SOME RECENT ADVANCES IN THE EPIDEMIOLOGY AND
CONTROL OF HELMINTH INFECTION IN SHEEP

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Summary

Recent studies on the free-living stages of gastro-intestinal worm parasites of sheep show that their rates of development to the infective stage is slower and the mortality of infective larvae in pastures is lower than was believed hitherto. This, together with findings on the natural regulation of worm populations in sheep, suggests that worm burdens do not increase through a rapid succession of generations. Therefore, the concentration of free-living stages in pastures when susceptible animals begin to graze or at the beginning of periods favourable for parasite replication will have an important influence on the ultimate size of the worm burden. These concepts are exemplified by control measures for strictly winter-rainfall regions, based on drenching during the hot, dry summer when larval availability in pastures is very low. In accordance with the same principles, it is likely that practices adopted at weaning will be much more important in preventing production losses due to parasitism in young sheep than drenching ewes at lambing time. Preliminary findings suggest that drenching lambs at weaning and moving them to clean grazing can provide prolonged protection from parasitic disease independently of weather favourable for parasite transmission.

1. INTRODUCTION

At present, the Australian sheep industry depends almost solely on the regular use of anthelmintics to control gastro-intestinal worm parasite infection with species in the genera *Haemonchus*, *Ostertagia*, *Trichostrongylus*, *Nematodirus*, *Oesophagostomum* and *Chabertia*. The concept of strategic drenching, which involved giving drenches on a number of occasions through the year at specified times, was introduced some 25 years ago. Simple grazing management practices, limited largely to short-term pasture spelling and rotational grazing, were also advocated as aids to control. This approach is essentially a preventive one with drenches directed chiefly at limiting pasture contamination with worm eggs and only secondarily at the removal of damaging or potentially damaging worm burdens present in the animal (Gordon 1948), although Brunsdon (1967) remarked that the former aspect is almost invariably neglected in the application of anthelmintic treatment.

Earlier control programmes were based on the prevailing view that the free-living stages did not survive long in pastures and, therefore, that any interruption to pasture contamination produced by drenching or spelling would be followed quickly by a reduction in pasture infectivity. In recent years, a number of studies in a variety of environments has shown that the free-living stages are capable of much longer survival than had been believed, and the value of spelling pastures for periods less than about eight weeks has been generally discredited (Donald 1969), although this might have been inferred from the comprehensive studies of Kates (1950). The unreliability of short-term pasture spelling has tended to imply a greater reliance on drenching, but this will not always be effective in a preventive sense if pastures remain infected for long enough to reinfect susceptible sheep. Misgivings have been expressed concerning the efficacy of strategic drenching to the extent that drenching

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when symptoms first appear has been proposed as an alternative (Cole 1967). However, any failure of control measures based on incomplete epidemiological knowledge does not invalidate the view that preventive control, directed towards limiting the rate of infection from pastures, is both possible and desirable.

II. NATURAL REGULATION OF PARASITE POPULATIONS

(a) Free-living Stages in Pastures

The number of parasite generations that occur in a year is much less than the theoretical maximum (Michel 1969), upon which much earlier thinking was based. Not only can infective larvae survive in pastures much longer than was thought, but the time required for eggs deposited in faeces to reach the infective larval stage and migrate to the herbage varies greatly with seasonal weather, and is usually more prolonged than was believed.

Several studies, both in Australia and overseas, have revealed that infective larvae developing from eggs deposited in autumn show prolonged survival through the winter (Gibson and Everett 1967, 1972a; Donald 1968; Boag and Thomas 1970; Donald and Waller 1973), and can be present in substantial numbers in early spring, although their rate of death accelerates as temperatures rise. For some genera, e.g. *Ostertagia* and *Trichostrongylus*, development is possible in winter, especially where winters are mild, but the proportion of eggs surviving to reach the infective stage is less and their rate of development is slower than for eggs deposited in autumn (Donald 1968; Gibson and Everett 1972a). Autumn contamination of pastures is likely, therefore, to be an important source of larval availability throughout the winter, especially if rates of egg output by grazing sheep tend to be lower in winter than in autumn (James and Johnstone 1967; Anderson 1972). On the other hand, provided that moisture is not severely limiting, the rising temperatures of spring tend to result in a sharp increase in infective larval numbers on pasture resulting from the coincident completion of development of eggs deposited over a period of several weeks (Michel 1969). This may coincide with or closely follow the rapid disappearance of over-wintered larvae (Donald and Waller 1973).

