

## THE ECOLOGICAL CONSEQUENCES OF MYXOMATOSIS IN AUSTRALIA

by F.N. RATCLIFFE

*Officer-in-Charge,  
Wildlife Survey Section,  
Commonwealth Scientific and Industrial  
Research Organisation.  
Canberra, N.S.W., Australia.*

### *Introduction*

The sudden wholesale eclipse of a key herbivore, like the rabbit, in a country's fauna is bound to have far-reaching ecological consequences, which could well be very complex. In Australia, however, the ecological results of myxomatosis appear to be relatively simple in character — though it is possible that we have been misled in our assessment simply because our observations and data are inadequate.

By far the greater part of the rabbit-infested regions of Australia consists of land that is utilised for grazing (of sheep mainly, but with cattle important in some areas) and, moreover, that has been grazed since the early days of settlement. Much of it looks hospitable, and as if it should be a good habitat for native animals — a partly cleared savannah woodland, or grass plains, with scattered patches of forest or scrub. Actually — thinking of the original mammal fauna — the pastoral country has been more grossly impoverished than any other type of land in Australia. This I think has been due mainly to the erratic climate of all but the coastal fringes of the continent, combined with the artificial provision of stock water from wells and bores. Very few areas under pastoral settlement will not have experienced a dozen major droughts during the past century or less, in which the stock have been kept on the land until they have started to die of starvation. The varied and originally abundant herbivorous marsu-

pials could not stand up to this type of competition, and they have virtually disappeared — a striking contrast to the situation in the forested coastal ranges or the central deserts.

There are only two types of native mammal that have maintained a satisfactory status in the pastoral belt — that largest and most mobile of the Macropodidae, exemplified by the red or plains kangaroo, and arboreal forms such as the possums and gliders. The big kangaroos, though they have disappeared from much of their original range, are still numerous in the inland grazing country, at times and in places reaching pest proportions. They tend to appear in numbers on the sheep and cattle stations in good seasons, and to disappear in bad ones; and despite the claims and complaints of graziers probably do not rank as serious competitors of domestic stock. The arboreal marsupials are not grazers, and need not be considered in our equation. With the small and medium-sized Macropodids reduced to vanishing point and, in general, a complete absence of an abundant small rodent fauna (such as is so important in the northern hemisphere), I think it can be claimed that the ecological framework in which the effects of the abundance and reduction of the rabbit have to be assessed is in truth relatively simple, as ecological situations go. The rabbit has, in Australia to-day, only one important direct competitor — man's domestic stock — and the main effect of any gross change in its status will take the form of qualitative and quantitative changes in the pasture vegetation and resultant changes in the well-being and abundance of sheep and cattle.

The predator position in the pastoral country — insofar as it affects the rabbit with any reasonable degree of directness — seems also to be relatively simple. The native *Dasyures* have suffered the same general reduction in numbers, if perhaps less complete, as the small and medium-sized wallabies of the plains and open country, and are rare or local to-day. The dingo has been virtually eradicated from all but the sparsely settled parts of the rabbit-infested country. Thus to all intents and purposes we need only consider the introduced fox, birds of prey, and perhaps feral cats. (Australia did not make the same mistake as her sister Dominion, New Zealand. No *Mustelids* — other than the ferret, which has not succeeded in establishing itself in a feral state — have been introduced to this country).

What little information we have on the fox and the

wedge-tailed eagle (*Aquila audax*) will be mentioned below. We have no information on feral cats, beyond the revelation from our field work that they are surprisingly abundant. Although it appears that they have spread and can maintain themselves far from white settlement (*vide* Finlayson, « The Red Centre »), we suspect that the general population level is maintained by frequent augmentations from farmhouses, station homesteads etc., so it should be rapidly adjustable to changes in the rabbit position — assuming, as seems reasonable, that the easily obtained food supply provided by young rabbits is the mainstay of cats' breeding in the feral state.

There are several species of hawks that are casual predators of rabbits, particularly the young, and one species, the little eagle (*Hieraetus morphnoides*), which seems to be essentially a hunter — i.e. does not turn to carrion as an alternative source of food, as do so many of the larger Australian Raptores, including the wedge-tailed eagle — and to have developed a dependence on the rabbit almost comparable with that of the buzzard in Britain. The little eagle must undoubtedly have been affected in its habits and abundance by the eclipse of the rabbit population; but unfortunately we have made no « post-myxomatosis » observations on this rather uncommon bird.

