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Myxomatosis on the Western Plains of Victoria

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SUMMARY

Myxomatosis on the Western Plains is an enzootic disease in contrast with the epizootic pattern which is general in eastern Australia. The most unusual aspects are the presence of significant numbers of diseased rabbits throughout the winter and the continuously low percentage of rabbits with antibodies to myxoma virus.

Climatic and topographic conditions are unsuited to the production of the high densities of mosquitoes necessary for widespread epizootics. Under these conditions the effects of less efficient methods of myxomatosis transmission are apparent. The unusual epidemiology of myxomatosis has resulted in selection for virulence of the virus similar to that which has occurred under summer epizootic conditions. All field strains are now in the mid range of virulence.

INTRODUCTION

The time of occurrence of epizootics of myxomatosis in Australia has been largely controlled by the presence in sufficient numbers of mosquito vectors (Fenner & Ratcliffe, 1965). In Victoria generally these vectors are most abundant during the summer or early autumn and epizootics occur during this period. However, winter outbreaks of myxomatosis were reported from the Western Plains (Fig. 1), soon after the myxoma virus was released in the area in 1951. Most reports from farmers indicated that the disease appeared to move gradually but steadily through the rabbit population and that some infected rabbits could be found throughout the year.

Answers to a questionnaire sent to farmers in late 1958 suggested that the disease had continued since 1951 at a low level of activity with no spectacular outbreaks. Most replies stressed that the disease seemed to be more effective in the winter although, in some years, there seemed to be increased summer activity. Investigations were begun in 1958 in an attempt to find an effective winter vector. The attempt was unsuccessful but the epidemiology of myxomatosis in the area was clarified.

Interest in the Western Plains was re-stimulated by the introduction into Australia of the European rabbit flea (*Spilopsyllus cuniculi* (Dale)) as a myxoma vector (Sobey & Menzies, 1969; Sobey & Conolly, 1971) and the investigations were resumed in 1967.

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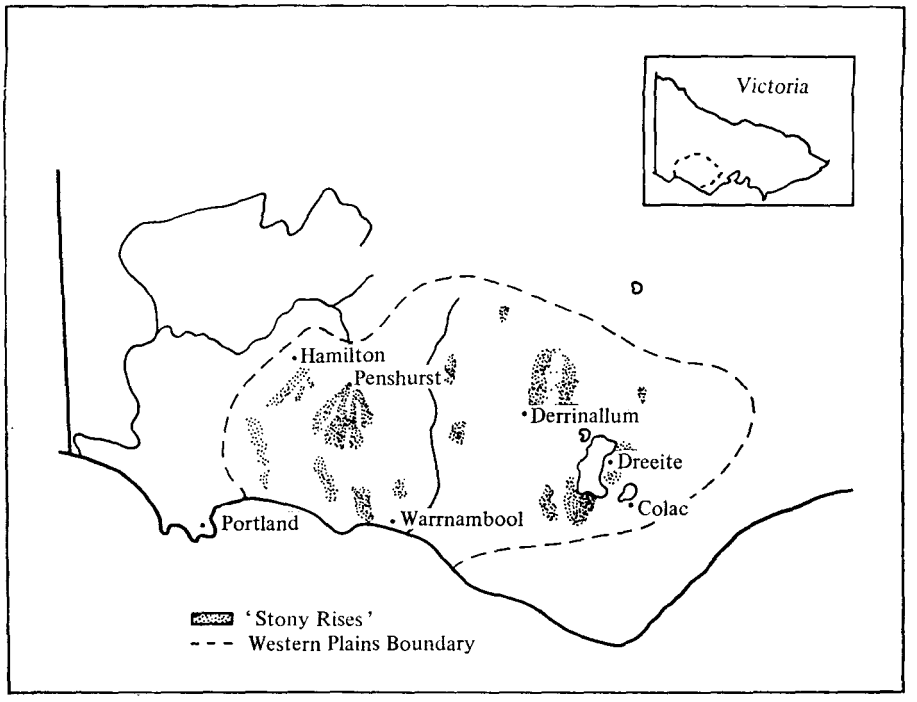

Fig. 1. The Western Plains of Victoria.

