Breeding for Resistance to Infectious Diseases in Small Ruminants

G.D. Gray, R.R. Woolaston
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Preface

This collection of papers represents a broad overview of an approach to controlling livestock disease which has been under consideration for over half a century but which has, in recent times, attracted renewed interest. In theory at least, animals bred for resistance to one or more diseases do not incur any costs associated with chemical treatment or prevention and the associated risks of toxicity and contamination of animal products. Likewise there is no risk that therapeutic chemicals can damage the ecosystem of which the livestock are part. Neither is there any risk of developing resistance to chemicals, already widespread in helminths and bacteria.

On the other hand, breeding is a relatively slow process, much slower than the introduction of a new chemical or drug. It is difficult to implement in many production systems and only now are we acquiring enough information to design breeding programs with predictable consequences.

Each chapter in this volume represents a different geographical viewpoint (allocated roughly on a continental basis), biological approach (from molecular genetics to immunology) or group of pathogens (from viruses to arthropods). ACIAR's objective in bringing together these approaches is to review the topic in a single volume, provide a basis for potential new collaborative research projects and a tool for animal health and production planners to assess the potential of genetic approaches to disease control. It is not a complete picture, but we hope that the papers and the literature cited by their authors will provide comprehensive access to the field.

We, as editors, and ACIAR, particularly John Copland of the Animal Sciences Program and Peter Lynch of the Communications Unit, would like to thank all who contributed their time, enthusiasm, thought, imagination and insight which is evident in these papers. All the papers in this volume have been reviewed by referees whose efforts are much appreciated.

Measuring the success of a publication is never easy but one outcome that would particularly please authors, referees, editors and ACIAR would be the generation of further international collaborative efforts to explore and utilise genetic variation for improved, sustainable livestock production. That has already happened among those who have contributed to this monograph and we sincerely hope such collaboration continues among its readership.

Final thanks are due to Jan Jopson and Dallas Blakely for their contribution to this project.

G.D. Gray R.R. Woolaston B.T. Eaton

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G.D. GRAY

ABSTRACT

Evidence for genetic variation to parasites has been found both within, and between, host populations and for a number of important parasite species including nematode worms, coccidian protozoa, flies and ticks. For this genetic variation to be exploited successfully, the requirements of livestock farmers must be identified clearly and an appropriate breeding objective established. The consequences of breeding for parasite resistance need also to be assessed for resistance to diseases that are not the subject of selection, and productivity in terms of cash, investment security, social and religious characteristics, and avoidence of risks such as the development of resistance to drugs used for disease control. The concepts of resistance and resilience can be more clearly defined in terms of the criteria used for selection, the breeding objective and the environment in which the selection takes place. 'Environment' in this context should include nutritional status, exposure to disease, age and immune status as well as usual features such as temperature, humidity and rainfall.

There is ample evidence from studies on humans, domestic livestock and experimental animals for genetic variation in resistance to internal and external parasites, both within and between populations. We are, however, almost completely ignorant of the nature of the genes that confer resistance to diseases caused by parasites. As we start to exploit genetic variation to improve resistance to parasites and reduce their impact on small ruminant production a major question arises. Can we, knowing so little about the genetic basis of resistance, predict the outcome of breeding programs? The answer to that question is a qualified 'yes'.

Genetic variation to parasitism must be viewed in the context of successful breeding programs for other production traits. The criteria for inclusion of a trait in a breeding program—being heritable, variable and able to be measured—are met by resistance to several diseases of small ruminants. The prospects for breeding for resistance are therefore very good. But this interaction of host and parasite should also be seen in an evolutionary context. Host and parasites have evolved together and we should certainly not be complacent that parasites will not adapt to genetic changes in the host imposed by breeding programs. There is no evidence (Woolaston and Eady, this volume) that suggests this can happen but it is worthwhile to be reminded that genetic adaptation by the parasite, genetic resistance to anthelmintics, has stimulated much of the research on breeding approaches to parasite control.

There have been a number of comprehensive reviews of genetic variation in host response to parasites (Chandler 1932; Wakelin 1988, 1989; Dargie 1982; Mitchell 1979; Albright and Albright 1984; Grencis 1990). In this paper more practical aspects of breeding for resistance to parasites will be addressed.

Genetic Differences Between Hosts

Between species

One option for increasing resistance to parasites is to select other livestock species that may meet the commercial objectives of the farmer, for example replacing goats with sheep, sheep with cattle, pigs with chickens, or even mixing species that can be husbanded together. Host specificity of parasites can make this an attractive option and strategies have been developed in which cattle and sheep are grazed alternately with the purpose of controlling sheep parasites that do not survive in cattle (Barger 1978; Reinecke and Louw 1991). There may be many social and practical reasons to restrict the choice of livestock species but it is one option that should always be considered.

Intraspecific variation

Evidence acquired in the last 40 years has shown clearly that a significant proportion of intraspecific variation is genetically determined. An early example of simple genetic control of variation was demonstrated in *Plasmodium falciparum* infections of humans. Allison (1954) established that the abnormal haemoglobin S, determined by a single gene locus, confers resistance to falciparum malaria and this, in turn, ensures that this harmful allele is maintained in populations affected by malaria. Such simple allelic variation has been difficult to find in other host–parasite systems although there has been considerable interest in the association of the major histocompatability complex and resistance to disease in many species. Immune response is certainly implicated in the genetic resistance of sheep to worm infections (Gray and Gill 1993)—and lines of sheep successfully selected, on the basis of the response to vaccination against *Trichostrongylus colubriformis* (Windon 1990), provide further evidence that there is genetic variation in the hosts' ability to respond to vaccination as well as to infection. The possible role of the MHC in resistance to nematode infections is discussed by Blattman and Beh (this volume).

There are some good examples among small ruminants where knowledge of the breed has predictive value for resistance to parasitic infection. Such resistant sheep breeds include the Red Maasai, Florida Native and St Croix.

In large ruminants it has been shown repeatedly that N'dama and West African Shorthorn cattle are more resistant than other breeds to the effects of trypanosomes (Trail et al. 1991) and *Bos indicus* more resistant to tick infestation (Utech et al. 1978, de Castro 1991).

To obtain accurate estimates of the genetic component of variation within populations it is usually necessary to perform large experiments. For sheep this may involve measuring more than a thousand offspring of more than 50 sires. In almost all cases where genetic variation has been sought it has been found. For nematode infections of sheep, the proportion of variation that can be attributed to genetic effects (heritability) varies between 0.2 and 0.4 (Woolaston et al. 1991). At such levels there are prospects for selective breeding for improved resistance (Gray 1991).

Consequences of Breeding Nematode-resistant Sheep

Resistance to other parasites

When sheep are selected on the basis of resistance to one parasite it is important to assess if resistance extends to other related parasites of importance. Experiments on a number of selection lines indicate that this is the case. One such experiment (Fig. 1) determined that sheep bred for resistance to one parasite (*H. contortus)* were resistant to at least one other nematode (*Trichostrongylus* sp.). Further, the resistance was expressed when the lambs remained undrenched or were drenched according to local recommendations. The design of this experiment was to graze resistant lambs on the same pasture for the entire experiment—random-bred lambs grazed separate pastures. To avoid confounding genetic background with the effect of the pasture *per se* on resistance it was necessary to replicate each genotype-pasture combination. In this experiment there were three replicates of each genotype–drench regime combination resulting in a total of 12 separate pastures being used. Full details are given in Gray et al. (1992).

Responses to vaccination against other diseases

Merino lambs are routinely vaccinated against 5 species of clostridial disease using a multivalent vaccine. Antibody response to the *Clostridium tetani* component were measured over two years in lambs from lines of sheep selected for resistance to *Haemonchus*. In neither year was there any difference between the selection lines (Table 1). This response to vaccine does not necessarily correspond to resistance to clostridial disease but certainly indicates that there has not been a marked correlated response which may impair the effectiveness of vaccination in lambs selected for resistance to worms.