In hot dry summers, there are very few larvae available on pasture and little parasite transmission takes place, even when there are occasional heavy falls of rain in mid-summer (Parnell 1962; Anderson 1972). On summer-wet pastures, however, development of the free-living stages of all species can proceed relatively quickly, but even here some eggs deposited in summer do not reach the herbage as infective larvae for several weeks, and pastures may not become substantially free of infection for at least three months. This may be illustrated by some results from a recent study in Canberra (Axelsen, Donald, Donnelly, Morley and Waller unpublished).

Duplicate 0.4 ha *Phalaris* plots were grazed by naturally infected weaners at a stocking rate of 25/ha for 28-day periods in each of the months December 1970, January, February and March 1971. Before and after contamination, each plot was subjected to the same grazing pressure with weaners drenched fortnightly to prevent worm egg output. At intervals, pairs of worm-free "tracer" sheep were grazed on the plots for two weeks and subsequently slaughtered for total worm counts. Results for the two most important and abundant genera, *Ostertagia* and *Trichostrongylus*, are shown in Table 1.

December contaminated plots carried substantial numbers of larvae to the beginning of March, but were effectively "clean" by the end of April. On January and February contaminated plots the rate of decline of larval numbers was slower and maximum levels of larval availability on February plots were not recorded until the latter half of April. Although March plots were tested on two occasions only, very high levels of larval availability were recorded at the end of May despite lower
rainfall during the contamination period. Substantial numbers were still available on March plots in mid-winter.

**TABLE 1**

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<tr>
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</thead>
<tbody>
<tr>
<td>Rainfall (mm):</td>
<td>78</td>
<td>135</td>
<td>167</td>
<td>30</td>
</tr>
<tr>
<td>Parasite Genus:</td>
<td>O T</td>
<td>O T</td>
<td>O T</td>
<td>O T</td>
</tr>
<tr>
<td>Tracer Grazing Period</td>
<td>20/1/71-3/2/71</td>
<td>5000 5240</td>
<td>2460 1900</td>
<td></td>
</tr>
<tr>
<td></td>
<td>17/2/71-3/3/71</td>
<td>430 700</td>
<td>1820 2200</td>
<td></td>
</tr>
<tr>
<td></td>
<td>17/3/71-31/3/71</td>
<td>80 10</td>
<td>750 460</td>
<td></td>
</tr>
<tr>
<td></td>
<td>14/4/71-28/4/71</td>
<td>730 400</td>
<td>1390 3590</td>
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</table>

(b) Host Responses

With age and experience of infection, sheep develop a strong resistance to the establishment of infection at least with certain species, e.g. *Nematodirus* spp. and *Trichostrongylus* spp., which is generally sufficient to prevent the occurrence of clinical disease. Resistance to *Haemonchus contortus* and *Ostertagia* spp. tends to be more labile (Michel 1969). However, there is now good evidence not only that immune competence against helminth infection is slow to develop in sheep and is not fully expressed until about six to nine months of age, but also that exposure of lambs or weaners to heavy infection may impair their capacity to develop resistance (Manton et al. 1962; Ross 1970; Silverman, Mansfield and Scott 1970; Gibson and Parfitt 1972). This emphasizes the importance of preventing exposure of young sheep to heavy infection, and explains why drenching weaners without reducing exposure to reinfection can lead to the rapid re-establishment of worm burdens at least as great as those in undrenched animals (Boag and Thomas 1973). The immediately pre-parturient and the lactating ewe may also show increased susceptibility because there is a temporary relaxation of immunological control of worm infection which is directly associated with lactation (Connan 1968a; O’Sullivan and Donald 1970; Dineen and Kelly 1972). Although resistant adult sheep exposed to high levels of larval intake may show no signs of disease, substantial reductions in wool growth have been reported (Anderson 1972; Barger 1973; Barger, Southcott and Williams 1973). This represents a previously unsuspected penalty from grazing adult sheep on heavily infected pastures, and suggests that measures aimed at reducing the rate of infection might be beneficial in all classes of sheep.