#### *Effect of rabbit reduction on pastures and stock*

Myxomatosis « escaped » from one of our test sites in the Murray Valley in 1950; and in the first (1950-51) season produced « ribbon » kills along the waterways of much of central New South Wales, and what amounted to a regional crash of the rabbit population over an extensive area of northern N.S.W and southern Queensland. Every year since then the disease has increased its geographical spread in eastern Australia; though only slightly during the past two seasons, for the simple reason that the spectacular spread of 1952-53 left very few rabbit-infested areas unaffected. Since then also, allowing for certain local irregularities, epidemic outbreaks have dealt effectively with the susceptible population that has bred up from the survivors of the previous outbreak. Thus for several years now the benefits of myxomatosis have been regularly consolidated and even, in the main, augmented.

An important factor in the present satisfactory

situation has been the favourable run of seasons that eastern Australia, at any rate, has enjoyed since about 1947. There have been minor local droughts — sequences of a few dry months in this or that area — but by and large the rainfall has been such that one might be tempted to think that the climate was moving into the humid period of some long-term cycle. This has of course affected the stock-carrying capacity of the pastoral country and the regeneration of vegetation that has suffered overgrazing for a short or long period. It is probably difficult for workers in European countries, with their more reliable rainfall and less extreme summer climate, to appreciate just what the « luck of the season » means to Australian sheep and cattle men, and how frequently anxiety for the welfare and nutrition of their stock is in their minds. Up to a point, good seasons and high rabbit numbers tend to go together; and where rabbit increase is ineffectively controlled, serious infestations may outweigh the effect of a favourable season, and graziers will start talking of a « rabbit drought ». These points are mentioned merely to explain why it has not been easy to differentiate satisfactorily between the effects of good seasons and of rabbit scarcity on the vegetation and productivity of the Australian pastoral country in recent years.

Immediately prior to the liberation of myxomatosis, a combination of circumstances had led to a build-up of rabbit numbers to very high levels over much or most of their range; and the situation in many areas could only be described as desperate. This gave an almost exaggerated emphasis to the change that was manifest over the next few years, often with startling suddenness where individual properties and districts were concerned. The change, because good seasons have enabled the vegetation to take full advantage of the relief from the pressure of rabbit grazing, has been almost miraculous: the landscape in some areas has been virtually transfigured. Hills that had been grazed to the soil for decades, and whose slopes had appeared grey and red on the horizon, are now clothed in grass. The broad margins of country roads, lying outside the boundary fences of grazing properties, tended to carry dense rabbit populations and as often as not showed it in the poverty of their ground cover. It is now usual to see tall grass and herbage to the road's edge. Looking over the fences, it is now very rare to see a paddock without a dense and healthy pasture.

The area that has been affected by myxomatosis is

so huge, and the conditions within it so varied, that it would be futile to try and assess the changes that have occurred in anything but general terms. On some holdings there has been no change, other than that attributable to the favourable seasons; for they had been maintained rabbit-free for long periods, inside the protection of netted boundaries. It is from the study of such properties that we base our conclusion that the difference between freedom from rabbits and a tolerated light-to-medium infestation may represent a doubling of stock-carrying capacity and an ability to negotiate minor droughts without loss of condition in the stock or the expense of hand-feeding. Myxomatosis has naturally benefited the poor manager more than the good one — the man who, over the years, has gone to the trouble and expense of keeping his rabbits under control — and it is on properties and in districts where rabbits had got the upper hand (and there were many such in 1949) that the greatest changes are to be seen.

Only one serious attempt has been made to assess the increased productivity of grazing land, resulting from myxomatosis, in quantitative terms — in fact, in terms of hard cash. Using the statistics of wool and fat lamb production, and making all possible allowances for the effect of favourable seasons and other contributing factors, the Bureau of Agricultural Economics estimated that « during 1952-53 in the sheep industry alone... myxomatosis resulted in increased production to the value of more than £ 30 million ».