MATERIALS AND METHODS

Study areas (Fig. 1)

The Western Plains are generally flat, open, and highly developed agriculturally except for basalt flows, the 'stony rises' which have supported very large rabbit populations. The surface of the stony rise country is very irregular. Basalt barriers 3–20 m high may be crowded together or widely spaced with flats between them. The tops of the barriers are usually flat, although there may be sunken areas of variable depth.

The stony rises were originally covered by basalt boulders ranging in size up to 2 m in diameter. Farmers have cleared the boulders from many of the flats leaving mounds of large boulders and have used the smaller boulders in hollow stone fences. These fences provide harbour for the rabbits. Further harbour is provided by patches of vegetation, especially bracken (*Pteridium esculentum* (Forst. f.) Nakai), shore thistle (*Carduus tenuiflorus* Curt.) and spotted thistle (*Silybum marianum* (L.) J. Gaertn.).

The climate has the typical Mediterranean pattern of southern Victoria with hot dry summers and wet winters. The mean annual rainfall ranges from about 600 to 650 mm.

The areas chosen originally for study were the Penshurst district south of the extinct volcano, Mt Rouse, where about 100 square miles abutting Mt Rouse were examined and the Dreeite district east of Lake Corangamite, about 100 square

miles dominated by the Warrion group of extinct volcanoes. Studies were extended in 1967 to an area north of Derrinallum.

Disease activity

Field staff of the Department of Crown Lands and Survey have made regular observations of the occurrence and severity of myxomatosis as part of their routine duties. From 1958 until 1960 and from 1967 until 1970 these observations were supplemented by research staff of the Department.

Observations were made from a slow-moving vehicle and by walks where the terrain was too rough for vehicles.

Serum samples

Rabbits were captured by trapping, digging out or spot-lighting, and blood samples were taken. The sera were tested for the presence of antibodies to the soluble antigens of myxoma by gel diffusion techniques (Mansi, 1957; Sobey, Conolly & Adams, 1966).

Field strains of virus

Throughout the study period, samples of infected tissue were taken from diseased rabbits. The method used to determine virulence was that described by Marshall & Fenner (1960). The grading system is that used by Fenner & Marshall and described in detail by Fenner & Ratcliffe (1965).

Vectors

During 1958–60 and 1969–70 mosquitoes (Culicidae), black flies (Simulidae) and ectoparasites of the rabbit were collected on visits made at 4–7 week intervals. Observations were also made of other possible methods of transmission.

Culicidae and Simulidae

Larval and pupal stages. On each visit an assessment of all water areas was made so that potential breeding areas for mosquitoes could be located. All types of water were tested using a regular scooping procedure.

Adults. Attempts to detect adults were made during the regular water sampling visits. Various techniques were used, including warren exit traps and cone traps (Myers, 1956), human bait, sweeping of vegetation, examination of potential resting areas and blowing exhaust gases through rabbit warrens.

Ectoparasites

Freshly killed rabbits were examined for ectoparasites on all visits to the Penshurst area during the first year of observations. All parts of the carcase were examined.

Live rabbits were examined in the field during the spring of 1969 and 1970.

Table 1. *Myxomatosis occurrence on the Western Plains; severity and time of peak activity*

Year	District: Penshurst	Colac (including Dreeite)	Derrinallum
1960	Mild, summer	Severe, summer–autumn	Mild, summer
1961	Mild, winter	Moderate, summer	Mild, spring
1962	Moderate, summer	Moderate, summer* Mild, winter	Mild, autumn*–winter
1963	Moderate, summer* Low, winter	Moderate, summer* Mild, winter	Moderate, summer* Mild, winter
1964	Severe, spring–summer	Moderate, autumn* Low, spring	Moderate, autumn
1965	Moderate, spring	Mild, autumn–winter	Mild, summer
1966	Moderate, winter	Mild, summer* Mild, winter	Moderate*, autumn–winter
1967	Severe, winter	Moderate, winter	Moderate, spring
1968	Severe, winter	Low, no peak	Mild, autumn
1969	Severe, winter	Mild, autumn	Mild, autumn* Mild, spring
1970	Moderate, autumn	Mild, spring	Mild, autumn
1971	Severe, autumn–winter	Severe, summer–autumn	Low, no peak

* Two peaks of activity recorded.