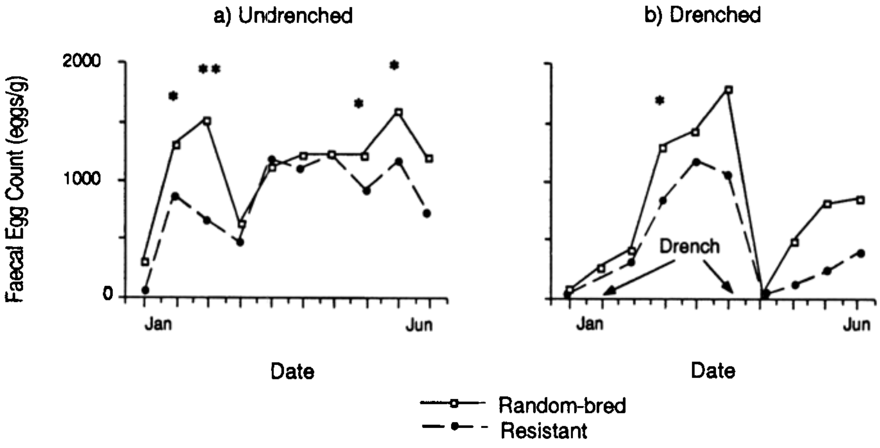

Figure 1 Mean faecal worm egg counts of 4 groups of 30 lambs which were grazed from weaning until nine months of age on pasture contaminated with larvae of *Haemonchus contortus*, *Trichostrongylus colubriformis* and *Ostertagia circumcincta*. Lambs were sired by either a genetically resistant ram or random-bred rams (determined by the response of previous progeny to artificial *H. contortus* infection). Half the resistant and half the susceptible lambs were given strategic anthelmintic treatment and the remainder remained untreated. The dominant species in all faecal samples and in worm counts (not shown) was *T. colubriformis*. These genetic differences were maintained while the lambs were subject to strategic anthelmintic treatment (Gray et al. 1992).

Defining the host response to parasitism

In the mosaic of diseases, environments and host breeds and species referred to in this monograph, a number of terms are used that have proved extremely useful in describing the interaction of infectious organisms with their hosts. These are *resistance*, *susceptibility*, *resilience* and *tolerance*. These are brief definitions:

Resistance. The ability of a host to reduce the number of parasites that establish, reproduce or survive.

Susceptibility. The inverse of resistance. A host with higher resistance is, by definition, less susceptible.

Tolerance. The ability of a host to thrive in the presence of parasites. This term has been widely used for trypanosome infections.

Table 1 Mean (±SEM) serum antibody levels (Ab Units) of lambs vaccinated with a commercial vaccine against *Cl. tetani*. Serum samples were collected two weeks after the second vaccination in 1988 (Year 1) or 1989 (Year 2). (n= number of animals.)

Year	Resistant (n)	Random (n)	Susceptible (n)
	280±40 (101)	400±40 (63)	340±50 (108)
2	170±30 (24)	200±20 (37)	180±30 (14)

Resilience. The same as tolerance, but first coined to avoid confusion with immunological tolerance. This term has been used mostly to describe sheep that perform well in the face of large worm burdens.

Essentially, therefore, we have two concepts: resistance/susceptibility which is a measure of the hosts effect on the parasite, and resilience/tolerance which is the ability of the host to perform despite the presence of the parasite. Are these in conflict? Is it possible to breed for both? Before considering these questions it is worthwhile to consider the possible outcomes of a breeding program that includes any disease.

Resistance and resilience as selection criteria and breeding objectives

Strictly, neither resistance nor resilience can be measured: they have no units. In the real world the traits that could be included in a breeding objective are those that can be quantified, such as weight of potential breeding animals at one-year old (HW), fleece weight (FW), wool fibre diameter (FD), and faecal worm egg count (FEC), in wormy and non-wormy environments (Table 2).

The benefits of selection for resistance (FEC) alone will accrue from the phenotypic effects of fewer worms, including a lower impact on production, fewer drenches being needed for their control and reduced contamination of pasture. Other genetic effects will depend on the sign and magnitude of the genetic correlation between FEC and other traits in the breeding objective.

The benefits of selecting for resilience are that production is being measured directly and improvement is not dependent on favourable genetic relationship with FEC. There may not be phenotypic benefits from having fewer worms.

The benefits of any of these approaches depend on knowledge of the phenotypic and genetic relationship between all the traits in the objective and the traits used as selection criteria. The choice of which traits to use is

Table 2 **Combinations of traits in hypothetical breeding objectives in wormy and non-wormy environments.**

HW	FW	FD	FEC	Nature of Environment	This breeding objective could be defined as:
				Wormy	Resistance
				Wormy	Resilience
				Non-wormy	Increased production
				Wormy	Resistance and resilience

much more important than the choice between the two concepts of resistance and resilience, which, when the hard decisions have to be made, become redundant.

Increased 'usefulness': the favourable outcome of a breeding program

Small ruminants are kept for many purposes, only one of which is to increase short-term profitability of a cash-based enterprise. Other reasons include security and mobility of assets, social integration and religious festivals (Orskov and Viglizzo 1994). It is conventional to assign economic weights to traits in a breeding objective and so quantify success in dollar terms. Clearly, that is not always appropriate and, for each enterprise or production system, it is necessary to fully define a favourable outcome. With that definition, it is then possible to work back and define what characteristics of the animals (the breeding objective) will produce that favourable outcome and, in turn, decide what can be best measured (selection criteria) in order to achieve that objective. Figure 2 illustrates such a scheme.

Another way of approaching this concept is to consider the objectives and strategies of modern worm control programs. Extrapolation of results from parasitological experiments on artificially infected animals to the field is difficult because of the nature of the helminth–pasture–sheep interaction. In pens, independent observations are made on single animals and statistical inferences, for example on the effectiveness of a drug, are based on a number of degrees of freedom which approaches the total number of animals in the experiment. In the field, however, measurements on individual animals are not independent: sheep contaminate pasture, pastures infect sheep and the level of infection in one animal is partly dependent on the level of infection of its grazing mates.

The solution to the problem in field experiments (Gill 1990) is to replicate groups of animals on their own pasture. Each treatment within the experiment then has two or more replicated groups, not individuals, allocated to it.

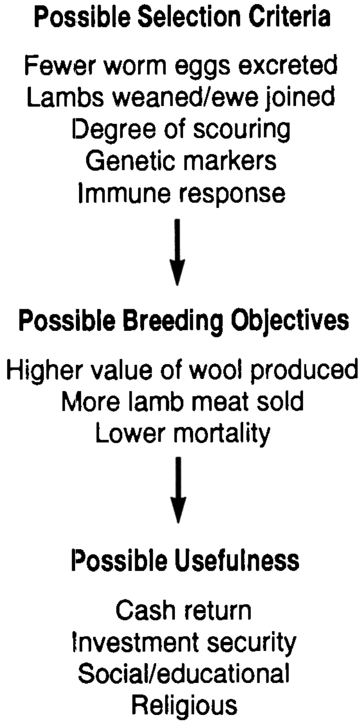

Figure 2 The relationship between possible selection criteria, breeding objectives and the overall usefulness of small ruminants to humans.

The statistical analysis is then performed with degrees of freedom approaching the total number of groups in the experiment, not the total number of individuals.

Modern methods of strategic worm control are based on a similar philosophy: chemical control and other measures are applied with the intention of reducing the numbers of parasites circulating in a grazing flock. This is commonly expressed as 'reducing pasture contamination' and is the cornerstone of the 'flock health' approach to worm control.

