Rabbit Burrows as Environments for European Rabbit Fleas, *Spilopsyllus cuniculi* (Dale), in Arid South Australia

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Abstract

The temperature and humidity of air within rabbit burrows was recorded for sites on either side of the margin of the distribution of the rabbit flea, *Spilopsyllus cuniculi*, in South Australia. The microclimate in the burrows differed significantly across this margin, and the differences in temperatures and humidities were large enough to have significant effects on flea populations. At sites where fleas occurred, the relative humidity of burrow air was above 70% and usually between 80 and 90% RH for at least 4–5 months during the winter and spring. This not only provided optimum conditions for the survival of flea larvae in the rabbits' nests, but also should have enabled the flea populations to achieve their full reproductive potential. High humidity of burrow air at these sites during summer would also favour the survival of free-living adult fleas. At those sites where fleas did not occur, the humidity of burrow air is generally unsuitable for the survival of larvae or free-living adult fleas.

Introduction

European rabbit fleas were introduced into Australia in 1969 as vectors of myxoma virus to assist with the biological control of the introduced European rabbit, *Oryctolagus cuniculus* (L.) (Sobey & Menzies 1969; Sobey & Conolly 1971).

However, they have been unable to colonise inland Australia where rainfall averages less than 200 mm annually (Cooke 1984; King *et al.* 1985) even though rabbits are relatively common in areas receiving as little as 125 mm annually.

The reasons for the failure of *Spilopsyllus* to become established are not precisely known. Cooke and Skewes (1988) have investigated the effects of temperature and humidity on development and survival of each life stage of the rabbit flea and have found that, although flea eggs and pupae can tolerate low humidities, flea larvae generally require humidity in excess of 70% RH to survive and grow normally. *Spilopsyllus* lays eggs in the nests of grass and belly fur which female rabbits make for their young. These nests are usually in cul-de-sacs off one of the burrows in the rabbit warren. The young rabbits warm the nest, thereby quickening the development of the flea larvae. To some extent the young rabbits' urine and exhaled air also humidifies the nest, reducing water loss from the flea larvae. However, this benefit appears to be small, and if the burrow air is too dry these urinary and evaporative water losses are not enough to maintain adequate levels of humidity for the flea larvae to survive.

It is also known that adult fleas are intolerant of hot dry air. Consequently, in inland Australia those rabbit fleas which leave their host may risk desiccation, because Hall and Myers (1978) found that in arid western New South Wales the air within rabbit burrows was often relatively hot and dry during summer. The air in rabbit burrows is not always cool and moist as suggested by Hayward (1961).
From the correlation between the distribution of rabbit fleas and rainfall it would be expected that the burrows on the edge of the distribution of the fleas would be cooler and moister than those outside it. More important, the absolute values of temperature and humidity should be such that these differences would be expected to exert a strong influence on the development and persistence of adult fleas or larvae.

In this paper, data are presented on the seasonal changes in the temperature and humidity of rabbit burrows at several sites in and around the Flinders Ranges in inland South Australia. These enable comparisons to be made between sites in which the fleas persisted and those which were uninhabited. In addition, the data on burrow microclimates have been reviewed against the laboratory data of Cooke and Skewes (1988), to assess their probable influence on the survival of larval and adult fleas.

Methods and Materials

Study Areas

Measurements of the microclimates of rabbit burrows were made at seven sites in two transects across the Flinders Ranges in South Australia. The general climate and topography of the area has been described by Laut et al. (1977). The specific sites have also been described previously (Cooke 1984) and so here it suffices to list each site and its approximate average annual rainfall. They are: Oraparinna (300 mm), Belton (275 mm), Witchitie (220 mm) and Koonamore (200 mm), stretching across the southern Flinders Ranges, and Angepena (250 mm), Balcanoona (190 mm) and Moolawatana (150 mm) in the northern Flinders Ranges. Rabbit fleas are common at Oraparinna, Belton and Angepena, and can be found in most years at Witchitie. However, they have never persisted at Koonamore, Balcanoona or Moolawatana despite temporary episodes of colonisation following their release or natural spread into these sites (Cooke 1984).

During the period in 1984 and 1985 in which the measurements of microclimate were made, the seasonal conditions, as judged from rainfall and pasture conditions, were a little wetter than average.