Table 2. *The seasonal occurrence of peaks of myxomatosis activity on the Western Plains of Victoria*, 1960–71

Season	Number of peaks recorded*: Penshurst	Colac	Derrinallum
Summer	3 ½	4 ½ ½	3
Autumn	1 ½	1 ½ ½	4 ½ ½
Winter	6 ½	4 ½	1 ½ ½
Spring	1 ½	2	3

* Peaks which occurred from one season into the next are shown as ½ in each season.

RESULTS

Disease activity 1960–71

Observations made by field and research staff are summarized in Table 1. This table gives a subjective estimate of the severity of the disease in each year and the time at which most disease activity was apparent. The grading used in the table is: severe = considerable reduction in rabbit numbers over a short period, many diseased rabbits or carcases seen; moderate = reduction in rabbit numbers over a 2–3 month period with a definite but not sharp peak in disease activity; mild = no great reduction in rabbit numbers but an increase in disease activity above the usual low level.

There is no simple correlation between the times of annual peaks of disease activity in the three districts. When the data are considered on a seasonal basis

Table 3. *Occurrence of antibodies to the soluble antigens of myxoma virus*

Date	No. tested	With antibody (%)	District
May 1958	50	8	Penshurst
Nov. 1958	13	45	Penshurst
Feb. 1959	36	14	Penshurst
April 1959	66	8	Penshurst
July 1959	47	23	Penshurst
Dec. 1959	37	17	Penshurst
May 1958	50	6	Dreeite
Nov. 1959	45	11	Dreeite
July 1967	17	29	Derrinallum
July 1967	45	16	Colac
Oct. 1968	34	24	Derrinallum
April 1969	26	31	Derrinallum
May 1969	45	20	Derrinallum
Aug. 1969	40	22	Derrinallum

(Table 2) there is evidence of considerable differences in occurrence patterns between the districts.

All districts had peaks of activity in all seasons but most peaks at Penshurst and Dreeite occurred in winter or summer with few peaks in autumn or spring whereas peak activity at Derrinallum seldom occurred in the winter. Peaks at Derrinallum were most common during the autumn.

Two peaks of activity in one year have been recorded four times in 11 years at Colac and Derrinallum, once at Penshurst.

Peak activity at Penshurst has been most severe with five peaks graded as 'severe' in 11 years. Two peaks were graded as 'severe' at Colac, none at Derrinallum although small pockets of intense disease activity have been recorded in the Derrinallum district.

Antibodies to the soluble antigens of myxoma virus

The results of tests of the occurrence of rabbits with antibodies are shown in Table 3. The data from Penshurst show the generally very low percentage of antibody positive rabbits except in the very small collection in November 1958. The increase from April to July 1959 (8–23 %) followed an early winter outbreak of myxomatosis. The data from Dreeite show similar very low percentages. The percentages were higher at Derrinallum but the highest recorded, 31 % in April 1969, contrasts with 91 % recorded at the same time in the summer epizootic area of north-western Victoria (Edmonds, Shepherd & Nolan, unpublished data).

The Derrinallum data show a remarkable consistency in percentages which do not vary significantly with disease activity or breeding season.

Field strains of myxoma virus

The grading of field strains collected on the Western Plains is shown in Table 4. All field strains collected since 1960 have been in the moderate range of virulence.

Table 4. *Field strains of myxoma virus collected from the Western Plains*

Year	Grade I	II	III	IV	V
1956	—	—	4	—	—
1957	—	—	3	2	3
1958	—	1	8	1	—
1959	—	3	7	—	—
1960–67	—	—	14	5	—
1968–74	—	—	14	2	—

Table 5. *Adult mosquito activity at Dreeite*

Date	Temperature at dusk (°F)	Biting man*		Biting rabbit*	
		Anopheles annulipes	Other species	*Anopheles annulipes*	Other species
5 Aug. 1958	52	0	0	0	0
13 Oct. 1958	56	0	2	0	2
26 Nov. 1958	56	0	0	0	0
27 Nov. 1958	74	6	0	4	0
5 Jan. 1959	73	14	0	6	0
6 Jan. 1959	53	3	0	0	0
23 Feb. 1959	57	3	0	1	0
5 Jan. 1960	61	9	0	1	0
5 Jan. 1960 (9 p.m.)	56	3	0	0	0
6 Jan. 1960	76	16	0	2	0
7 Jan. 1960	85	16	0	2	0

* Period of observation approximately 1½ h.