This therefore is the object of a chemical control strategy. Even though drenches are applied to individual sheep according to their requirements (age, body weight, physiological state), it is the intention to 'treat' the 'flock–pasture' system. Likewise with a breeding program: the 'breeding objective' applies to characteristics of individual sheep in which we want 'reduced FEC' or increased resistance, but that is only one component of the overall objective of the sheep enterprise. For this reason it is useful to consider several important levels of intent in the breeding process:

1. The farming objective of increased usefulness—in this case, better worm control or reduced pasture contamination.
2. The breeding objective—the qualities we would like the animals to have, for example, greater resistance or productivity.
3. The selection criteria by which these animals are chosen for breeding: faecal worm egg count or other trait that can be measured readily.

It is important to stress that the selection criteria may or may not be the characteristics which are in the breeding objective.

Strategies for increasing resistance and production

Breeding for resistance to parasites cannot take place in isolation. It must relate to and, if possible, be integrated into the breeding objectives of the small ruminant enterprise. In addition, it must be seen as a component of ongoing parasite control programs, and not seen as a replacement for them.

It is unlikely that a breeding program would have resistance to parasites as its sole objective. More likely the objective would be expressed in units of production or in the value of production. Therefore, genetic relationships with other traits in the objective, for example liveweight gain, fleece weight or resistance to other diseases and the economic weights of all the traits in the objective, may be as important as those of resistance itself.

Similarly the usefulness of resistant breeds depends on commercial requirements of the producer. If resistant sheep breeds are better producers of meat or wool than breeds in current use, then a change to the resistant breed may be advantageous. Comparison of the resistant Red Maasai breed with the susceptible Dorper breed in Kenya has shown that the Red Maasai are just as productive as the Dorpers (Baker et al. 1993). Not all such comparisons favour the resistant breeds but detailed studies of the breed productivity, including reproductive, survival and production characteristics, all measured in a realistic commercial environment are required. It should be noted that not all reports of resistant breeds take into account between-sire differences, and the perceived breed difference may really be due to the effects of a few resistant sires. In addition to their potential as productive replacements for existing breeds, these parasite-resistant genotypes are of extreme interest for investigating the genetic basis for resistance and how resistance genes may be expressed.

Selection within breed has not resulted in any association with loss of production (Albers et al. 1987; Windon and Dineen 1984; Woolaston et al.

1990). It has, however, been suggested that selection for resistant animals actually results in increased or no loss of production (Albers et al. 1987; Baker et al. 1993). Piper and Barger (1988) using the best-available genetic correlations between parasite resistance and production traits estimated that the rate of genetic gain would increase by about 10% for a typical Merino flock. However, it should be emphasised that marginal economic gains are not nearly as important as those from preventing devastating losses due to anthelmintic resistance in the parasite population.

References

Albers, G.A.A., Gray, G.D., Piper, L.R., Barker, J.S.F., LeJambre, L.F. and Barger, I.A. 1987. The genetics of resistance and resilience to *Haemonchus contortus* infection in young Merino sheep. International Journal for Parasitology, 17, 1355–1363.

Albright, J.F. and Albright, J.W. 1984. Natural resistance to animal parasites. Contemporary Topics in Immunobiology, 16, 1–51.

Allison, A.C. 1954. Protection afforded by sickle cell trait against subtertian malaria. British Medical Journal, 1, 290–294.

Baker, R.L., Reynolds, L., Mwamachi, D.M., Audho, J.O., Magadi, M. and Miller, J.E. 1993. Genetic resistance to gastrointestinal parasites in Dorper and Red Maasai × Dorper lambs in coastal Kenya. Proceedings of the 11th Scientific Workshop of the Small Ruminant Collaborative Research Support Program (SR - CRSP), 3–4 March 1993, Nairobi, Kenya, 228–241.

Barger. I.A. 1978. Grazing management and control of parasites of sheep. In: Donald, A.D., Southcott, W.H. and Dineen, J.K. ed., Epidemiology and control of gastrointestinal parasites of sheep in Australia. Melbourne, CSIRO Division of Animal Health, 53–63.

Chandler, A.C. 1932. Susceptibility and resistance to helminthic infections. Journal of Parasitology, 18, 135–152.

Dargie, J.D. 1982. The influence of genetic factors on the resistance of ruminants to gastrointestinal nematode and trypanosome infestations. In: Owen, D.G. ed., Animal models in parasitology. London, MacMillan, 17–51.

de Castro, J.J. 1991. Resistance to Ixodid ticks in cattle with an assessment of its role in tick control in Africa. In: Owen, J.B. and Axford, R.F.E. ed., Breeding for diseases resistance in farm animals, Proceedings of an International Symposium, Bangor, Wales, Sept. 1990. Wallingford, U.K., CAB International, pp. 244–262.

Gill, J.L. 1990. Uses and abuses of statistical methods in research in parasitology. Veterinary Parasitology, 36, 189–209.

Gray, G.D. 1991. Breeding for resistance to trichostrongyle nematodes in sheep. In: Owen, J.B. and Axford, R.F.E. ed., Breeding for diseases resistance in farm animals, Proceedings of an International Symposium, Bangor, Wales, Sept. 1990. Wallingford, U.K., CAB International, 100–125.

Gray, G.D. and Gill H.S. 1993. Host genes, parasites and parasitic infections. International Journal for Parasitology, 23, 485–494.

Gray, G.D., Barger, I.A., LeJambre, L.F. and Douch, P.G.C. 1992. Parasitological and immunological responses of genetically resistant Merino sheep on pastures contaminated with parasitic nematodes. International Journal for Parasitology 22, 417–425.

Grencis, R.K. 1990. Genetically determined variation in host response and susceptibility to pathological damage. In: Behnke, J.M. ed., Parasites: immunity and pathology. London, Taylor and Francis, 120–145.

Mitchell, G.F. 1979. Responses to infection with metazoan and protozoan parasites in mice. Advances in Immunology, 28, 451–511.

Orskov, E.R. and Viglizzo, E.F. 1994. The role of animals and spreading risks and other non-economic functions: a new paradigm for animal science. In: Sustainable animal production and the environment, Proceedings of the 7th AAAP Animal Science Congress, Bali, Indonesia, 125–142.

Piper, L.R. and Barger, I. A. 1988. Resistance to gastro-intestinal strongyles: feasibility of a breeding programme. Proceedings of the 3rd World Congress on Sheep and Beef Cattle Breeding, Paris. 2, 593–611.

Reinecke, R.K. and Louw, J.P. 1991. Disinfestation of irrigated sheep pasture by alternating grazing with cattle. Journal of the South African Veterinary Association. 62, 156–157.

Trail, J.C.M., d'Ieteren, G.D.M. and Murray, M. 1991. Practical aspects of developing resistance to trypanosomiasis. In: Owen, J.B. and Axford, R.F.E. ed., Breeding for diseases resistance in farm animals, Proceedings of an International Symposium, Bangor, Wales, Sept. 1990. Wallingford, UK, CAB International, 224–243.

Utech, K.B.W., Wharton, R.H. and Kerr, J.D. 1978. Resistance to *Boophilus microplus* (Canestrini) in different breeds of cattle. Australian Journal of Agricultural Research 29, 885–895.

Wakelin, D. 1988 Helminth infections. In: Wakelin, D. and Blackwell, J.M. ed., Genetics of resistance to bacterial and parasitic infection. London, Taylor and Francis, 153–224.

——1989. Nature and Nurture: Overcoming constraints on immunity. Parasitology, 99, S21–S35.

Windon, R.G. 1990. Revue Scientifique et Technique, Office International des Epizooties, 9, 555–576.

