On the trail of the rabbit

Few things done in the 200 years of European settlement of Australia have been as destructive as the introduction of the rabbit. The settlers who brought it here for food and sport, and as a reminder of the English countryside, made a terrible mistake, which rapidly became apparent.

The population explosion began about 1860, in southern Victoria. Within 30 years, rabbit numbers had reached plague proportions over large parts of southern Australia, and landholders were resorting to desperate measures to protect pastures and crops. Some poisoned their dams, to kill rabbits when they came to drink. Strychnine and phosphorus baits were spread around the countryside in mass-poisoning campaigns.

But for a few people, the arrival of the rabbit was good news. Rabbits could be sold as food, and their pelts had value as fur and as the basic material for the felt-hat industry. To expand their sources of supply, trappers and shooters carried rabbits hundreds of kilometres to areas not already infested.

The activities of these people combined with natural spread to populate the vast portion of Australia suited to the rabbit by the early 1900s. Rabbits are at home in environments ranging from arid stony deserts to subalpine valleys, sub-tropical grasslands, and wet coastal plains. They inhabit more than half of Australia's 7·7 million-sq-km land area, mainly to the south of the Tropic of Capricorn.

The people most concerned by the rabbit have, of course, been farmers—mainly because of pasture losses. The animals display marked preferences in their choice of food, generally going for the most nutritious species available. In improved pastures their first choices are clovers, ryegrasses, and other valuable species, and they have the additional damaging habit of digging out the roots. Pastures are then likely to be invaded by less useful grass species and weeds.

Rabbits and sheep—competitors.

A victim of myxomatosis.

Rabbits do much harm to the native vegetation, but it is often hard to tell just how much. For example, there is no way of sorting out the rabbit's impact on plants, and hence on native animals, from the effects of grazing by sheep and cattle. All have contributed to the disappearance of small marsupials from vast areas, and the extinction of some species. Also, over huge tracts of lower-rainfall country, grazing by both stock and rabbits has degraded the vegetation cover and led to erosion.

In 1887, the New South Wales Government offered a prize of $25 000 to anyone who could rid the colony of the pest. But nobody had the answer, and numbers continued to build up until 1901–02, when much of Australia was hit by severe drought. Large numbers of sheep and cattle died, and rabbit populations plummeted. Heavy grazing by hungry animals did great damage to pastures.

Although most estimates of rabbit populations are inevitably subjective and unreliable, numbers seem to have built up again quite slowly after that drought. Long-term pasture damage caused by severe over-grazing may have been a major reason for the slow recovery, and control attempts by poisoning, shooting, and fumigation of burrows must have had some impact. But by 1950, numbers had grown to such an extent that the rabbit was threatening the livelihood of farmers over wide areas.

Myxo.

Then came myxomatosis. In 1896, disease almost wiped out the laboratory rabbit population at the Hygiene Institute in Montevideo, Uruguay, and a virus that produces only minor symptoms in its natural host, South America's forest cottontail, was found to be responsible. Myxomatosis had not been observed before in the European rabbit, the species that was brought to Australia and from which laboratory varieties have been bred.

As early as 1919, a Brazilian scientist studying myxomatosis suggested that it might have the potential to stem the rabbit plague in Australia. Some experiments with the virus were conducted in this country in the 1920s and 1930s, but attempts before World War II to establish it in the wild rabbit population failed.

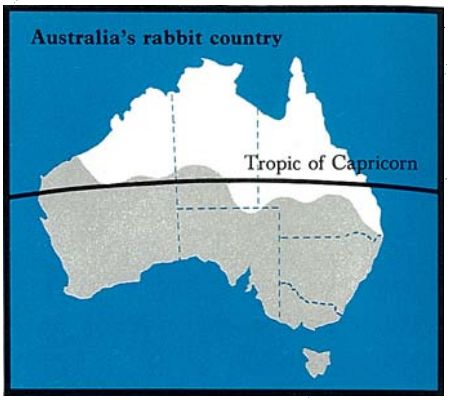
The story was very different after the War. In the summer of 1950–51, after a release of the virus near Corowa on the Murray River, rabbits died by the million. Very few that contracted the disease survived, and the rate of spread was remarkable. By 1953, virtually all rabbit populations in south-eastern Australia—from southern Queensland through New South Wales and Victoria to South Australia—were affected. Numbers fell to very low levels in most districts.

Inevitably, however, there were survivors. With the development of less virulent strains of the virus and resistance among rabbits, myxomatosis has since become a less effective rabbit-killer. But it is still important in keeping numbers down, and no further decline in average virulence has been detected for 10 years or more.