Under certain conditions, the development of some worms acquired by sheep may be arrested at the early fourth larval stage for several months exerting little if any harmful effect, even when present in large numbers. The conditions which determine whether an infective larva enters the state of inhibition are not yet clearly understood, but it is associated predominantly with larvae acquired from pasture during winter (James and Johnstone 1967; Muller 1968; Connan 1971; Reid and Armour 1972). The phenomenon occurs in *H. contortus*, *Ostertagia* spp., *Trichostrongylus axei* and *Nematodirus* spp., but not in the intestinal *Trichostrongylus* spp. Its importance lies in the potential of inhibited larvae to resume development at a time relatively remote from the time of their acquisition from pasture. While the precise conditions stimulating resumption of development are also not known, simultaneous redevelopment of large numbers of *H. contortus* and *Ostertagia* spp. inhibited larvae can occur in the
lactating ewe (Connan 1968b; Procter and Gibbs 1968). Ostertagia spp. inhibited larvae acquired in winter have also resumed development in dry sheep during summer when larval intake was reduced to very low levels (Parnell 1962; James and Johnstone 1967), although this does not always occur (Anderson 1972).

(c) General Implications

It is now clear that worm burdens do not increase exponentially through a rapid succession of discrete generations, and therefore the initial level of larval availability on pasture to which susceptible animals are exposed has an important influence on the level of parasitism which they experience (Michel 1969). When susceptible young sheep are drenched and put to graze on pastures which are relatively clean (but not necessarily free of all infection), even at times when free-living parasitic development proceeds most actively, worm burdens are unlikely to increase to dangerous levels before weather and pasture conditions become less favourable for parasite transmission or host resistance begins to develop, or both. Conversely, a single drench given to infected sheep on infected pastures may have little, if any, effect on the level of larval availability and only a temporary effect on worm burdens. 

These concepts are exemplified by some recent studies on epidemiology and control.

III. EPIDEMIOLOGY AND CONTROL IN WINTER RAINFALL REGIONS

In Western Australia, Parnell (1962) showed that worm burdens in spring-born lambs weaned in December were very much lower during the summer than those in autumn-born lambs weaned in August. This resulted from a decline in larval availability in late spring and the almost complete absence of larval intake during the hot, dry summer. He first advocated drenching in late spring or early summer to remove both immature and adult worms before the main period of nutritional stress, and when reinfection rates would be low. This, together with studies by Gardiner and Craig (1961) and Gardiner and Butler (1964), led to the general recommendation for Western Australia by Butler (1967) to drench weaners and two-tooths in early summer. He mentioned the additional benefit that pastures would not be heavily contaminated at the time of the autumn break, and suggested that because of post-drenching reinfection, pre-lambing drenching of ewes due to lamb in winter or spring would be of doubtful value, proposing instead that ewes be drenched in summer. Anderson (1972, 1973) has described the natural history of worm infection in sheep in Western Victoria, and has confirmed that larval availability on pasture is high from June to October but falls to very low levels during summer. He has also demonstrated the lack of effect on animal performance of frequent drenching during winter when reinfection rates are high, whereas sheep drenched in summer after larval availability on pasture had fallen to low levels showed greater liveweight gains and grew more wool than undrenched animals. Moreover, two drenches given in October and January respectively, resulted in at least a ten-fold reduction in the rate of pasture contamination with worm eggs.

For regions with reliable hot, dry summers, Anderson (1973) has proposed drenching all sheep twice only during summer, with the primary object of preventing pasture contamination over an extended period. If the numbers both of worms in sheep and of free-living stages on pasture are very few at the time of the autumn break, then worm burdens are unlikely to reach high levels over the following winter and spring. This control programme is being evaluated experimentally in a large sheep enterprise in western Victoria and although rainfall has been above average in two of three summers, it has resulted in substantial increases in sheep production and economic returns to the producer (Anderson, personal communication). This represents a successful example of strategic drenching as originally proposed by Gordon (1948).