They are similar in virulence to the field strains collected from southern Victoria generally (Edmonds, Nolan, Shepherd & Gocs, 1975).

Vectors

Culicidae Culex pipiens australicus (Dobrotworsky and Drummond) larval and pupal stages were found during spring, summer and autumn, generally in very low numbers (1 per 2–5 scoops) in permanent swamps but peaking to 20–30 per 5 in scoop in roadside pools and shallow swamps after heavy spring or autumn rain.

Anopheles annulipes (Walk.) larvae and pupae were found in very low numbers in permanent swamps. They reached peak numbers at about the same time as *C. pipiens australicus* but the peak was generally less than one per 5 in scoop.

Aedes alboannulatus (Macquart) and *Aedes nigrithorax* (Macquart) were found in small numbers in roadside pools but did not approach the numbers reported in other areas of Victoria by Douglas (1958).

Aedes notoscriptus (Skuse) larvae were found once in a disused tank.

No larvae or pupae were found during the severe drought of 1967–68. Breeding stopped completely as described in the Wimmera (Edmonds & Gocs, 1970).

Adult activity was always low compared with other regions of Victoria. Table 5

shows adults caught biting man and rabbit at Dreeite. The numbers caught in January 1960 (16 in a 1½ h period) were the highest recorded during any visit to the Western Plains. The highest number caught at Penshurst was six biting man in November 1958.

Numbers caught in warren exit traps were never high. The highest numbers recorded were twelve *A. annulipes* (at Dreeite in January 1959) and two *C. pipiens australicus* (at Penshurst in February 1959 and at Dreeite in January 1960). This compares with collections of up to 300 of each species under similar conditions in northern Victoria (A. Gocs, unpublished).

Species recorded at any time biting man were: *Anopheles annulipes*, *Aedes alboannalatus*, *A. notoscriptus*, *A. camptorhynchus* (Thomson) (a single specimen at Derrinallum in April 1969).

Species recorded biting rabbit were: *Anopheles annulipes*, *Aedes alboannalatus*.

Simulidae

Austrosimulium furiosum (Skuse) and *Simulium ornatipes* Sk. larvae were collected in the Penshurst area in late winter and spring. Pupae of both species were found throughout the spring.

Occasional adult specimens of *A. furiosum* were recorded biting man during the summers. A. Neboiss (personal communication) found a few adults of *A. furiosum* and *S. ornatipes* in the Penshurst study area in July and August 1953. He also found the same two species at Branxholme, 40 miles west of Penshurst, at the same time. However, this winter activity of the flies was not detected in this study.

No running water occurs in the Dreeite and Derrinallum study areas and simulids were not found.

Ectoparasites

The three common ectoparasites of the wild rabbit in Australia, the louse *Haemodipsus ventricosus* (Denny) and the mites *Leporacarus gibbus* (Pagenstecher) and *Cheyletiella parasitivorax* (Megnin) were found at all sites. *H. ventricosus* and *L. gibbus* occurred in similar numbers to those recorded from the Werribee district of Victoria (Shepherd & Edmonds, 1973). However *C. parasitivorax*, although present on almost all rabbits, was found in lower numbers than at Werribee.

DISCUSSION

The recurring myxomatosis epizootics of south-eastern Australia require a successful rabbit breeding season to provide a sufficient population of susceptible rabbits, and a rapid and heavy build-up in numbers of one or more of the three important mosquito vectors, *Anopheles annulipes*, *C. pipiens australicus* and *Culex annulirostris*.

On the Western Plains rabbit breeding goes on at a low level during the winter with a peak during almost every spring, occasional late autumn peaks in favourable years, and little or no breeding during late summer–early autumn. This is not greatly different from the breeding patterns in other parts of Victoria although the

main breeding season on the Western Plains is more prolonged and may extend from late winter to mid summer.

Agents generally accepted as low level vectors of myxomatosis are present on the Western Plains in similar numbers to other areas in southern Victoria where they do not play any major part in myxomatosis occurrence (Shepherd & Edmonds, 1973).

The two outstanding differences between the Western Plains and the neighbouring epizootic areas are the very small numbers of mosquito vectors and the continuously high percentage of susceptible rabbits.

It seems clear that low mosquito counts are due to the open windswept nature of the plains rather than any limitation of breeding sites which are as numerous as in other Victorian districts.