In 1949, CSIRO set up a Wildlife Survey Section, now the Division of Wildlife Research. The rabbit was the Section's dominant concern at the start, and the scientists' main activities initially were releasing myxomatosis and monitoring its spread and impact.

However, it was clear that myxomatosis would not provide the complete answer to the rabbit problem, and that other approaches to control were still needed. Recognizing the importance, in pest control as in war, of 'knowing the enemy', the Division of Wildlife Research expanded its research into rabbit behaviour and ecology. A vast amount of information has been gathered; this article describes only a small part of it. Much of the research on rabbit behaviour has been pioneering work that has yielded important insights into animal behaviour generally.

They inhabit more than half of Australia's 7·7 million-sq-km land area.



Some outlying populations live north of the shaded area.

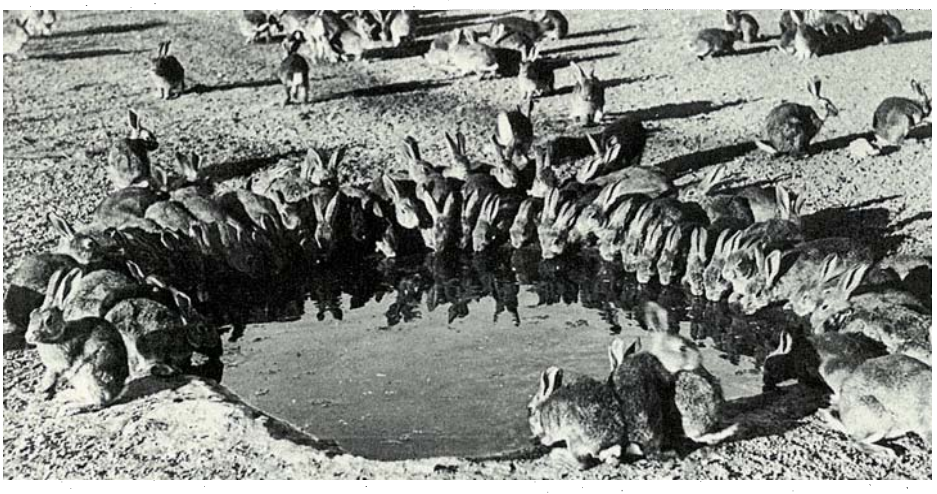
The problem varies

Legislation in each State requires that rabbits be controlled, and makes individual landholders responsible for control on their holdings. With research backing from CSIRO and elsewhere, success has been achieved to the extent that numbers are largely in check in the higher-rainfall agricultural areas. Myxomatosis still kills many rabbits in these areas, and predators—mainly foxes and feral cats—help keep numbers down. Ripping of warrens and poisoning campaigns, planned with knowledge of rabbit behaviour, are the main additional controls encouraged or implemented by the State authorities.

In outback pastoral areas and unused land in the arid zone, however, numbers sometimes still rise to plague proportions. Myxomatosis strikes less often in these parts, and ripping and poisoning are usually impracticable because of cost and the huge areas involved. The CSIRO rabbit researchers are now directing most of their attention to this type of country.

Results of a survey by Dr Brian Cooke of the South Australian Vertebrate Pest Con-

A dramatic illustration of the damage rabbits can do. The fence kept them out of the right-hand paddock but they were free to infest the one on the left.



Rabbits caught by drought converge on a waterhole in a denuded paddock. This photo was taken before the introduction of myxomatosis in 1950–51.

trol Authority, during a recent plague in the north-east of that State, illustrate the size of the problem in the outback. He estimates that there were more than 2000 rabbits per square kilometre, eating something like 1 tonne of saltbush each night. The animals killed shrubs and trees by biting off their bark. Plagues like this may cause irreparable damage to the naturally delicate balance of the arid ecosytem.

They breed like rabbits

The ability to multiply very rapidly is perhaps the best-known attribute of rabbits. Under ideal conditions, females can produce a litter per month in the breeding season, and litters of four to six kittens are normal. The young can start breeding at an age of 3–4 months.