In areas with significant summer rainfall, the weather alone cannot be relied upon to produce clean pastures, and positive management action may be required. In these regions, therefore, optimum control programmes aimed at limiting rates of
infection might well vary from property to property. Nevertheless, at least for lambs and weaners, a better understanding of the epidemiology of infection is beginning to emerge, and this should influence the choice of control measures.

IV. EPIDEMIOLOGY AND CONTROL IN LAMBS AND WEANERS

(a) Sources of Infection

Where ewes lamb in spring on clean pastures, the sole source of infection for lambs is the post-parturient rise of worm egg output in ewes derived from previously acquired worms. Large numbers of infective larvae developing from these eggs are unlikely to become available on pasture much before lambs are eight to 12 weeks old, and liveweight gains of lambs to weaning at about 12 weeks have been little, if at all increased by drenching ewes before lambing (Heath and Michel 1969; Boag and Thomas 1971, 1973; Thomas and Boag 1972; Salisbury and Arundel 1970; Donald and Waller 1973). Nevertheless, to take full advantage of the initially clean pasture, it is highly desirable to drench ewes before movement onto the lambing paddock, as lambs can safely remain there after weaning. Worm burdens in lambs from ewes drenched before lambing on clean pasture have remained low throughout the summer, and no advantage was gained by either drenching or moving the lambs at weaning (Boag and Thomas 1973).

Where ewes have lambed in spring on pastures carrying residual over-wintered larvae, these have tended to negate the effects of a pre-lambing drench. In some instances, drenched ewes have, nevertheless, shown a rise in egg output after lambing resulting from post-drenching reinfection (Arundel and Ford 1969; O'Sullivan and Donald 1970; Arundel 1971). Even when this has not occurred, or when ewe egg output has been completely suppressed by fortnightly drenching, over-wintered larvae have infected lambs as soon as they began to graze. These early infections have not generally affected liveweight gains of suckling lambs. However, eggs produced by this first generation of worms in young lambs have substituted for ewe egg output as a source of pasture contamination, such that a second generation has resulted in disease in weaners which have continued to graze on the lambing paddock (Thomas and Boag 1972; Gibson and Everett 1972b; Donald and Waller 1973).

Where ewes lamb on contaminated pastures, time of lambing, weather and management will have important effects on the level of infection to which lambs will be exposed. However, the value of drenching ewes is doubtful both on epidemiological grounds and because, as Donnelly, McKinney and Morley (1972) have pointed out, apart from one year of a study by Leaning et al. (1970), a significant effect of ewe drenching on liveweight gain of lambs to 12 weeks of age has not been reported. It may be justified for ewes in a therapeutic sense, especially if they are in poor condition or are known to be heavily infected. It is possible, particularly in a late spring or early summer lambing, for young lambs to acquire heavy H. contortus infections from the rapid development of eggs deposited by their dams, although the findings of Southcott, George and Lewis (1972) in an H. contortus endemic area lend no particular support to this view. Where it is common for lambs to be weaned later than about 12 weeks, drenching ewes might have significant effects on lamb growth before weaning. However, in view of the fact that most ewes in Australia are unlike to be lambing on genuinely clean pastures, it is difficult to escape the conclusion that if lambs are weaned no later than about 12 weeks of age, then practices adopted in weaning are likely to be much more important than ewe drenching in preventing production loss due to parasitism.
(b) Effects of Drenching and Residual Pasture Infection at Weaning

Recent studies in Britain by Gibson and Everett (1968, 1971) and Boag and Thomas (1973) have shown that if lambs were drenched at weaning and moved to pastures not contaminated since the end of winter, worm burdens remained low and weight gains were excellent over the remainder of the summer and autumn. In 1971-72 an experiment was conducted at Canberra to examine the effects of drenching and pasture infection at weaning on the worm burdens and performance of weaners. Although this work will be reported in detail elsewhere (Axelsen, Donald, Donnelly, Morley and Waller, in preparation), some results are presented here.