Burrow Microclimate

Rabbit warrens have numerous entrances and are sufficiently well ventilated for the temperature and humidity of air within the burrows to change slowly throughout the day, although to a much lesser extent than the air at the surface of the soil. This presented some difficulty in making comparisons between sites, because temperature and humidity were often recorded at different times of the day and often under widely different weather conditions. However, initial observations showed that most of the daily changes in the relative humidity of burrow air can be attributed to the daily warming and cooling of the burrow, and that the absolute humidity within a given burrow changes very little. As an example, at Witchitie, in a burrow which was continuously monitored over 24 h, relative humidity fell to only 72% at 1915 h but rose to 81% by 0800 h the following day. However, the absolute humidity, estimated over the same period, varied only between 20.2 and 21.5 mg H₂O L⁻¹ air. Absolute humidity was read from the tables of Weast (1973).

As a consequence of these observations, initial data on the relative humidity of burrow air from each site were also expressed in terms of absolute humidity. In effect, this corrected the data for differences in temperature and brought the data into a standard form enabling direct comparisons to be made between sites.

Likewise, it was found for soil and burrow temperatures that most of the daily changes in temperature occurred within 0·5 m of the soil surface. At greater depths temperature changed very little from day to day, although it did change slowly from summer to winter. On this basis the temperature of the soil at 1 m depth was used for making comparisons between sites.

Records of temperature and humidity were made at different times of the year, so that some idea of the seasonal changes in burrow microclimate might be obtained. All sites were visited four times during 1984 and early 1985, but one additional set of temperature measurements was made at Oraparinna, Belton, Witchitie and Koonamore.

Humidity Measurements

A number of electronic devices are available for measuring humidity, but of those tried for this work none seemed to be able to provide accurate readings, under field conditions, when humidity was low. Similar difficulties appear to have been encountered by Hall and Myers (1978), who recorded relative humidities of 0% at some sites. Such readings appear to be related to the malfunction or lack of sensitivity of the recording devices at low humidities rather than real humidities; air is never completely dry in natural environments.
For this study a small aspirating hygrometer was designed and built. A 12-V car vacuum-cleaner was used to draw air through an insulated tube (2 cm internal diameter) inserted 1-2 m into the burrow entrances. These entrances were sealed with plugs of earth before air was drawn from the burrow, to ensure that air entering the hygrometer came from within the warren and was not a mixture of burrow air and air entering the burrow mouth. Entrances to burrows in close proximity (within 2 m), or likely to be connected to those used for measurements, were also plugged with earth. The air drawn into the tube passed through a small chamber containing wet- and dry-bulb thermometers; the humidity was calculated from the difference between the wet- and dry-bulb readings, by means of tables published by the Commonwealth Bureau of Meteorology. Air speed within the recording chamber was maintained at approximately 3 m s⁻¹. It was necessary to use two filters—one of phosphor-bronze 200 wire mesh and the other of fine, brushed nylon—to remove dust from the air to prevent fouling of the wet bulb thermometer. This hygrometer was calibrated, in the open air, against a whirling-hygrometer (Casella, London) and good agreement was obtained over the range of 20-90% relative humidity \( (r^2 = 0.98, y = 0.97x + 0.67, n = 16, \text{where } y \text{ is the reading from the aspirating hygrometer and } x \text{ is the reading from the whirling hygrometer, both expressed as percentage RH})\).

At each site recordings were made from two burrows in each of five warrens. These warrens were usually of moderate size, each having between 15 and 30 entrances. In addition, the temperature and humidity of the air 25 cm above the ground was recorded at the time the measurements were made within the burrows.

**Temperature Measurements**

At the beginning of the study, lengths of aluminium tubing, 8 mm internal diameter, were buried vertically in the soil at each site, enabling a Digitemp thermistor probe to be lowered to a given depth to record temperature. On visits to each site recordings were normally taken at the surface and at depths of 10 cm, 25 cm, 50 cm and 1·0 m, to provide profiles of soil temperature against depth. However, other depths were occasionally used where it was important to determine the shape of the profile more exactly. Although these temperature-measuring probes were placed up to 25 m apart at some sites, the temperatures recorded at any given time were usually within 0·4°C for each other.