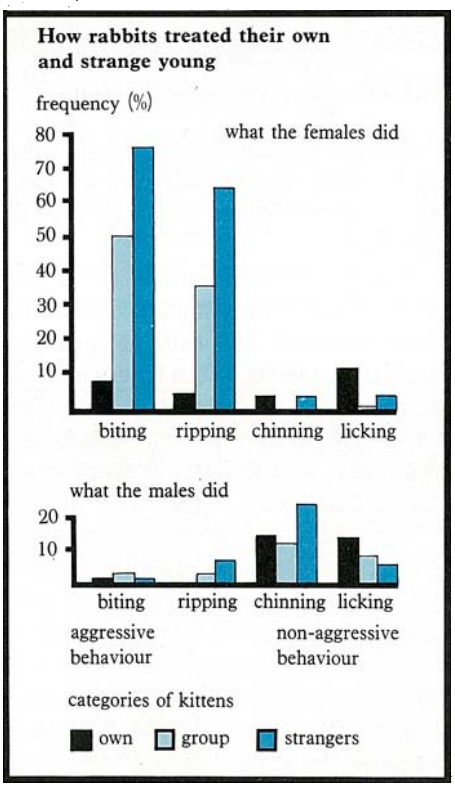
During the 1960s, Dr Ken Myers and colleagues from the Division of Wildlife Research sampled rabbits from five parts of Australia to see, among other things, how closely rates of reproduction in the field approached the rabbit's potential. They found that reproduction performance varied widely with location.

Rabbits turned out to be most productive in a temperate mediterranean climate—the conditions found in southern Europe, where they originated, and in much of south-eastern and south-western Australia. The females in these areas produced an average of 5·2 litters per year, each averaging 5·65 kittens; this means that the typical female produced 29·4 young per year—quite a performance. If a population is to remain stable under these conditions, more than 80% of the young must die within 3 months of birth. Clearly, the potential exists for an explosive population increase.

The next most productive regions among those examined were sub-tropical Queensland (averaging 18·5 young per female) and the New South Wales south coast (16·7). Performance was poorest in semi-arid north-western New South Wales, where the average was 13·4 young per female, and in the subalpine Snowy High Plains, where the figure was 13·1. Conditions appear most precarious for the rabbit in the subalpine area, where Dr Myers' calculations indicate that a death rate any greater than 17% in the 0–3 months age group would send the population into decline.

The warren

The centre of rabbit society, and the place where most young are born, is the warren.



The charts show some of the results of tests in which kittens were put in pens with pairs of adult rabbits. Females usually attacked strange kittens, but not their own. The males more often sought to protect the young, and frequently attacked aggressive females.

Smell is a most important and complex means of communication.

By observing the behaviour of rabbits in a 0·7-ha enclosure and a 33-ha paddock near Canberra, Dr Roman Mykytowycz, Dr Peter Fullagar, and other Division of Wildlife Research scientists have learnt much about the importance of the warren and the way rabbits behave around it.

Warrens are networks of tunnels with a diameter of 15–20 cm. Does dig breeding chambers of about twice that diameter in short offshoots from the main tunnels, and make their nests there. Some warrens have more than 20 separate entrances, but most have only a few. The does that breed outside warrens dig short 'breeding stops' nearby.

During the breeding season, rabbits form social groups of one to three males and one to seven females; many groups can occupy one warren. Strict hierarchies form among both the males and females in the groups, status being won in fights and displays of aggression.

Rabbits are gregarious animals, showing little inclination to set out on their own or establish new warrens away from the ones they were born in or near. For example, during 5 years of observations, the rabbits in the 33-ha paddock near Canberra restricted their activities to a limited area around two warren complexes. In that time, the population varied from an initial 53 adults, down to a single breeding pair after an outbreak of myxomatosis, and up to a maximum of 271, including young.

When the population was high, subordinate females attempting to secure breeding sites in the warrens were repulsed by the dominant does. Despite this, they made no attempt to establish new warrens. Instead, they nested nearby in exposed breeding stops. Young produced by these does tried to attach themselves to the warrens, and they, too, were greeted with hostility.

From observations of the rabbits' behaviour, Dr Mykytowycz and Dr Fullagar allocated one of four status classes to each adult female in the paddock. The dominant class, 24% of the total, were those that came out on top in all their aggressive encounters. The second and biggest group (43%) dominated some females, but were subservient to the top 24%. The third group lost all encounters, and the bottom-rankers engaged in no aggressive encounters with

When the rains come and the desert blooms, rabbit numbers can rise rapidly to plague proportions.

other females, evidently accepting without argument their subordinate position.

A clear correlation showed up between social status and reproductive success. Although the dominant does constituted less than one-quarter of the breeding population, they produced 51% of the young. The second-ranking does produced all but 7% of the remainder. As the dominant bucks do most of the mating, it is largely the genes of dominant rabbits that get passed on from generation to generation.