Windon, R.G. and Dineen, J.K. 1984. Parasitological and immunological competence of lambs selected for high and low responsiveness to vaccination with irradiated *Trichostrongylus colubriformis* larvae. In: Dineen, J.K. and Outteridge, P.W. ed., Immunogenetic approaches to the control of endoparasites. Melbourne, CSIRO, 13–28.

Woolaston, R.R., Barger, I.A. and Piper, L.R. 1990. Response to helminth infection of sheep selected for resistance to *Haemonchus contortus*. International Journal for Parasitology, 20, 1015–1018.

Woolaston R.R., Windon R.G. and Gray G.D. 1991. Genetic variation in resistance to internal parasites in Armidale experimental flocks. In: Breeding for disease resistance in sheep. Gray G.D. and Woolaston R.R. ed., Melbourne, Australian Wool Corporation.

Australian Research on Genetic Resistance to Nematode Parasites

R.R. WOOLASTON AND S.J. EADY

ABSTRACT

Australian research into quantitative genetic aspects of breeding for worm resistance is reviewed. Five selection experiments have each resulted in Merino lines with different levels of worm faecal egg counts (FEC). Heritability estimates for FEC in these lines have ranged between 0.21 and 0.47, depending on the worm species and number of counts recorded. Studies of 57 Merino bloodlines found that between-flock variation in resistance was biologically insignificant compared with within-flock genetic variation. Sheep with superior levels of resistance have not been found to be consistently more or less immunocompetent with respect to other diseases, indicating that resistance to nematodes has not been gained at the expense of resistance to other diseases. Between-age correlations in FEC appear to be positive and high, but further work is required before clear recommendations can be made about the best age to test for resistance. Methods for combining FEC and production data are discussed, as are the practicalities of breeding for resistance in the Australian Merino flock.

During recent years internal parasites of sheep have developed resistance to all of the main classes of anthelmintics. This is particularly the case for roundworms, in which drug resistance is now widespread throughout Australia (Overend et al. 1994). Strategic drenching programs have assisted in worm control, but parasites have continued to develop further anthelmintic resistance to the point where there are often very limited management options for their control. Instances of resistance to ivermectin have now been reported in two states of Australia, and this has led breeders and researchers to consider alternative control measures. Genetic variation in resistance of the Merino to worms has been the subject of research for some time in Australia and the purpose of this paper is to review some aspects of this research.

Resistance and Resilience

There has been much discussion amongst researchers and breeders as to whether it is preferable to improve resistance (the ability of animals to resist infection by parasites), or resilience (the ability of animals to maintain production during infection). Resistant animals should reduce the total number of worms in the production system, as resistant animals presumably harvest the same number of worm larvae from pastures, but pass out fewer eggs in their faeces than less resistant sheep. This in turn, should mean that pastures will be less contaminated, leading to a progressive reduction in pasture contamination each worm generation.

It has been argued however, that selecting resistant hosts poses a direct challenge to the parasites' existence and as parasites can adapt to threats from chemicals, they can probably also adapt to resistant hosts. If this is true, then worms, having a far higher reproduction rate than sheep and a much shorter generation interval, should have little trouble keeping ahead of genetic changes in their hosts. Resilience, on the other hand, allows worms and sheep to co-exist, without necessarily placing any selection pressure on the parasite. Barger and Sutherst (1991) were sceptical about such arguments, pointing to examples where parasites have seemingly been unable to adapt to resistant hosts (such as cattle ticks on *Bos indicus* cattle). They also suggested that the pressure on parasites to adapt may not be as great as might be imagined, because the majority of a parasite population is invariably harboured by a minority of the hosts, even in relatively resistant flocks. Consequently, most of the adult parasites are in hosts that are imposing very little threat to their existence.

Albers et al. (1987) were the first workers to experimentally compare the feasibility of breeding for resistance or resilience to internal parasites of sheep. They found that resilience appeared to be far less heritable than resistance and that the two traits had a favourable genetic correlation anyway, so that selection for increased resistance should lead to an automatic improvement in resilience. Furthermore, resilience is a difficult trait to measure, because to obtain a measure of how much an animal's production is affected by worms, it is necessary to know levels of production with and without a challenge infection. Thus animals must be measured twice, and it is not a simple procedure to obtain accurate measures of wool growth over short periods of time, particularly as sheep acquire natural immunity progressively over their first year of life. By comparison, resistance can be measured quite simply and cheaply using faecal egg count (FEC). Thus Australian researchers have concentrated on improving resistance rather than resilience, reassured by the recent finding that worms may not be capable of adapting to resistant sheep (these results are detailed in a later section), and that FEC is a valuable trait in its own right as a measure of the degree to which an animal is contaminating pastures with worm eggs.

Within-flock Variation in Resistance

The earliest investigation of genetic variation in resistance of Merinos to internal parasites was reviewed by Piper (1987). This work involved a study of the heritability of faecal egg counts (FEC) in unselected 18-month-old Merino rams following artificial challenge with infective *H. contortus* larvae. Based on the maximum FEC observed during four counts recorded 3–6 weeks after infection, the heritability was estimated at 0.27±0.13, or 0.23±0.13 when the data were log-transformed. This was similar to the estimated heritability of anaemia over the same period, as indicated by packed cell volume decline (0.25±0.13). The heritability of individual FEC determinations from the same data set has not been estimated, nor has there been any attempt to determine whether the change in faecal egg counts for each animal over the measurement period was under genetic control.

After it was confirmed that FEC was heritable in Merinos, two major projects were established at Armidale to study in closer detail the role of genetic variation in the host as a means of parasite control. The first of these, based at the CSIRO Pastoral Research Laboratory, is a long-term selection experiment with divergent lines of Merinos selected on FEC after artificial challenge with *H. contortus* larvae (first described by Piper 1987). The second project is on descendants of a sire whose progeny were found to be extremely resistant to *H. contortus*, the so-called 'Golden Ram' (Albers et al. 1987) and this flock is located at the University of New England. Meanwhile, another flock of Merinos was established near Sydney by CSIRO Division of Animal Health to select animals with high and low responsiveness to vaccination with irradiated *Trichostrongylus colubriformis* larvae (Windon and Dineen 1984). In 1990, this flock was also moved to Armidale, when a fourth flock was established, based on resistant animals from all three experimental flocks (the 'nucleus flock').

In the 1980s, two other experimental Merino flocks were established to study resistance to nematode parasites: one, at Hamilton in Victoria, based predominantly on resistance to *Ostertagia* spp. (Cummins et al. 1991); and a flock in the south-west of Western Australia, drawn from about 100 contributors (Karlsson et al. 1991) and based initially on natural worm challenge.

CSIRO *Haemonchus* Selection Flock

The origins of this finewool flock, its management and the procedure for artificial challenge have been described in detail by Woolaston et al. (1990). Established in 1978, the flock comprises divergent selection lines and an unselected control line, with selection based on the maximum FEC recorded after artificial challenge with infective larvae. Although the number of sampling periods has varied slightly between years because of variation in the rate of infection, there have usually been at least three FEC determinations, approximately three to six weeks post-infection.

Heritabilities of FEC and packed cell volume decline (PCVD) in this flock have been estimated using an animal model (Woolaston and Piper, unpublished). The heritability of FEC was 0.23±0.03 and of PCVD was 0.21±0.03. A cube root transformation was found to be effective in normalising FEC data and reducing the range of within-selection line-birth year variances from 118-fold to 10-fold. Transforming FEC data increased the heritability to 0.29±0.03 and reduced selection bias due to heterogeneity of variance, but the further step of pre-adjusting the transformed data to a common variance had only a trivial effect. Heritability estimates for FEC in years with high means and variances were similar, as were estimates for transformed FEC. The estimated genetic correlations between measurements in years with high and low means and variabilities ranged from 0.77 to 0.91.