### Table 1. Seasonal changes in the absolute humidity of burrow air at each site

<table>
<thead>
<tr>
<th>Site</th>
<th>Humidity during:</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Autumn</td>
<td>Winter</td>
</tr>
<tr>
<td>Oraparinna</td>
<td>9·15 ± 1·94</td>
<td>8·88 ± 0·46</td>
</tr>
<tr>
<td>Belton</td>
<td>10·40 ± 0·68</td>
<td>9·10 ± 0·18</td>
</tr>
<tr>
<td>Witchitie</td>
<td>8·02 ± 1·45</td>
<td>9·12 ± 0·24</td>
</tr>
<tr>
<td>Koonamore</td>
<td>6·75 ± 0·51</td>
<td>7·52 ± 0·48</td>
</tr>
<tr>
<td>Angepena</td>
<td>8·48 ± 1·65</td>
<td>10·00 ± 0·54</td>
</tr>
<tr>
<td>Balcanoona</td>
<td>8·43 ± 1·43</td>
<td>11·65 ± 3·60</td>
</tr>
<tr>
<td>Moolawatana</td>
<td>5·38 ± 2·01</td>
<td>10·93 ± 0·51</td>
</tr>
</tbody>
</table>

**Results**

**Burrow Humidity**

The average (±standard error) of the absolute humidity of air within burrows at each site is given in Table 1. Although there are some differences in burrow humidity between sites and between different times of the year, the factors which determine absolute humidity are complex, and it is not possible to see obvious seasonal patterns. In particular, the irregularity of rainfall at most sites meant that seasonal changes in absolute humidity were not regular and predictable.

**Soil Temperatures**

Temperatures recorded at 1 m depth at each site were compared in the following way. Data collected at different times of the year were used in a linear mathematical model in which soil temperature was fitted against a cosine transformation of the time of the year \( [\cos (\text{day} \cdot 360/365)] \) which made allowance for the fact that changes in soil temperature
lag behind the peaks and troughs in annual solar radiation. An iterative fit of the data in which lag periods were progressively increased showed that a lag of 38 days after the solstices gave the least residual variance. An analysis of variance showed that there was no differences in the slopes of the fitted curves ($F_{6,18} = 2.28$, NS) but the intercepts differed ($F_{6,24} = 22.8$, $P < 0.001$). This meant that at all sites the temperatures followed similar trends during the year, but at some sites soil temperatures were always significantly warmer than at others. The amplitude of measurements about the mean temperature averaged 7.35°C (Table 2).

Table 2. The calculated means and seasonal amplitude of deep burrow temperatures for each of the experimental sites, based on temperatures recorded at 1 m depth

<table>
<thead>
<tr>
<th>Site</th>
<th>Mean temperature (± SE)</th>
<th>Amplitude (± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orararinna</td>
<td>19.07 ± 0.40</td>
<td>7.97 ± 0.56</td>
</tr>
<tr>
<td>Belton</td>
<td>17.43 ± 0.40</td>
<td>6.82 ± 0.56</td>
</tr>
<tr>
<td>Witchitie</td>
<td>21.01 ± 0.40</td>
<td>8.23 ± 0.56</td>
</tr>
<tr>
<td>Koonamore</td>
<td>21.11 ± 0.40</td>
<td>7.39 ± 0.56</td>
</tr>
<tr>
<td>Angepena</td>
<td>19.87 ± 0.46</td>
<td>5.74 ± 0.69</td>
</tr>
<tr>
<td>Balcanoona</td>
<td>22.32 ± 0.46</td>
<td>6.35 ± 0.69</td>
</tr>
<tr>
<td>Moolawatana</td>
<td>24.75 ± 0.46</td>
<td>8.19 ± 0.69</td>
</tr>
</tbody>
</table>

Soil Temperature Profiles

Fig. 1 shows how temperature changes with depth in the soil. It also shows how most daily variation in temperature occurs within 50 cm of the soil surface. Because heat penetrates the soil slowly, the soil at a depth of 10–25 cm remains cooler than the rest of the warren during the morning, but it eventually warms up during the afternoon and then remains warm during the evening, well after the surface soil has cooled down again.

**Fig. 1.** Soil temperature profiles at three sites in the southern Flinders Ranges in late summer 1984. There is little diurnal temperature change below 50 cm in comparison to that seen in the surface layers.