Communications

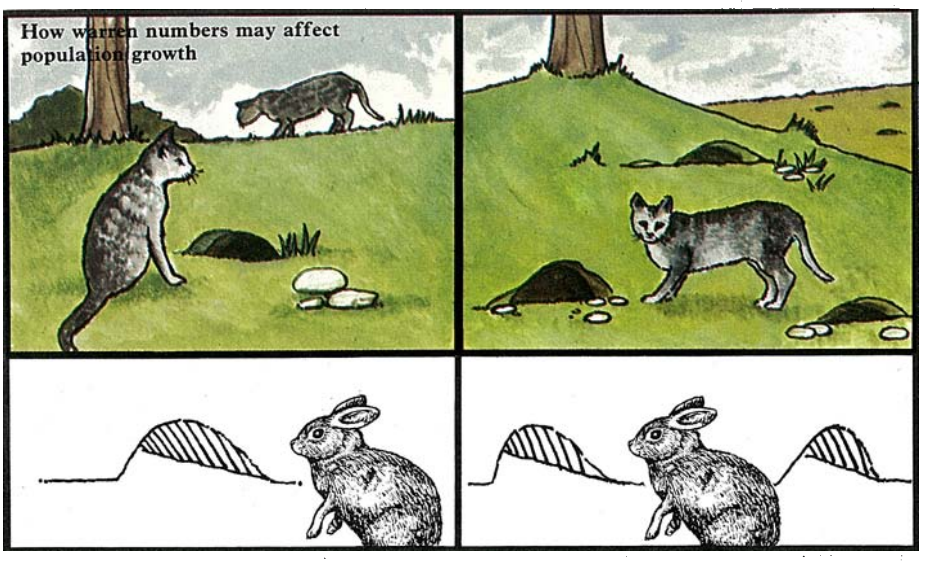
To run their warren societies, rabbits have to communicate with one another. They are not noisy animals, and they can make only limited use of visual communication because they live in dark burrows and perform most of their outside activities at night. Touching—either a friendly lick or an aggressive attack—is one method they use. Another is foot-stamping. Research led by Dr Mykytowycz shows that smell is a most important and complex means of communication.

Rabbits deposit odour signals with their faeces and urine. Also, some parts of their bodies, including the chin, groin, ears, and areas around the eyes, contain special odour-producing glands. Working out what different odours mean is complicated by the fact that rabbits respond in different ways to the same message. Social status, age, sex, and stage of the reproductive cycle are some of the factors that affect the response.

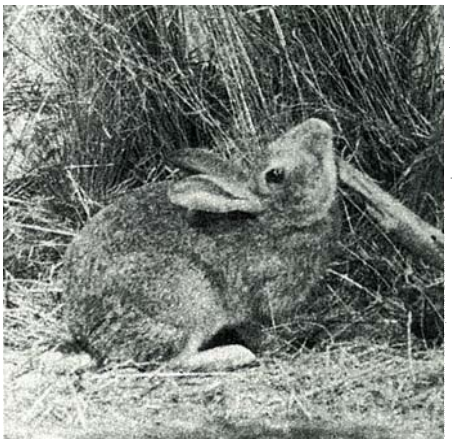
The studies revealed that rabbits use secretions from the chin and anal glands to mark out territory, and from the groin gland for identification of individuals.

By dissecting out and measuring large numbers of glands, Dr Mykytowycz found that the size and secretory activity of the chin and anal glands vary with social status. Males, which do most of the territory marking, have bigger glands than females, and the dominant bucks have the biggest of all.

Rabbits have two characteristic ways of marking out their territory above ground—establishing dung hills and rubbing objects with their chins. Both are predominantly male activities. Faecal pellets are coated



Predators such as feral cats hunt young rabbits by waiting at burrow entrances for them to emerge. Hence, a small population scattered through many warrens may have a better chance of growing to plague proportions than the same population confined to a few warrens.



A rabbit marks out its territory by chinning.

with secretions from the anal gland as they are excreted, and rubbing of objects with the chin leaves behind secretions from the chin gland.

Females block the entrances to their breeding nests with soil marked with their faeces and urine. This marking apparently repels other rabbits. When kittens leave the burrow at an age of 18–21 days, they initially restrict their movements to the area where they can detect their mother's odour, learnt in the nest.

Territorial marking by members of a group has two effects—warning strangers and giving rabbits confidence on their home ground. To study the confidence-inducing properties of the various secretions, the researchers carried out a series of tests in a 4-square-metre pen. In each test, faecal pellets or pads impregnated with rabbit secretions were placed on the floor, and then two rabbits were put in the pen.

Inducing confidence

Rabbits tested in the presence of their own or familiar odours were regarded as 'home' animals, and the others as being 'away'. The scientists judged the confidence of animals by observing fights, attempts to escape from the pen, amounts of movement, and general deportment.

The confidence-inducing effects of the chin and anal secretions showed up clearly. Urine seemed to have less territorial significance for males than for females, which acted confidently in the presence of both their own and their male partner's urine. This difference between the sexes may be related to the fact that females mark the sealed entrances to their breeding nests with their urine.

