) working at Urana in southern New South Wales found fleas throughout the rabbit population living in a 223 ha paddock 18 months after release. These findings contrast with our finding that a few rabbits remained uninfested four years after the release.

Williams (1973) recorded peaks of 125 and 175 fleas on adult rabbits living in 0·2 ha enclosures near Corowa, New South Wales 1 year after release. At Werribee it took 4 years to reach a mean of 125 fleas per rabbit and 6 years for an average of 175 or more fleas per rabbit to be found. If rabbits confined in a small enclosure are allowed to breed and no spread is possible then flea numbers can increase rapidly. The flea numbers in 0·2 ha around the Werribee release sites were much lower than those reported by Williams.

Although pregnant, lactating Werribee does generally carried a higher number of fleas than Mallee does at a similar stage of pregnancy, none reached the high numbers (up to 756) reported by Sobey & Conolly (1971). The infestation numbers on the 32 does found carrying more than 200 fleas in October 1975 ranged from 212 to 512, the highest number found on any doe at Werribee. We have found numbers comparable with those reported by Sobey & Conolly on wild rabbits at Frankston only (maximum 769) but the numbers at Werribee are generally similar to the lower numbers found by Allan (1956) on rabbits in Scotland.

The transect counts carried out along the 12 km coastal strip showed that the fleas had no significant effect on the rabbit population during the establishment period.

We are grateful to all staff of the Keith Turnball Research Institute who gave excellent technical assistance especially Mr I. Nolan, Mr I. Lane, Mr A. Gocs, Miss R. Lewis and Mrs Q. Dam. The work could not have been carried out without the complete co-operation of the Melbourne and Metropolitan Board of Works and in particular the unstinting help of Mr D. Williams.

The work was supported by the Wool Research Trust Fund.

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