Burrows as Environments for *Spilopsyllus*

By themselves, the data on absolute humidities of the burrow air are of little use for comparing sites as environments for *Spilopsyllus*. Because of the large differences in soil
Fig. 2. Humidity of rabbit burrows at seven sites in the pastoral area of South Australia. The shaded area indicates the optimum humidity for development of *Spilopsyllus cuniculi* larvae; the dotted line indicates the lower limit for larval survival. Solid symbols, sites where *S. cuniculi* occurs; open symbols, sites where *S. cuniculi* does not persist. Site locations: ■ Witchitie; ▲ Belton; ● Orparinna; △ Koonamore; ★ Angepena; □ Balcanoona; ○ Moolawatana.
temperature between sites and at different times of the year, these humidity data alone provide a poor measure of the real environmental stress imposed. Cooke and Skewes (1988) have shown that relative humidity and the saturation deficit of air are much more relevant measures as far as the survival of fleas is concerned. Consequently, for each study site, estimates of the relative humidity and saturation deficit in soil at 1 m depth were taken to be the most useful estimates of the severity of the burrow microclimates. It was assumed that these would approximate the conditions in deep burrows. The data on the seasonal changes in relative humidity in deep burrows are given in Figs 2a and 2b, which show data from the southern and northern Flinders Ranges separately.

Discussion

Climate and Flea Distribution

The data collected from the field establish quite clearly that there are significant differences between the microclimates of the rabbit warrens from one study site to the next. It is also clear that these differences are correlated with the apparent suitability of each site for rabbit flea populations. Only the more humid sites support permanent populations of rabbit fleas. At Witchitie, which is a marginal habitat for fleas in some years (Cooke 1984), the microclimate of the rabbit burrows is intermediate between those sites which support fleas and those which do not.

Rainfall is highest in the more elevated parts of the Flinders Ranges and, because of the adiabatic effect, these areas are also cooler than the surrounding plains. As a consequence there are steep gradients in burrow microclimates along each of the transects across the Flinders Ranges. Burrows at elevated sites like Belton or Angepena, where annual average rainfall generally exceeds 200 mm, remain relatively cool and humid throughout the year, while the burrows at the low-lying sites of Koonamore or Moolawatana are warm and relatively dry.

The field data appear to be in general agreement with those previously published. Near Albury, N.S.W., where rainfall is about 500 mm annually, the air in rabbit burrows remained near saturation throughout the summer (Hayward 1961). However, at Calindary in western New South Wales annual rainfall averaged only about 200 mm and in summer the humidity in rabbit burrows often fell below 30% RH (Hall & Myers 1978).

It is to be expected that there would be a correlation between the rainfall in any given period and the humidity of burrow air at each site. Certainly the humidity of the burrows at Moolawatana was high during the 1984 winter because of very heavy rains in the previous autumn, whereas at Koonamore, which missed the rains, the burrows were relatively dry (Figs 2a, 2b). Such observations provide an explanation for the occasional, temporary colonisation of arid sites by the rabbit fleas (Cooke 1984).

The observation that maximum burrow temperatures lagged about 38 days behind the peak in solar radiation is in broad agreement with Prescott (1942), who calculated a lag of 25–30 days of mean air temperature behind solar radiation for inland South Australia. Temperatures 1 m deep in the soil would be expected to lag substantially behind mean temperatures at or above the soil surface. However, the mean amplitude of temperature changes within the rabbit burrows over the course of a whole year is quite similar to the annual amplitude of mean monthly air temperatures observed by Prescott, i.e. 7.5°C. The amplitude is half the annual range in observed temperatures.

The maximum temperatures recorded 1 m below ground at low-altitude sites such as Moolawatana (31°C) are within the range expected by interpolating data given by Parer and Libke (1985) for sites elsewhere in South Australia (e.g. 26°C at a site in the south of the state and 34°C in the far north).