In most cases, secretions from the groin gland had no impact on the animals' confidence. By far the biggest effect of these secretions was to increase the amount of time that the animals spent sniffing one another.

This observation supports the conclusion that secretions from the groin gland help rabbits recognize their fellows. Additional evidence came from experiments in which rabbits from an established group were smeared with secretions from strangers. Other members of the group attacked the treated rabbits as if they were unknown outsiders. In many cases, the attacks persisted until the smeared rabbits were killed or removed from the group.

The role of odour, although not necessarily from the groin gland, in recognition also showed up strongly in a study of the behaviour of adult rabbits in the presence of their own and strange kittens. Ten pairs of rabbits took part in the tests, together with 155 kittens. The kittens were divided into three categories—'own' for those born to the adult pair being tested, 'group' for others from the same breeding

colony, and 'strangers' unknown to any of the adults.

When a 'stranger' was put in the experimental pen with a pair of adults, the female almost invariably attacked it viciously. Females bit kittens and ripped them with the claws of their hind legs. Frequently, the males sought to protect the young and attacked their mates. They also often 'chinned' and urinated on the strange kittens.

Attacks by females on 'group' kittens were less frequent, but still quite common. They never occurred on 'own' kittens below weaning age, but older 'owns' were sometimes attacked.

To assess the importance of odour in recognition, the scientists blindfolded the adult rabbits for some of the tests. Although the masks inconvenienced the animals, the females still showed marked aggression towards strange kittens—much more than towards the 'group' kittens used in these tests. The blindfolded animals seemed to identify kittens solely by smell.

In the wild, young kittens normally escape attack, as they spend their first 18–21 days in the nest with their mother and then restrict their movements outside to areas where the mother's odour prevails. However, kittens born in breeding stops away from a warren are likely to be attacked and may be killed when they try to attach themselves to the warren.

The protective activities of males are interesting. By chinning, licking, and urinating on strange kittens, they impregnate them with odours familiar to other members of the group and gradually make them acceptable to the group.

Strict hierarchies form among both the males and females.

Young rabbits survey a barren landscape from their warren entrance.

Population pressure

Observations in the field show that rates of aggression increase with crowding in and around warrens. One result is an increase in the death rate of kittens. Stress-linked physiological changes have been measured among rabbits living in crowded conditions. So have considerably reduced growth rates among kittens.

The conclusion seems to be that population density and social factors can limit the growth of rabbit numbers. Australia's experience shows, however, that numbers can grow very large despite this.

Numbers were very high near Urana, in the Riverina district of southern New South Wales, when CSIRO conducted its first study of rabbit numbers there in 1951. The 12-ha study site supported about 5000 rabbits—that's more than 400 per hectare. The Riverina has a mediterranean climate, the type that seems to suit the rabbit best.

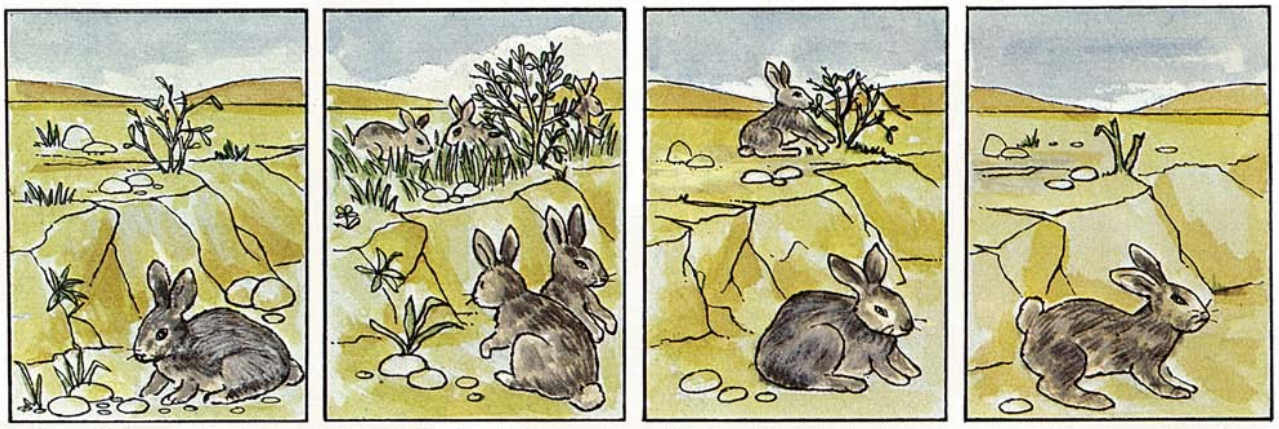
Myxomatosis swept through the area in October-November 1951, and reduced numbers to well below 1% of their previous level.