The experiment was a $2^2$ factorial comparing drenching vs. no drenching at weaning in November 1971 with movement onto clean or infected pastures, in four replications. Two replicates were given a second drench in February 1972, converting the experiment into a $2^3$ factorial in two replications. Experimental units were 0.4 ha *Phalaris* plots stocked at 25/ha, reduced to 20/ha in February. All plots had been grazed with sheep intermittently at the same grazing pressure between August and November 1971, but those animals on plots destined to be 'clean' were drenched fortnightly to prevent contamination. Rainfall in September (37mm) and October (43mm) was poor, but it exceeded 76 mm in each of the months November, December and January. Estimates of pasture infectivity at the beginning of the experiment showed that 'clean' plots carried small residual populations of *Ostertagia* spp. and *Nematodirus* spp. larvae only. On "infected" plots there were more larvae of *Ostertagia* spp. but similar numbers of *Nematodirus* spp. larvae, compared to "clean" plots. In addition, the "infected" plots carried substantial numbers of *Trichostrongylus* spp. larvae but only very few of *H. contortus*. Two 'animals from each plot were slaughtered for worm counts in February 1972 just before the second drenching treatment. These results, together with counts from a sample of the lambs taken at weaning, are shown in Table 2.

<table>
<thead>
<tr>
<th>Parasite</th>
<th>Slaughtered at weaning 23/11/71</th>
<th>Slaughtered 2/2/72</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Infected pasture</td>
<td>Clean pasture</td>
</tr>
<tr>
<td><em>H. contortus</em></td>
<td>7</td>
<td>3071</td>
</tr>
<tr>
<td><em>Ostertagia</em> spp.</td>
<td>4042</td>
<td>8535</td>
</tr>
<tr>
<td><em>T. axei</em></td>
<td>3</td>
<td>1055</td>
</tr>
<tr>
<td><em>Trichostrongylus</em> spp.</td>
<td>717</td>
<td>3822</td>
</tr>
<tr>
<td><em>Nematodirus</em> spp.</td>
<td>1188</td>
<td>4635</td>
</tr>
</tbody>
</table>

In the undrenched groups, except for *T. axei*, there was no significant effect of pasture infection. However, in the drenched groups the relative abundance of species reflected the availability of larvae on clean and infected pastures at the beginning of the experiment with differences significant at least at the five per cent level for *Ostertagia* spp., *T. axei* and intestinal *Trichostrongylus* spp.

Prior to the second drenching treatment in February no sheep had died, but between February and April numerous deaths occurred, due predominantly to *H. contortus*. Their incidence with respect to treatments is shown in Table 3.
No deaths occurred in those weaners originally drenched onto clean pastures and
the second drench obviously had no effect. Moreover, the February drench did not
prevent deaths amongst animals which were not drenched at weaning in
*November*, and grazed on infected pastures. However, in those groups drenched onto infected pastures or
not drenched onto clean pastures in November, the February drench had an effect just
significant at the five per cent level. Although in the conditions of this experi-
ence: the drench at weaning was more important than the level of pasture infection,
drenching onto clean pasture at weaning provided complete protection from parasitic
disease throughout a wet summer without the need for any further measures.

The concept of combining drenching with movement to clean pastures is not new.
However, the criteria on which pastures can be judged to be effectively clean and the
measures required to produce them have been undefined, and are still far from certain
Moreover, the role of residual pasture infection at weaning has received little
attention until quite recently and more studies are needed. If clean grazing at
weaning can be shown to result in prolonged protection from losses due to parasitism
in weaners independently of the weather, this would constitute a strong incentive to
provide it. However, the benefits would need to be measured against the
practicability and costs of providing clean grazing relativeto the alternative of
more frequent drenching. In some conditions of weather and management, the grazing
provided at weaning may be effectively clean anyway., particularly, for example, where
lucerne aftermath or root or forage crops are used. For permanent grassland,
pastures not contaminated by sheep after the end of July are likely to be substantial:
free of infection by the end of October (Donald and Waller 1973), but spelling over
this period is clearly impracticable except where pastures are cut for hay.
Alternate grazing with cattle is a promising technique (Southcott and Barger 1973) and
is under investigation at the moment.

V. REFERENCES

BRUNSDON, R.V. (1967). In "Parasitism, anthelmintics production", Symposium of the Australian Society of Animal Production