It is also worth noting that the average temperature of the air in the rabbit warrens in summer was a little higher than the mean temperature of the surface air. For example, at Koonamore the temperature 1 m below ground was 28.5°C in late summer, yet Osborne et al. (1935) showed that average air temperature in February at Koonamore is only 24.6°C. Similarly, the maximum temperature of burrows at Oraparinna, 27.1°C, was higher than expected from mean air temperatures, 25.5°C, at Angorichina nearby. At Albury, the mean air temperature in January, 22.2°C, was lower than the temperature of 25°C recorded in
rabbit burrows by Hayward (1961), and the mean temperature for Broken Hill in January, 25.3°C, is lower than the averages of 28-29°C recorded in rabbit warrens at Calindary (Hall & Myers 1978). Rogers (1970) found that at Koonamore temperatures 0.5 cm below the soil surface occasionally reached 65°C, and sometimes remained above 60°C for up to five consecutive hours during the day. Air temperatures at the same time were in the order of 45°C. Presumably it is this extreme heating of the soil surface which creates the higher than average temperatures below ground.

Launay (1989) working at La Fauqa, Haute-Garrone, France, found that burrow temperatures at 1 m depth were about 1°C higher than average air temperatures during the year. His data also suggest that burrow temperature fluctuations lag some time behind air temperature fluctuations. This observation is in accord with the discrepancy noted earlier between peak soil temperatures and the seasonal peak in average air temperature.

Microclimate and Flea Survival

The data gathered on the temperature and humidity of burrow air at each site are of great importance in establishing the range of conditions to which fleas are likely to be subjected in the field. They provide the basis for comparisons with the results of laboratory experiments to test the tolerance of the fleas to warm, dry conditions.

As mentioned earlier, newly hatched rabbit flea larvae cannot tolerate relative humidities of less than 70%, and if burrow air contains less water than this the water loss from nestling rabbits may not add sufficient humidity to the air in the nesting chamber to enable the flea larvae to persist. The flea larvae develop most successfully if the humidity is between 80 and 90% RH.

On this basis it can be seen from Figs 2a and 2b that at sites like Koonamore, Balcanoona and Moolawatana, the humidity of the air in deep burrows probably rose above 70% RH only briefly during the winter or spring months, and at no stage could it be said that the air within burrows would have presented optimum humidities for the development of the flea larvae over extended periods. By contrast, at the other sites, where fleas persist, the relative humidity of burrow air should have been well above 70% throughout the winter and spring at least. Such data fit the idea of Andrewartha (1961) that one important resource for animal populations is time—in the sense that conditions must remain favourable for sufficient time for animals to reproduce effectively.

For example, fleas need time to accumulate on the female rabbits at the start of the breeding season, and those fleas which have persisted through summer as quiescent pupae in disused rabbits' nests are likely to begin breeding bit by bit over several months as rabbits progressively revisit old nest sites and clean them out, causing the new adult fleas to emerge.

In addition, it is quite likely that, once breeding has begun, fleas which develop sufficiently rapidly to leave the nest with the newly weaned young rabbits have a chance of producing further generations each year. However, in considering this possibility, it must be remembered that the development of fleas from eggs to adults takes 3 weeks at least, and the first generation of fleas must then spend a further 7-10 days on a pregnant rabbit to reach full sexual maturity. Consequently, it is most unlikely that many individuals from an initial generation of fleas would be ready to breed before female rabbits began producing their second litters 28 days after the first. Nevertheless, the fleas could produce a substantial second generation if the rabbits bred a third time.

On this basis it is apparent that a short breeding season would prevent the fleas from reaching their full reproductive potential. It can be argued further that the humidity of rabbit warrens would need to remain high (i.e. more than 70% RH and preferably between 80 and 90% RH) for at least 3 months for the fleas to produce substantially more than one generation each year.

In support of this, evidence from Witchitie and Moolawatana (Cooke 1984) suggests that fleas died out in those years when the rabbits bred only briefly. It is also worth reiterating that at those sites where fleas persisted during 1984-85 the humidity of deep burrows would have been in excess of 70% RH for at least 5 months during the winter and spring. At all other sites the humidity exceeded 70% for only 2 or 3 months at most.
With respect to adult fleas, the observations of Williams (1971) and the analysis of data of Allan (1956) by Muirhead-Thompson (1968) provide good evidence that rabbit fleas spend some time off the host living free in the rabbit burrows during the summer months. In southern France, Launay (1980) collected free-living *Spilopsyllus* from burrows during summer, usually within 1 m of the burrow entrance.