PCVD and pre-adjusted transformed FEC had a phenotypic correlation of 0.48. Estimates for the genetic correlation ranged from 0.76 in the decreased resistance line to 1.00 in the increased resistance line and 0.87 with pooled data. Other effects on resistance included birth type and dam age, with twins and progeny of maiden dams being more resistant than their cohorts. Sex effects were unimportant for FEC but males had higher PCVD than females in most, but not all, years. Younger animals had higher FEC and PCVD than older animals. Maternal genetic effects were found to be unimportant, as were the effects of low levels of inbreeding found in the flock. Genetic trends in the flock are shown in Figure 1.

University of New England 'Golden Ram' flock

This flock was formed at the University of New England (UNE) in the early 1980s and resulted from progeny-testing fine and medium wool Merino rams from several sources for their parasite resistance. A full description of the animals and the experimental protocol can be found in Albers et al. (1987). The rams were given an oral dose of infective (L3) larvae, and nematode eggs in the faeces counted 4–5 weeks later. In the work reported by Albers et al., 60 progeny groups were involved, and a histogram of the sire group means for 4-week egg count is shown in Figure 2.

The data summarised in Figure 2 describe a group of sires approximating a normal distribution for resistance, but with one notable outlier. It was postulated that this ram, dubbed the 'Golden Ram', was probably the carrier of a

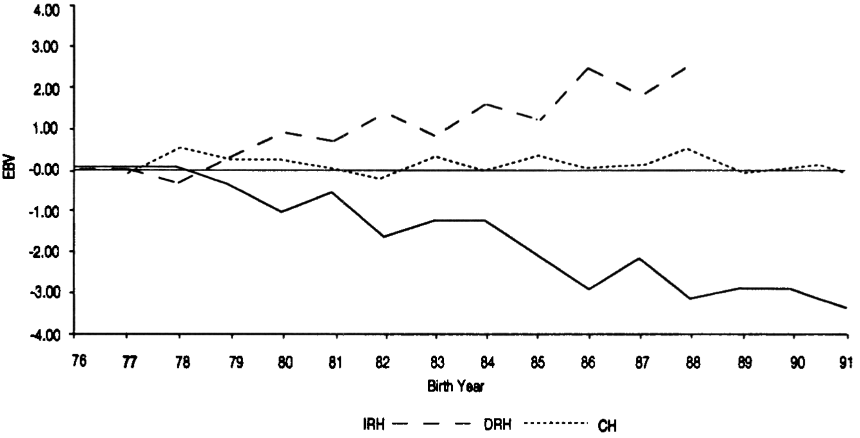

Figure 1 Estimated breeding values (EBV) for cube-root transformed faecal egg count, classified by birth year and selection line (Increased Resistance IRH, Decreased Resistance DRH and Control CH).

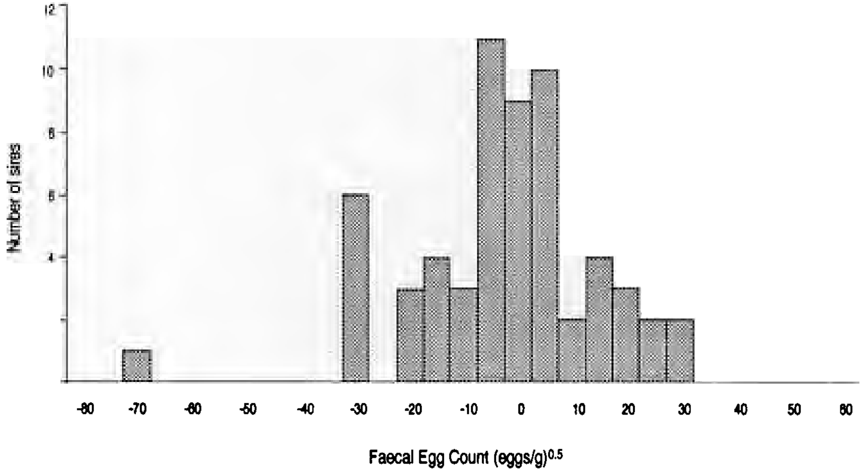

Figure 2 Frequency distribution of deviations of sire group means from the overall mean for four-week egg counts, square-root transformed (after Albers et al. 1987).

major gene for parasite resistance. Following this discovery, matings were made in an attempt to elucidate the mode of inheritance of this putative gene, and studies were initiated to determine the physiological basis of resistance (see Gill et al. 1991). Various tests have been made to the data, including comparisons of within- and between-family variances, tests of segregation in F_1 and back-cross families and application of Famula's Major Gene Index (Woolaston et al. 1990). These tests, however, failed to provide convincing evidence for a major resistance gene and led to the conclusion that if a major gene is present, the nature of the trait makes it very difficult to detect using simple quantitative methods.

The failure to demonstrate the presence of a major gene for resistance prompted a re-examination of the flock's history. The original sires came from three sources. Most came from either the CSIRO Arding research station (31 sires) or the University's Kirby farm (23 sires). The origins of these lines are known and each could reasonably be regarded as a recognisable genetic entity. However, the third group (5 sires), was transferred from the University's Physiology Department and their history remains obscure. No records were kept of the origins of these animals, but it appears they were drawn from diverse sources. In the preliminary analyses described by Albers et al. (1987), flock (or sire origin) effects were tested but found to be unimportant. However, the possible heterogeneity of the small Physiology 'flock' was not taken into account, as only three origins were recognised. As the Golden Ram came from the Physiology 'flock', the possibility could be discounted that his apparent resistance was due to between-flock variation. Speculation that between-flock variation may be important led to a large scale study of resistance in a wide range of Merino flocks (discussed in a later section).

The 'Golden Ram' flock has provided information on the usefulness of one faecal egg count for assessing resistance to *H. contortus* following artificial challenge. Data were recorded on 2362 weaners born between 1981 and 1989 inclusive, with egg counts available from almost all animals at both 28 days and 35 days post-infection. The average egg count at 28 days was 13 365 eggs/g faeces (epg) increasing to 16 013 epg at 35 days. Full pedigree information was available on all measured animals and heritabilities have been estimated using an animal model. Following Albers et al. (1987), data were first subjected to a square-root transformation and on this scale the heritability of egg count 28 days post-infection was estimated at 0.22±0.04, not significantly different from the estimate for 35-day egg count (0.21±0.04). These estimates were lower than those reported previously by Albers et al. (1987) using a sub-set of the same data and a different method of analysis.

The genetic correlation between the 28-day and 35-day counts was estimated at 0.98, thus indicating that genetically, both counts are measuring essentially the same trait. When treated as a repeated observation of the same trait and after fitting a repeatability model which accounted for the same fixed effects, the repeatability was estimated at 0.60±0.01. Assuming the heritability of repeated measures of the same trait to be $2/(1+t)$, where t is the repeatability, then measuring egg counts twice, a week apart, should increase the heritability by about 25%. The average of the two square-root transformed egg counts was analysed as a trait and the corresponding heritability estimate was 0.24±0.04. Therefore, additional accuracy of selection can be obtained by using two egg count measures one week apart, but the gain is not great and the effort required to obtain the extra information may not be justified in many cases, particularly if mortalities from *Haemonchus* are likely to occur. The maximum of the two egg counts was examined as a potential selection criteria but with an estimated heritability of 0.20±0.04, this appeared to be no better than a single measurement.

Thus the heritability appeared lower in this flock than the CSIRO *Haemonchus* flock. In the absence of more detailed analyses, we cannot speculate as to whether this was the result of a flock effect, differences in experimental protocol or the fact that, in the CSIRO flock, the FEC was based on the maximum of three or more egg counts.