For 3 years from June 1967, Mr Ian Parer of the Division of Wildlife Research watched the progress of the rabbit population on a 280-ha site near Urana. He wanted to find out, among other things, what kept the population there from returning to pre-myxomatosis levels. No control work was done on the site during the study.

Numbers of adult rabbits fell from 153 to 90 in the first year, a time of severe drought. They recovered to 182 at the start of the third breeding season and had dropped back by just 2 when the study ended at the start of the fourth breeding season.

The potential for rapid population growth was there; counts of young emerging from burrows gave figures ranging from

Rabbits in the outback



small populations survive dry years in rocky warrens near drainage channels

after rain, the desert blooms and the rabbits multiply; sandy warrens are re-dug

as the land dries out, starving rabbits attack trees and shrubs as well as eating all available grass

permanent damage may have been done to the arid-land ecosystem; some rabbits remain near rocky channels

15·4 to 21·9 for the number of kittens produced per adult female in a year. These figures are underestimates, as many kittens would have died before they could be observed or trapped.

However, the death rate among kittens was very high. Only about one-quarter of those observed lived for more than 90 days.

Opportunities for predators

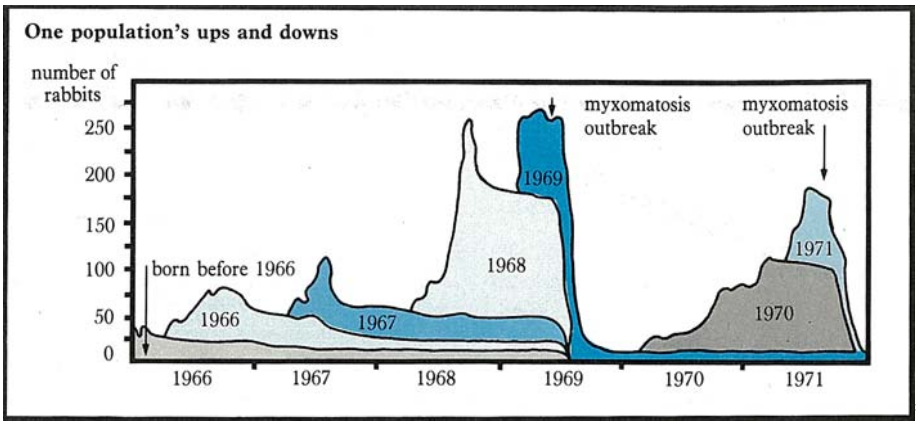
Mr Parer's observations indicate that myxomatosis was considerably less important than predators, particularly feral cats, as a killer of young rabbits. Counts of cats and predatory birds in 1968 and 1969 showed that there was one predator to every 15 adult rabbits on the study site during September and October, when kittens were emerging from the burrows. The ratio was much more strongly in the rabbit's favour—one predator to 155 adult rabbits— in 1951, before myxomatosis struck.

Mr Parer believes that the failure of rabbit numbers to return to high levels can be largely explained by the big reduction since 1950 in the number of warrens in the study area. After myxomatosis cut back the rabbit population in the early 1950s, many unoccupied warrens collapsed. Others were dug in by farmers.

He reasons that, as predators such as feral cats hunt young rabbits by waiting at burrow entrances for them to emerge, their killing capacity depends on the probability of young venturing out through the guarded entrances. Because of this, a small rabbit population scattered through many warrens would have a much better chance of growing to plague proportions than the same population confined to a few warrens.

The relatively low death rate from myxomatosis recorded at the Urana site in recent years contrasts with rates of 80% and higher seen in recent outbreaks in the New South Wales Southern Tablelands and Kosciusko National Park. These outbreaks occurred in winter, and the cold probably caused the mortality rate to be higher. The fact that only about 30% died when myxomatosis hit the same Kosciusko rabbit population in summer suggests this.

Also, unlike the summer outbreaks in the Riverina, the winter attacks were not annual events. As a result, less genetic resistance may have built up in the affected rabbit population.



This graph shows how the rabbit population in the 33-ha paddock near Canberra fluctuated. The different shades trace the fate of the young born in the years shown.

Myxomatosis unknowns

Mosquitoes have been the main transmitters of myxomatosis in Australia, and as they are most active in summer this is when most outbreaks have occurred. However, much remains to be learnt about the factors that initiate outbreaks and the means by which the virus spreads among members of a population of rabbits.