It therefore follows that if burrow air was hot and dry during midsummer it would adversely affect the survival of free-living, adult rabbit fleas. To illustrate the magnitude of the expected reduction in survival, data from Cooke and Skewes (1988) were used to derive a relationship between the survival time (days) of unfed fleas, temperature ($T$ in degrees Celsius) and saturation deficit ($SD$ in millimetres of mercury). This relationship, valid for temperatures around 20-30°C, was: \[ \ln(\text{survival time}) = 3.189 - 0.038T - 0.047SD. \]

Data collected at the end of the summer of 1984–85 were used in this formula to calculate the survival times given at Table 3. In general, the summertime microclimates of the warrens are least severe at sites where fleas survived.

### Table 3. Summer burrow temperatures, humidities and saturation deficits at the end of summer at seven experimental sites, and the estimated mean survival times of unfed, free-living fleas under such conditions

<table>
<thead>
<tr>
<th>Site</th>
<th>Temperature ($^\circ$C)</th>
<th>Relative humidity (%)</th>
<th>Saturation deficit (mm Hg)</th>
<th>Survival time (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oraparinna*</td>
<td>26</td>
<td>38</td>
<td>15.6</td>
<td>4.4</td>
</tr>
<tr>
<td>Belton*</td>
<td>24</td>
<td>85</td>
<td>3.4</td>
<td>4.4</td>
</tr>
<tr>
<td>Witchitie*</td>
<td>28</td>
<td>32</td>
<td>19.3</td>
<td>3.4</td>
</tr>
<tr>
<td>Koonamore</td>
<td>27</td>
<td>29</td>
<td>19.0</td>
<td>3.6</td>
</tr>
<tr>
<td>Angepena*</td>
<td>25</td>
<td>47</td>
<td>12.6</td>
<td>5.3</td>
</tr>
<tr>
<td>Balcanoona</td>
<td>28</td>
<td>35</td>
<td>18.4</td>
<td>3.6</td>
</tr>
<tr>
<td>Moolawatana</td>
<td>31</td>
<td>24</td>
<td>24.4</td>
<td>2.4</td>
</tr>
</tbody>
</table>

However, the data given in Table 3 tend to over-emphasise the problems which adult fleas would encounter. Cooke and Skewes (1988) have shown that those fleas which are able to feed on rabbits survive longer than unfed ones, even though this effect becomes less marked as temperatures increase. Clearly, survival would depend on how frequently the fleas were able to feed. Further, the temperature profile of the soil at each site suggests that fleas which left rabbits and lived in the burrows might gain considerable advantage by remaining in the cool humid parts of the burrows near the soil surface during the early part of the day, then moving deeper as the surface soil warmed. At night they could return to the burrows near the surface once the soil had cooled down.

At present it is not possible to say whether the limits to the distribution of *Spilopsyllus* are set predominantly by the effects of low humidity on the larval stages or on the adults. Yet it would seem that the period favourable for the increase of fleas is of great importance. If only a short time was available for fleas to breed each year, then maintaining a population would be doubly difficult; not only would recruitment into the population be low but the length of time until the next breeding season would also be prolonged. Even ignoring the risk that dry burrows pose for adult fleas, the chance of a small population surviving would be greatly reduced by the element of time alone.

To summarise: the observations give some insight into the mechanisms underlying the previously noted interrelation between climate and the distribution of *Spilopsyllus* in arid Australia; it was only in those sites where the relative humidity of the burrows remained high during winter and spring, that fleas generally persisted.

Burrow microclimate, particularly low humidity, appears to be a major factor limiting the distribution of *Spilopsyllus* in inland Australia. The data provide some empirical support for the contention of Holland (1979) and Marshall (1981) that, in general, the microclimate
of the host's nest (including burrows) is likely to be of critical importance in determining the distribution of many species of fleas.

Acknowledgments

I should like to thank Dr R. P. Henzell for assistance with the analysis of data on burrow microclimates and for helpful criticism of the manuscript. I should also thank Mr B. D. Sutton for assistance in the field and the construction and testing of the hygrometer. Mr P. L. Bird was also involved with field work and Ms F. W. Bartholomaeus drew the figures. This project was supported in part by funds from the Australian Meat and Livestock Research and Development Corporation as part of a project to find vectors of myxomatosis suitable for use in inland Australia.

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