The increase in production exemplified by these figures is a direct reflexion of the improved growth and quality of pasture vegetation following the lightening of rabbit grazing pressure. The improvement has been relatively straightforward and uncomplicated — a simple recovery from the impoverishment that had taken place in varying degrees according to local conditions. The recovery has been towards the state and balance of reasonably stocked and well-managed pastures in the particular region. There must often, of course, have been qualitative changes in the pasture vegetation, for rabbit grazing is selective; but no special observations or experiments have been undertaken to determine the nature of any changes in species composition and balance. In view of the variety and complexity of the plant associations that provide Australia's « native » pastures, such studies did not seem to be profitable or practicable; and in the case of the ecologically much simpler « improved » pastures, one can accept it as axiomatic

that anything but a very light rabbit infestation is incompatible with their satisfactory establishment and maintenance. The point of key importance, I think, is that in Australia we can produce no example of a « rabbit disclimax » that has any value or virtue — nothing, say, in any way comparable with chalk downlands of Britain.

Turning for a moment from grassland and pastures, the rabbit's habit of barking shrubs and small trees in times of drought, and defoliating and killing seedlings, has had a serious effect on the regeneration of certain components of the vegetation, especially on the light soils in the lower rainfall areas. Thus the natural regeneration of the mulga (*Acacia aneura*) seemed to have been completely suppressed in South Australia; and some years ago the Professor of Botany in Adelaide felt safe to offer a reward of £5 to anyone who could show him a mulga seedling growing naturally. *Callitris robusta*, one of the native or cypress pines which has high value as a timber tree, has suffered a somewhat similar fate in New South Wales; and the Forestry Department has found it necessary to net out and control rabbits in its pine reserves to insure natural regeneration. One of the results of the decimation of rabbits by myxomatosis has been a widespread and satisfactory regeneration of *Callitris*.

#### *Effect on predators, including man*

There are two important rabbit predators in Australia the behaviour and status of which one would naturally expect to have been affected by the success of myxomatosis — the wedge-tailed eagle and the introduced European fox. Just as we have no deliberately collected data to provide precise information on the re-establishment of overgrazed components of the pasture vegetation, we have had to depend on casual reports and unplanned observations for evidence of any noticeable changes in the feeding habits of the fox and eagle in recent years. Unfortunately, much of this evidence has to be taken with a grain of salt, as we have good reason to believe that many graziers tend to blame foxes and eagles for the killing of lambs that actually died, or would have died, as a result of bad management and unthriftiness. However, there does not seem to be much doubt that attacks on lambs by foxes and eagles have increased following the wholesale reduction in rabbit

numbers, although the extent of this increase, and the closeness of its correlation with myxomatosis activity in any region, cannot be satisfactorily estimated.

Objective data on eagle predation is rather scrappy. The most reliable reports of an increase in lamb killing which seemed correlated with the reduction in rabbits have come from inland New South Wales. In the State of Queensland the wedge-tailed eagle has a price on its head, and the bonus records for the years 1949-50 to 1952-53 inclusive are, in round figures, 9,000, 5,000, 10,000 and 12,000 respectively. The increase in the number of scalps paid for in the season of the first and greatest myxomatosis kill might be significant; though unless one could be assured that the main increase during 1951-52 came from the rabbit infested parts of the State one must remain sceptical.

The wedge-tailed eagle is protected in Tasmania, and the constant propaganda in its favour by ornithologists and conservationists generally has perhaps mitigated the war carried on against it by graziers, at any rate in the more populous mainland States. It must be classed, however, as a persecuted bird; and it occurs in numbers only in the more sparsely settled areas and in the neighbourhood of uncleared ranges. A food habit study on this species is long overdue; and although it would not be an easy one to carry out, we hope to be able to make a start on it before long. Examinations of the prey remains around nests — of which there have been many — leave no doubt that the eagle depends heavily on rabbits when feeding its young. It is a notorious trap robber; but I have met no-one who has seen an eagle hunt and kill a rabbit. On the other hand, I have watched rabbits feeding and behaving with complete unconcern while eagles circled low above them; and they continued to do so even when one of the birds landed among them and started to feed on a poisoned carcass.