CSIRO *Trichostronglus* Selection Lines

These lines (described by Windon and Dineen 1984 and Windon et al. 1987) are based on medium-wool Peppins. For the purposes of comparing heritability estimates with those described above, several features of the experimental design are worth noting. Until recently, all have been maintained worm-free in pens before vaccination with irradiated *T. colubriformis* larvae, whereas those in the other flocks were maintained on pasture. Weaners were infected at a relatively constant age, and the testing period was timed so that the range in ages was no more than two weeks. Faecal samples were taken at five fortnightly intervals, commencing three weeks after infection, and selection was based on the average egg count recorded during this period. After the flock was moved to Armidale in 1990, three lamb drops have been tested at pasture. This procedure has involved subjecting the lambs to artificial challenge, drenching, then reinfecting and measuring FEC at 3, 4 and 5 weeks after infection.

Analyses of individual FEC measurements on pen-tested lambs have been made on 1259 lambs (R.R. Woolaston and R.G. Windon, unpublished). The estimated heritability of FEC determinations (cube-root transformed) varied from 0.37±0.05 at three weeks post-infection to 0.47±0.05 eleven weeks after infection (Table 1). Counts recorded at 3, 5, 7, 9 and 11 weeks after infection were highly correlated genetically (Table 1), indicating that they were all measuring essentially the same phenomenon. It is interesting that the heritability for the mean of five counts was not significantly greater than that for any single count, which may indicate that the five counts were not perfectly correlated, or it may be a function of the transformation used.

More recent analysis of these data (R.R. Woolaston and R.G. Windon, unpublished) included records from 1504 animals tested in pens over the period 1975–93 inclusive and 412 animals tested at pasture during 1991–3. For these analyses, the average of the five FEC measures for pen-tested animals was treated as a separate, but correlated trait to the average of the three FEC measures for pasture-tested animals. Average egg counts were

Table 1 **Heritabilities, genetic correlations and phenotypic correlations of faecal egg counts recorded 3, 5, 7, 9 and 11 weeks post-infection in the *Trichostrongylus* selection lines. Also shown is the estimated heritability of the mean of 5 counts. Data were cube-root transformed before being analysed.**

	3	**5**	**7**	**9**	**11**	
3	0.36±0.04	0.97	0.99	0.93	0.93	
5	0.78	0.35±0.04	0.98	0.96	0.95	
7	0.73	0.79	0.37±0.04	0.95	0.96	
9	0.66	0.71	0.79	0.38±0.04	0.97	
11	0.60	0.65	0.75	0.81	0.45±0.05	
Average						**0.40±0.04**

cube-root transformed before REML analysis with an individual animal model. Fixed effects fitted included test period, vaccination (some of the randomly-bred animals were not vaccinated), sex, birth type and dam age. Of these, dam age did not account for a significant proportion of the variation and was excluded from the final model. Birth type was found to be unimportant for pen-tested lambs, but had a significant effect on paddock-tested lambs. An additional animal effect for dams was fitted, as described above for analysis of the CSIRO *Haemonchus* selection lines, but again this was found to be unimportant and excluded from the final model.

The estimated heritability of pen-tested FEC (average of five counts) was 0.37±0.04, marginally lower than figures reported earlier (Windon et al. 1987, Woolaston et al. 1991). The estimate for paddock tested animals (average of three counts) was 0.39±0.11 with the genetic correlation between the two traits estimated at 0.72.

Armidale Nucleus Flock

This flock is a collaborative effort between the CSIRO Divisions of Animal Production and Animal Health and the University of New England. Foundation animals were drawn from the three flocks described above, after detailed genetic analyses to find animals with low estimated breeding values for FEC. Comparisons of sires from the three sources used in 1992 indicate similar levels of resistance to *H. contortus* and *T. colubriformis* (Fig. 3).

The Nucleus flock is now linked to industry flocks through sire evaluation schemes in the New England region of NSW and at Hamilton in Victoria. A sire used in the Nucleus flock in 1993 and 1994 was entered in both schemes in 1993. Following the release of progeny-test results in 1994–95 for resistance and production characteristics, animals from this flock will be made available to industry.

Hamilton Selection Lines

These lines were described in detail by Cummins et al. (1991) and only a summary will be given here. The Hamilton breeding program was established after a whole blood microtitre culture assay (WBLC) to measure in vitro lymphocyte stimulation to trichostrongylid antigens, an indirect trait for parasite resistance was developed. The program began with heritability estimates being made for both WBLC and FEC, after natural infection, and these were 0.29±0.13 for log WBLC and 0.42±0.14 for log(FEC+30). The sires for this study were drawn from across a number of Victorian fine-wool Merino flocks and the heritability estimates may be biased because between

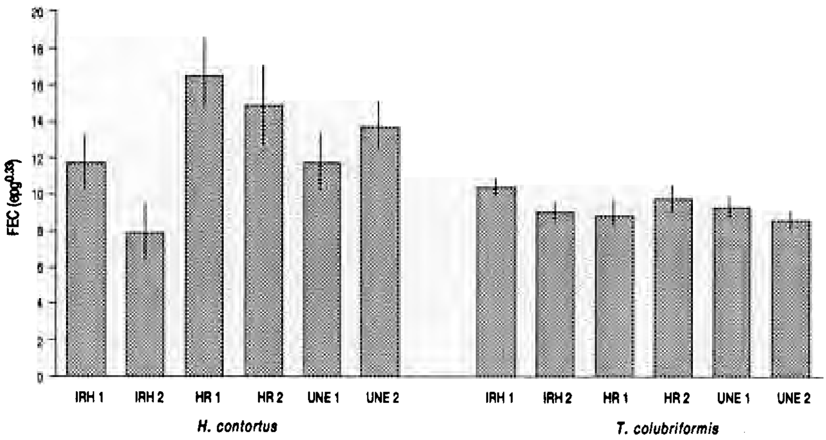

Figure 3 Mean faecal egg counts of progeny sired by two rams from the *Haemonchus* flock (IRH1 and IRH2), the *Trichostrongylus* lines (HR1 and HR2) and the Golden Ram line (UNE1 and UNE2), when artificially infected with either *H. contortus* or *T. colubriformis.* Bars show mean (and standard error) FECs 4–10 weeks after challenge, on a cube root scale.

flock differences in the sire component of variance were included. Closed selection lines were then formed and both WBLC and FEC after natural infection were used as selection criteria for the resistant and susceptible flocks. Two intermediate flocks were also formed to allow the relative contribution of both selection criteria to parasite resistance to be assessed. Further heritability estimates, using sire–offspring correlations in the selection flocks, gave heritability estimates of 0.11±0.08 for log WBLC and 0.38±0.08 for log(FEC+30).

Progeny produced in the first two years of the resistant and susceptible selection flocks showed significant differences in WBLC and FEC with the intermediate flocks between the two. Parasites common in this region of Australia include *Trichostrongylus* spp. and *Teladorsagia circumcincta.* Recent analyses of the selection lines have shown that in the high resistance line, selected for low FEC and high WBLC, FEC has contributed most to resistance and this flock has continued to be selected with FEC as the sole selection criterion (L.J. Cummins, pers. comm.). The selection lines at Hamilton have demonstrated that it should be feasible to breed sheep for resistance to parasites in this region, using FEC as a selection criterion. This has occurred even though—with *T. circumcincta*, one of the major species present—FEC can be independent of the number of nematodes present (Symons et al. 1981, Callinan and Arundel, 1982).