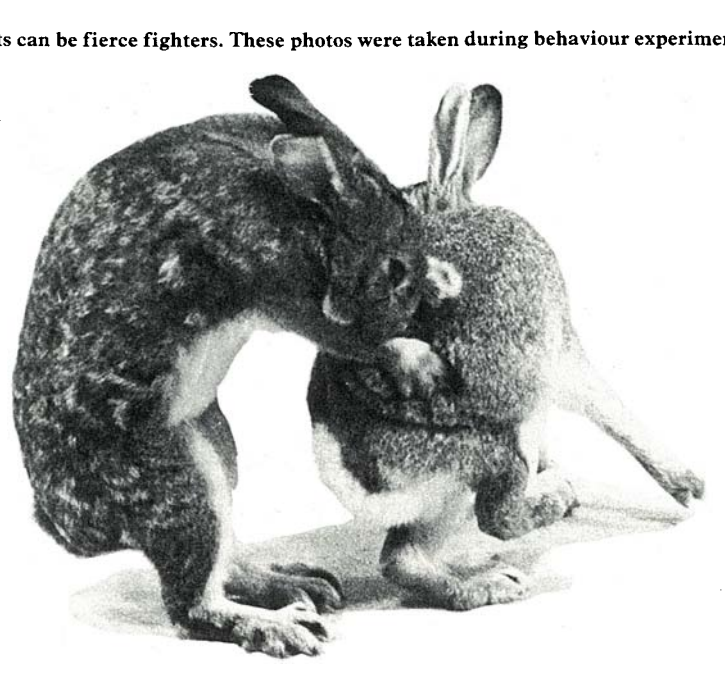
One of the biggest unknowns is the cause of the winter outbreaks, as flying insects that could carry the virus are few and far between in the colder months. It seems that the disease may arise within the population—probably from rabbits that have survived myxomatosis and still carry the virus, or from their descendants. What brings on the revival remains to be determined, as does the means of transmission of the disease. Studies have shown that contact between rabbits can spread the virus without the assistance of a carrying insect.

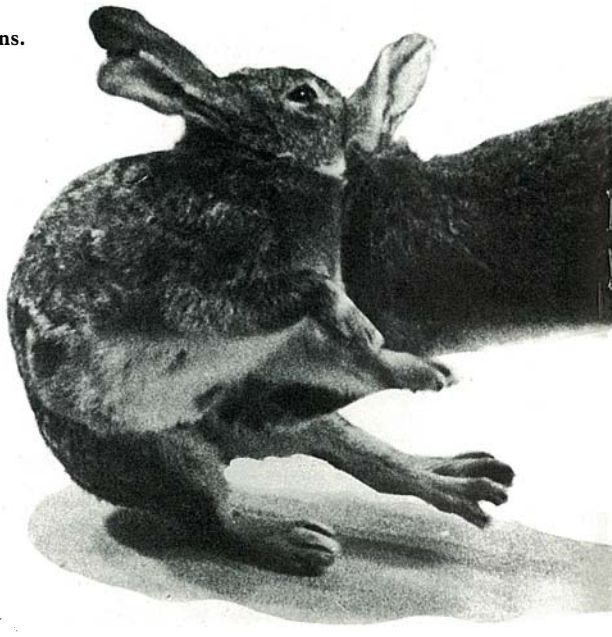
In 1966, Dr Bill Sobey, then with the Division of Animal Genetics and now at the Division of Wildlife Research, imported rabbit fleas to see whether they could improve transmission of myxomatosis. They are the main carriers of the virus in England.

Control authorities in a number of States are now breeding and spreading the fleas. Although their impact has not been dramatic, in some areas where regular myx-

Myxomatosis is still important in keeping numbers down.

Rabbits can be fierce fighters. These photos were taken during behaviour experiments in pens.





omatosis outbreaks used to occur in summer they are now occurring in spring due to the fleas' activities. As spring is usually the height of the breeding season and the weather is cooler then, the outbreaks may kill a bigger proportion of rabbits. Some evidence suggests that this is happening.

One of the main aims of the research now being intensified on rabbits in arid areas is to see whether the fleas can survive there and transmit myxomatosis effectively. At present, only sporadic outbreaks occur, presumably initiated by mosquito-borne virus.