The evidence on foxes is more substantial; and the Queensland scalp bounty statistics are of particular interest in this connection. The bounty payment — 5/- per head — is not sufficiently high to stimulate fox hunting as an economic proposition, and therefore any substantial local increase in the numbers of scalps paid for almost certainly reflects an increase in fox nuisance value. During the four years mentioned above (1949-50 through 1952-53) bounties were paid on the following numbers of scalps : 14,319, 14,342, 35,717 and 16,469. The sudden big increase took place in the year of, and

immediately following, the rabbit crash, and it was due almost entirely to an increase in pay-outs in the southern (i.e. rabbit infested) portion of the State. The report of the Authority responsible for vermin control in Queensland, for the year in question, includes this statement :

« Since the considerable reduction in the rabbit population in the years 1951 and 1952 by the disease myxomatosis, severe losses of sheep have occurred from attacks by foxes, and an « all out » drive is being made by landholders to reduce fox numbers. A comparison between the 5,170 foxes destroyed in one southern shire during 1951-52 and the annual average of 383 for the Shire gives some indication of the activity being displayed by landholders to destroy the fox. »

Fox predation on sheep and lambs, like eagle predation, is an old story in Australia, erratic and usually subjectively reported. It is thus not easy to draw a baseline for comparison. Over much of south-eastern Australia the main myxomatosis kill took place in the 1952-53 season, and one would have expected a major switch on fox feeding habits to have been manifest in that year. I recollect that my impression at the time was that the reports of fox attacks on lambs were fewer than might have been expected; but this impression may have been quite erroneous, for my colleagues and I were heavily engaged with other aspects of myxomatosis just then, and did not go out to collect and analyse these reports. One member of the Wildlife Section was able to record that in the East Gippsland district of southern Victoria there was a marked increase in fox trouble immediately after the first effective myxomatosis epidemic, which took place that year. All in all, it is probably safe to assume that what happened here also happened elsewhere, in greater or lesser degree.

The European fox has found conditions in Australia very much to its liking, and it is now an extremely abundant and widely distributed animal. Its range on the continent is more extensive than that of the rabbit. There is no doubt that it preys substantially on rabbits (though it seems to have considerable difficulty in catching the adults). Nor, I think, can there be much doubt that it must depend very largely on rabbits for the feeding and rearing of its own young. If this dependence indeed exists, and is strong, one would have expected that the great reduction in rabbit density that took place between 1950 and 1953 (and amounted to virtual extermination in some areas) would have been reflected in a noticeable decrease in the general level of the fox



population during the last two of three years. As far as we have been able to ascertain, however, nothing like this has happened — fox numbers, if anything, have been abnormally high.

A complicating factor in the situation has been the prevalence of sarcoptic mange in the fox population during the past decade or more. It has been very severe in its manifestations, and reports indicate that it has had a marked effect on fox population levels — for instance, an 80 per cent reduction has been estimated for certain areas. It is only during the last few years that the incidence of the infection has noticeably and generally declined, with badly affected animals being the exception rather than the rule; and it is possible that the recovery of the fox population in health and numbers may have masked the tendency, which might otherwise have been manifest, for the density of this predator to have adjusted itself to that of its rabbit prey.

As is probably the case elsewhere, the most important predator on rabbit in Australia is man, represented by certain sections of the rural community. Consideration of the effects of myxomatosis on the human predator leads one inevitably into the realms of sociology, but the picture would not be complete if this aspect of the situation were ignored. Human predators on the rabbit fall into two main categories, the landholders (farmers and graziers) on the one hand, and rural employees and « free lance » workers on the other. In their attitude to the rabbit these two groups stand in striking contrast. In the early years of the Wildlife Section, when my colleagues and I were travelling widely and gathering information that would help us understand and assess the rabbit problem, we were impressed by the fact that the rabbit was a potential divider of classes, the employers being « anti » while the employees were substantially « pro », often to the extent of being classifiable as rabbit conservationists. The reluctance of what was probably the majority of country dwellers to treat the rabbit as a pest which had to be destroyed seemed likely to be a key factor militating against successful control on a national scale; but then myxomatosis spread, with no regard for human opinions and desires.