Rylington Flock

The flock at Rylington Park in Western Australia was established in 1987 with more than 90 sheep breeders interested in breeding parasite resistant Merinos contributing mated ewe hoggets (Karlsson et al. 1991). Rams used in the flock from 1988 to 1990 came from a variety of sources including: the UNE 'Golden Ram' flock; the CSIRO *Trichostrongylus* High Responder line; the CSIRO line with increased resistance to *Haemonchus* and the CSIRO closed flock at Yalanbee which has been run without anthelmintic treatment for over 20 years. The selection flock was closed with replacement breeding stock originally being selected on a combination of production traits and FEC after natural challenge with no drench intervention. Under these conditions the repeatability of FEC was low and the heritability estimates were highly variable from month to month. FEC is now assessed after artificial challenge with *T. colubriformis* and this gives a more reliable indicator of parasite resistance (L.J.E. Karlsson, pers. comm.). A control flock of 100 ewes is maintained to monitor genetic progress in the selection flock.

Summary of Within-flock Variation

The heritability of FEC in Merinos appears to be around 0.2 to 0.3 under typical challenge conditions. This figure can be higher if testing is carried out under highly controlled conditions or if the average of several measurements is used. While a heritability of 0.3 is at the lower end of the range (0.3–0.5) typically found for fleece weight, average fibre diameter and body weight (Turner and Young 1969), it is an extremely variable trait with a coefficient of variation often greater than 100%, compared with 7–15% in the usual objectively measured traits. Potential rates of genetic improvement are therefore quite rapid, and this topic will be further discussed in a later section.

Specificity of resistance

For convenience, most experimental Merino selection lines have been selected on the basis of resistance to only one species of parasite. In areas where worms are important, it is rare for the problem to be restricted to one species. For example, *Haemonchus* and *Trichostrongylus* species are often both found in humid and semi-humid temperate areas, while *Trichostrongylus* and *Teladorsagia* species are commonly found together in winter rainfall areas. It is therefore of some interest to know whether resistance to one species confers any resistance to other species. Logic suggests that this may not be the case, as worm species differ considerably in how they affect sheep.

Fortunately however, there appears to be a favourable association between resistance to the various species. When grazing contaminated pastures, animals in the CSIRO *Haemonchus* selection line bred for increased resistance have frequently been found to be passing fewer *Trichostrongylus*, *Teladorsagia* and *Oesophagostomum* eggs than unselected animals grazing the same pastures, even in the absence of *Haemonchus*. This observation has also been made in ewes nearing parturition and during lactation (Woolaston 1992). Similar results have been found for sheep bred for resistance to *T. colubriformis* (Windon 1990). While the genetic correlation between resistance to the various worm species has not been estimated and is unlikely to be perfect, it appears to be favourable and relatively strong.

Merinos are frequently run in areas characterised by unreliable rainfall and this is particularly the case in Australia. Under such conditions, a natural worm challenge severe enough to cause selection for resistance, is not always forthcoming. Thus, in experimental flocks, it has been expedient to artificially dose the sheep with infective worm larvae to guarantee positive worm egg counts in most sheep. Similar protocols have also been used in some commercial breeding operations.

It is important to know whether sheep identified as more resistant using artificial challenge are more resistant when infected naturally. No estimates of the genetic correlation have been made, but there is obviously a very close association between response to artificial and natural challenges. For example, sheep selected for increased resistance in the CSIRO *Haemonchus* selection line using artificial infections over a period of 12 years had geometric mean FECs of 2730 epg, compared with 12 720 epg in unselected sheep after the usual artificial challenge (Woolaston et al. 1990). When the infection was terminated with anthelmintic treatment and sheep were returned to contaminated pastures for six weeks, the respective mean egg counts were 140 epg and 3590 epg. These results have been corroborated on many other occasions where there has been no possibility of a residual effect from an earlier infection, and they indicate that selection using artificial infection is choosing the appropriate animals.

Between-flock Variation

Merinos have been developed to suit a broad range of environments, resulting in several relatively distinct strains. In general, finer types are found in higher rainfall areas, with the strong wool strains and bloodlines predominating in the more extensive systems typical of regions with limited rainfall. Worms tend to be a greater problem in wetter areas and whenever sheep are heavily stocked. Some ram breeders select their animals under a constant challenge from worms, while other breeders are selecting in environments where worms have little or no impact on production. Breeders in the same region also differ in the degree to which they use anthelmintics in their breeding flock. It is therefore reasonable to expect that differences between bloodlines might emerge over a period of time.

Until recently, little was known of the extent of variation in resistance between flocks. However, studies of 57 bloodlines across six research stations in various parts of Australia found that between-flock variation in resistance was quite small compared with within-flock genetic variation (Eady and Woolaston, unpublished). Of the total genetic variation in FEC, typically only 4% was accounted for by between-strain differences, 9% by bloodlines within strains and 85% by within-flock genetic differences (Fig. 4).

Evidence from sire evaluation schemes provides supporting evidence that most genetic variation in resistance is within-flock rather than between-flock. Sires from any one flock frequently have quite disparate rankings for FEC, indicating that results from one or two sires from a flock are a very poor guide to the resistance level of that flock (Fig. 5).

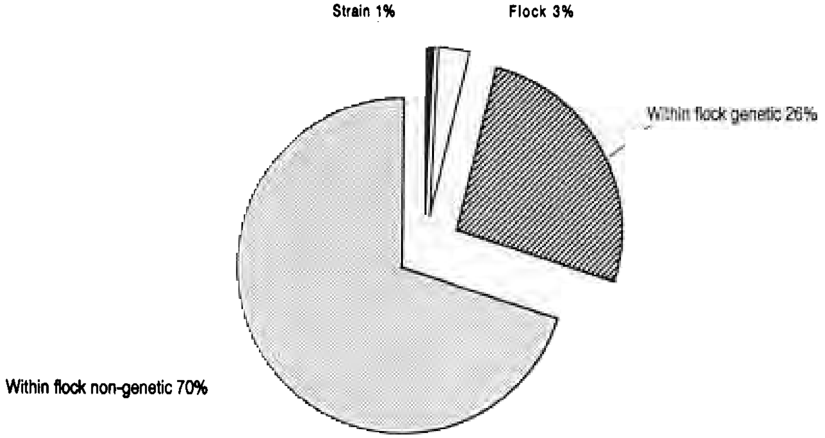

Figure 4 Sources of variation in faecal egg count in the Katanning Base Flocks (S.J. Eady, R.R. Woolaston and R.P. Lewer, unpublished).

These results suggest that there is little potential at present for breeders to improve the resistance levels of their flocks by finding a single source of resistant rams. However, for a breeder interested in making genetic progress towards greater resistance in his animals, it is pleasing to know that improvement should be achievable without the need to import animals from other flocks. Breeders already selecting for reduced FEC will undoubtedly make progress in future years and results from sire evaluation schemes should prove increasingly useful.

Relationship with other diseases

Although the immune system has been found to play a central role in determining the capacity of sheep to resist infection with internal parasites, sheep with superior levels of resistance are not consistently more immunocompetent with respect to other diseases (Gray et al. 1991). Importantly, the general immune responsiveness of nematode resistant sheep to other diseases does not appear to have been compromised either, indicating that resistance to nematodes has not been gained at the expense of resistance to other diseases.