The small number of mosquito vectors means that no epizootic occurs, that the percentage of susceptible rabbits is always high and therefore that inefficient vectors can maintain an enzootic in the susceptible rabbit population. When a very favourable season results in heavy rabbit breeding the resultant crowding of rabbits into limited warren space results in severe outbreaks which may be confined to single warren systems or to single stony rise barriers or occasionally may be widespread.

The differences in severity of activity between Penshurst and Derrinallum are probably due in part to more extensive rabbit populations at Penshurst. The Derrinallum populations are largely restricted to small, isolated stony rises with limited opportunity for rabbit or vector contact between populations. The extensive Penshurst and Dreeite populations have been difficult to control by routine methods. They tend to reach higher numbers than the Derrinallum populations.

The occurrence of high numbers of susceptible rabbits with easy vector interchange at Penshurst allows severe outbreaks of myxomatosis to occur fairly frequently. Severe outbreaks can occur only very rarely and in restricted systems at Derrinallum.

Dreeite populations probably occupy a situation intermediate between the Penshurst and Derrinallum populations.

The differences in time of peak activity between the districts probably reflect the same population effects. The numbers of susceptible rabbits are high enough to allow a moderate to severe outbreak at Penshurst once each year, the time depending on breeding conditions and control measures imposed by man. This outbreak causes severe mortality but the absence of mosquito vectors results in a high percentage of the survivors being uninfected. Low level disease activity can thus continue in the surviving population.

At Derrinallum the absence of any widespread severe outbreaks results in a susceptible population in which local outbreaks can occur whenever rabbit numbers in warren or stony rise systems become high enough. The increase may be due to breeding, to crowding as rabbits move in from denuded pastures or possibly to migration.

Edmonds *et al.* (1975) have reported on selection for moderate virulence of field strains of myxoma virus in Victoria. The grades of virulence of field strains col-

lected from the Western Plains are similar to those from southern Victoria generally. There is no evidence that the differences in epidemiology between the Western Plains and neighbouring regions have imposed any different selection pressure.

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REFERENCES

Douglas, G. W. (1958). Myxomatosis in Victoria. *Journal of the Department of Agriculture, Victoria* **56**, 779.

Edmonds, J. W. & Gocs, A. (1970). The occurrence of certain mosquito species under severe drought conditions in the southern Wimmera of Victoria. *Journal of the Australian Entomological Society* **9**, 71.

Edmonds, J. W., Nolan, I. F., Shepherd, Rosamond C. H. & Gocs, A. (1975). Myxomatosis: the virulence of field strains of myxoma virus in a population of wild rabbits (*Oryctolagus cuniculus* (L.)) with high resistance to myxoma. *Journal of Hygiene* **74**, 417.

Fenner, F. & Ratcliffe, F. N. (1965). *Myxomatosis*. Cambridge University Press.

Mansi, W. (1957). The study of some viruses by the plate gel diffusion precipitin test. *Journal of Comparative Pathology* **67**, 297.

Marshall, I. D. & Fenner, F. (1960). Studies in the epidemiology of infectious myxomatosis of rabbits. *Journal of Hygiene* **58**, 485.

Myers, K. (1956). Methods of sampling winged insects feeding on the rabbit *Oryctolagus cuniculus* (L.). *C.S.I.R.O. Wildlife Research* **1**, 45.

Shepherd, Rosamond C. H. & Edmonds, J. W. (1973). Observations of ectoparasites of the wild rabbit *Oryctolagus cuniculus* (L.) in the Werribee district of Victoria. *Journal of the Australian Entomological Society*, **12**, 195.

Sobey, W. R. & Conolly, D. (1971). Myxomatosis: the introduction of the European rabbit flea *Spilopsyllus cuniculi* (Dale) into wild rabbit populations in Australia. *Journal of Hygiene* **69**, 331.

Sobey, W. R., Conolly, D. & Adams, K. M. (1966). Myxomatosis: a simple method of sampling blood and testing for circulating soluble antigens or antibodies to them. *Australian Journal of Science* **28**, 354.

Sobey, W. R. & Menzies, W. (1969). Myxomatosis. The introduction of the European rabbit flea, *Spilopsyllus cuniculi* (Dale) into Australia. *Australian Journal of Science* **31**, 404.