The effect on the landholders as a group has been straightforward. The time and energy they had to spend on destroying rabbits was grudgingly given, and though vital for their well-being was, one might say, wasted. When they were very largely relieved by the

myxoma virus of the necessity of controlling the destroyers of their pastures and crops their energies were diverted, in the main, to more directly productive work on their holdings. The effect of the success of myxomatosis on the second category of human rabbit predators — man who kill rabbits for a living, either full or part time — has however been more complex.

Rural employees with memories of the great depression of the early thirties (when they turned to rabbiting to provide food for their families and something to replace lost wages) and who liked to see rabbits about because their exploitability provided an insurance against their being tied by adversity to an uncongenial employer, have only been affected by myxomatosis psychologically, so to speak. If they happen to have shared in the increased rural prosperity and security that has followed the eclipse of the rabbit, their attitude to the animal may well have changed from pro to anti. There remain the very large number of men in the country who were directly concerned, to a greater or lesser extent, with the rabbit skin and carcass industry. It is here, of course, that the strongest feelings and the greatest upset are to be found; for myxomatosis, where it has not virtually destroyed the industry, has changed it from a relatively secure livelihood with a readily available source of supply to one hedged with difficulty and insecurity.

The rabbit industry, however good and valuable the use to which its products are put, is essentially a parasitic industry that has thrived on the misfortune and at the expense of the primary producer. Whatever its apologists may claim, its contribution towards the control of the rabbit as a pest has been negligible. In fact, it has been much worse than negligible; for once the industry had become organised on a large scale it inevitably developed a widespread vested interest in the survival of the rabbit — and not merely its survival, but its survival in sufficient numbers to make its harvesting profitable and easy. (This fact has been recognised by New Zealand, which country recently took the courageous step of « decommercializing » the rabbit, even though it meant the loss of quite a valuable export trade in carcasses and skins.) The power and repercussions of this vested interest in the rabbit have varied from region to region and period to period; but only perhaps in Western Australia has its influence been negligible.

The extreme case is provided by a State (which need not be named) in which interest in the commercial-

ization of the rabbit had, I am convinced, adversely affected rural development and prosperity to a very real degree. Here the harvesting of rabbits was mostly carried out by employees on farms and grazing properties, as an off-time seasonal occupation, or by men who sought full-time employment on rural holdings for part of the year. The money they made out of rabbits was often more than their wages; and they naturally ranged themselves instinctively and strongly against any serious threat to their rabbit benefactor. The situation had developed over a considerable period; and the dependence of landholders on part-time rabbiters, for harvesting, shearing and other urgent and essential work, was such that the latter often found themselves in a position of being able to dictate to their employers on questions of rabbit control policy. I have heard landholders openly confess that they had to curtail rabbit eradication at a certain point to insure having adequate labour at harvest time. Methods of destroying rabbits which did not permit the recovery of carcasses and skins were discouraged or, quite often, actively sabotaged; and when an official campaign of myxomatosis dissemination was initiated, there were several attempts made to prevent landholders taking advantage of the service offered by the threat of « accidental » fires over their country when the pastures dried off in the summer.

The change in the situation in this State happened to be initiated by a hardening of the official policy towards the rabbits, which involved a radical overhaul of administrative machinery relating to vermin control; and myxomatosis did not have a significant effect on rabbit numbers until the change was well under way. The end result, however, did not differ materially from what it would have been had the disease been primarily responsible for the reduction in rabbit numbers. I wish I were in a position to say how the social adjustments that the change had forced on rural community were progressing; but unfortunately this would involve a survey or study that would be outside the function of my team. The State in question, as I have indicated, represents an extreme case; and changes — often radical — in the attitude and activity of a substantial number of people will be called for.

#### *The future of myxomatosis*

It is natural enough that there should be a call for an ecological stocktaking on the effects of myxomatosis

as soon as it became apparent that these effects were widespread and far-reaching. It seems to me, however, that in the European countries at any rate a stock-taking at this stage is rather like trying to assess the day's weather at breakfast time — quite an interesting and valuable exercise as long as one does not forget that it must be tentative.