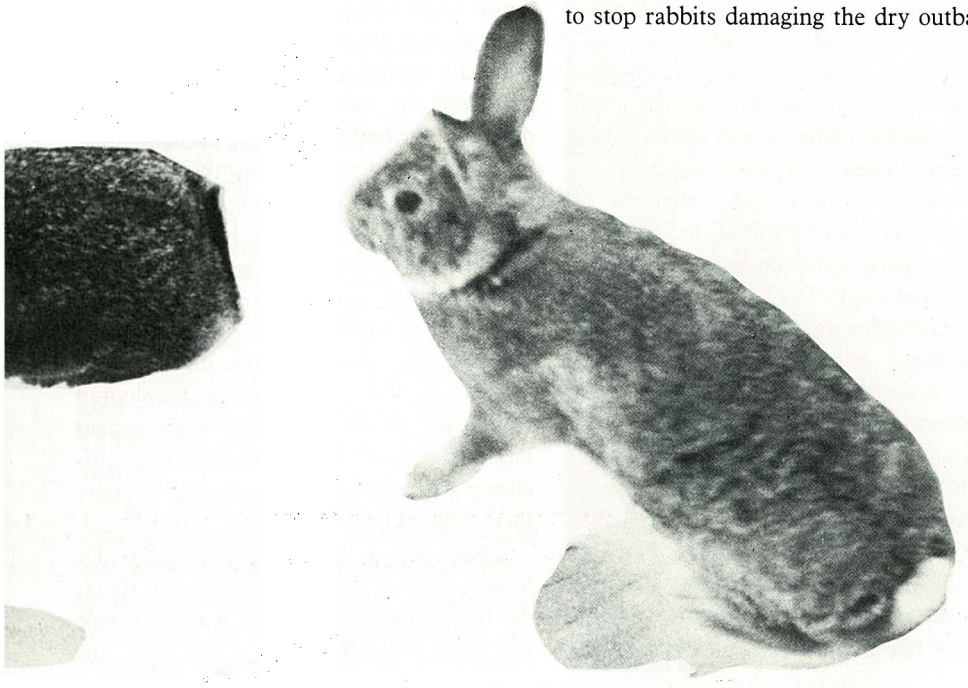
Close-up of a newcomer that has done very well in Australia — disastrously well.

He estimates that there were more than 2000 rabbits per sq km, eating something like 1 tonne of saltbush each night.

Surveys by Dr Myers and Mr Bruce Parker of the Division of Wildlife Research in the arid north-west of New South Wales show that, in dry years, rabbits with warrens in stony country close to drainage channels have the best chance of survival. These warrens provide more protection, particularly from foxes, than those in sand, and the rabbits find sufficient feed and moisture around the channels.

When the rains come and the desert blooms, rabbit numbers can rise rapidly to plague proportions. Warrens in sandy areas, deserted in the drought years, are re-excavated. After a succession of good years, the sandy country sometimes supports much greater rabbit numbers than the stony survival areas.

It is when the land dries out again that the damage is done, as the rabbit hordes eat anything that might provide some sustenance. Only by preventing the population explosions in good years will it be possible to stop rabbits damaging the dry outback.



More about the topic

A comparison of the effectiveness of the odours of rabbits, *Oryctolagus cuniculus,* in enhancing territorial confidence. R. Mykytowycz, E. R. Hesterman, S. Gambale, and M. L. Dudzinski. *Journal of Chemical Ecology,* 1976, **2**, 13–24.

Effect of social environment on reproduction in the rabbit, *Oryctolagus cuniculus* (L.). R. Mykytowycz and P. J. Fullagar. *Journal of Reproductive Fertility, Supplement,* 1973, **19**, 503–22.

Aggressive and protective behaviour of adult rabbits *Oryctolagus cuniculus* (L.) towards juveniles. R. Mykytowycz and M. L. Dudzinski. *Behaviour,* 1972, **18**, 97–120.

The population ecology of the wild rabbit, *Oryctolagus cuniculus* (L.), in a mediterranean-type climate in New South Wales. I. Parer. *Australian Wildlife Research,* 1977, **4**, 171–205.

Effect of severe drought on rabbit numbers and distribution in a refuge area in semi-arid north-western New South Wales. K. Myers and B. S. Parker. *Australian Wildlife Research,* 1975, **2**, 103–20.

Myxomatosis: the introduction of the European rabbit flea *Spilopsyllus cuniculi* (Dale) into wild rabbit populations in Australia. W. R. Sobey and D. Conolly. *Journal of Hygiene,* 1971, **69**, 331–46.

Observations on myxomatosis in a rabbit population with immune adults. P. J. Fullagar. *Australian Wildlife Research,* 1977, **4**, 263–80.

Rabbit fleas. W. R. Sobey. *Wool Technology and Sheep Breeding,* 1977, **25**, 37–40.

'Myxomatosis.' F. Fenner and F. N. Ratcliffe. (Cambridge University Press: Cambridge, 1965.)

'They All Ran Wild.' Eric C. Rolls. (Angus and Robertson: Sydney, 1969.)