We in Australia have now had over five years' experience of myxomatosis, and as far as we can tell its effects have been wholly, or at any rate overwhelmingly, beneficial. Our chief concern now is in the consolidation of the benefits that myxomatosis has brought, and with the question of how long we can expect the disease to carry on the good job.

The Wildlife Section has made a special study of the performance and transmission of myxomatosis in the field; and we have determined that the infection is spread in Australia almost exclusively by mosquitoes. Always making an allowance, in our minds, for the odd outbreak that cannot be satisfactorily explained, we now know with reasonable certainty that the performance of myxomatosis — the timing, extent and intensity of outbreaks — is a simple reflection of the abundance and activity of certain species of mosquitoes. This means, in turn, that it hinges on the amount and distribution of the seasonal rainfall, which introduces an element of considerable uncertainty, the climate of the continent being what it is. Forgetting for the moment the problem of changes in virus virulence and host resistance, continued effective control of the rabbit by myxomatosis will depend on the regular occurrence of outbreaks with a high infection rate in the local population. In regions where outbreaks are irregular or where the infection rate falls far below 100 per cent, effective control cannot be expected. The years since 1950 have, on the whole, been so exceptionally favourable for myxomatosis transmission that we cannot, on the basis of our observations to date, delimit on the map those areas in which the disease could be relied on to perform effectively over a run of « normal » seasons.

The secret of the success of myxomatosis is, of course, that it happens to be a « new » disease and experience for the European rabbit. No other type of infection could be expected to possess the combination of lethality and transmissibility required to produce frequent, extremely high mortalities in a wild mammal population. A « new » pathogen can be an effective controlling agent in this way simply because the host popu-

lation has not had a chance to develop a defence against it; but given time the parasite and host will arrive at some degree of mutual adjustment. This can be accepted as axiomatic. In the case of a virus parasite and a mammal host the mutual adjustment will be achieved by changes in virulence of the virus and in the innate resistance of the host.

Because the expected host-parasite adjustment would be of such great practical significance — and also because of the great scientific interest that would attach to its elucidation — a considerable part of the Australian myxomatosis research effort has been directed to this aspect of the problem. The leading spirit in the studies has been Professor Frank Fenner, of the Australian National University in Canberra, with whom my Section maintains close collaboration. The Animal Genetics Section of the C.S.I.R.O. has also been actively involved in the work.

Briefly, the story that is being unravelled is as follows. Strains of the myxoma virus with lowered virulence appeared as early as 1952, and now seem to have become dominant in the field. The prevalent « field » strains have a case mortality rate of about 90 per cent, with a mean survival time of something between 20 and 30 days in fatal cases — the comparable figures for the « standard » strain, originally liberated in Australia, being 99+ per cent and 10-12 days. Strains with a greater degree of attenuation than this have been recovered from natural outbreaks of the disease; and it was feared that their appearance might presage a progressive loss of virulence in field strains. However, the most recent data suggest that this is not happening: the prevalent strains to-day are still of the slightly attenuated type that appeared on the scene four years ago. The prevalent field strains, because of the longer period their cases remain infective for insect vectors, have a selective advantage over fully virulent strains, and it has been found impossible to replace them in the field by more virulent ones.

Laboratory tests have shown that the natural resistance of rabbits in areas where intense epidemics have occurred annually is building up at an appreciable rate; but so far the increased resistance (measurable in survival percentage and survival time) has not revealed itself in any obvious reduction in the efficacy of natural outbreaks. We attribute this to the fact that laboratory conditions probably permit the recovery of cases that would have succumbed in the field, and we assume that

the increase in resistance will be reflected in noticeably reduced field mortality when it has progressed a bit further, as it undoubtedly will.

Conditions in Europe, with different vectors responsible for transmission and an apparently more stable type of virus remaining dominant, may well be importantly different from ours; but I cannot help feeling that this difference, in the end, will merely mean that the rate of the inevitable host-parasite adjustment will be somewhat slower in the Northern Hemisphere. All told, I think we must conclude that myxomatosis cannot perform at anything like its present high level of effectiveness indefinitely; though whether we can expect the situation ultimately to stabilise at a point where rabbit numbers will never be permitted to build up to serious pest proportions is anyone's guess at the present time.