Instances of favourable associations with resistance have occasionally been found in Merinos, but often the sheep have had both diseases at the same time. Under such conditions, it is not always clear whether the presence of

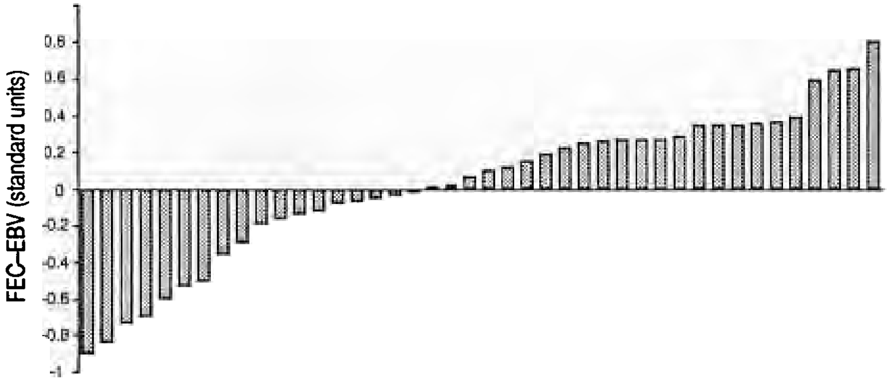

Figure 5 FEC-estimated breeding values (EBVs) for 42 sires evaluated in the New England Sire Evaluation Scheme, 1990–1993.

one disease is predisposing the animal to infection with the second, or whether there is a real genetic basis to the association. Favourable correlations have been found between resistance to nematodes and incidence of dermatophilosis; severity of dermatophilosis; fleece rot susceptibility; and footrot score and prevalence. However, in most cases these associations are weak. When sheep selected for enhanced resistance to *H. contortus* were vaccinated against clostridial disease, they were found to be no more or less responsive to *Clostridium tetani* than their unselected counterparts. In another experiment that involved testing Merino hoggets for resistance to *T. colubriformis*, a mild outbreak of pink eye (contagious opthalmia) was present in the flock. However, there was no significant association found between resistance to the two diseases.

Between-age correlations

Sheep are most susceptible to worm infection as lambs, with their natural immunity gradually increasing to about 12 months of age. After then, susceptibility is usually only a problem in the periparturient period—from the final one or two weeks of pregnancy through to mid-lactation. It is convenient to test Merinos for resistance to worms soon after they are weaned, so it is important to know whether selecting at this age will confer relative resistance at later periods during an the animal's first year and during the periparturient period.

To see if the same genes are responsible for the expression of resistance at various ages, it is necessary to estimate between-age genetic correlations. While no such estimates are available, evidence from experimental flocks is encouraging. In most Merino flocks bred for varying levels of resistance to worms, selections have been made on the basis of a test at 4–5 months of age. Resistance levels have been compared at various other ages in these flocks, and genetic differences begin to become apparent from about 85 days of age (R.R. Woolaston, R.L. Elwin and J.L. Ward unpublished), and persist through the lifetime of the animal. Recent results from the CSIRO *Haemonchus* selection flock are typical. Five weeks after an artificial challenge with infective larvae, 14-month-old sheep from the line bred for increased resistance had mean worm egg counts of 824 epg, compared with 6978 epg in unselected sheep and 12 648 epg in the line bred for decreased resistance. Comparisons of sheep during the periparturient period have yielded similar results. Merino ewes bred for increased resistance exhibited a less pronounced rise in FEC when grazing the same contaminated pastures as their counterparts which were either bred for decreased resistance or were unselected (Fig. 6). Comparisons of dry (non-reproductive) adult animals have consistently shown similar rankings of the three lines.

Parasite adaptation

It is possible that parasites may genetically adapt in response to any threat to their existence, including self-defence from the host organism. Thus it has long been a concern that genetically altering hosts to make them more resistant to worms is futile, as parasites have an adaptive advantage from a higher reproductive rate and shorter generation interval than their hosts. The longest-running experimental flocks have been selected using artificial challenge, so there has been no possibility of the parasite adapting—worm larvae used in one year are not usually descended from worms used the previous year.

Consequently an experiment was initiated to test the hypothesis that worms cannot adapt to selected Merino sheep. A fuller description of this work can be found elsewhere (Woolaston et al. 1992), together with an account of the results after 14 generations of worm selection. In this experiment, a diverse foundation population of *H. contortus* was created by assembling isolates from seven areas of Australia. From that point, the population was divided into two sub-populations, with one maintained in hosts bred for

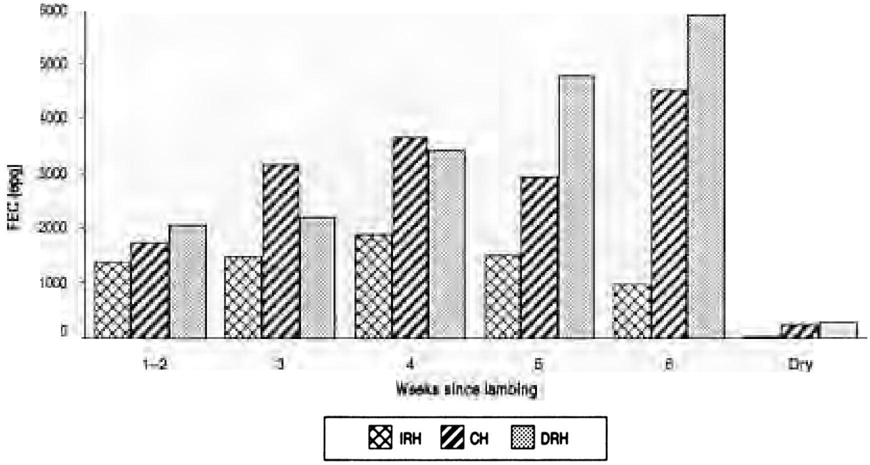

Figure 6 Faecal egg counts in lactating Merino ewes selected for increased resistance (IRH), decreased resistance (DRH) and unselected controls (CH). Means are classified by selection line and number of weeks since lambing. (Source: Woolaston et al. 1992).

enhanced resistance to the species and the other maintained in hosts bred for decreased resistance. Maintaining the sheep in an animal house facilitated a rapid turnover of worm generations, so that over a two and a half year period, 30 generations of selection were achieved. At the end of this period, a comparison was made of infectivity of the two selected sub-populations and the foundation population, which had been maintained in a frozen state. Tests were carried out in periparturient ewes and in younger (about 12 months old) ewes and rams. Results are shown in Figure 7.

Parasites that were encouraged to adapt by being maintained in relatively resistant hosts for 30 generations did not produce higher FECs than parasites maintained in relatively susceptible hosts, or unselected parasites (Fig. 7). This was the case in young sheep and periparturient ewes, regardless of the selection history of the sheep. The degree of anaemia suffered by each class of sheep during infection followed a similar pattern (not shown), indicating that FEC reflected the physiological burden to the animal. The conclusion is that worm adaptation should not be a problem for at least 30 generations, which is equivalent to about 15 years in a typical field situation where only

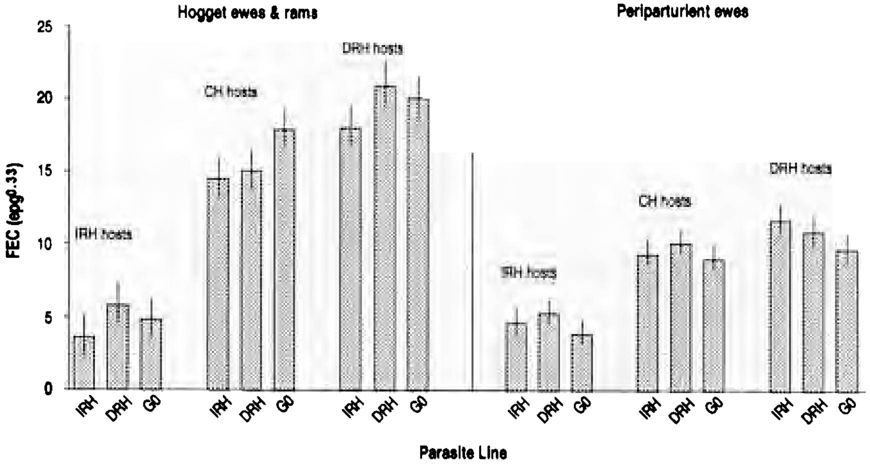

Figure 7 Faecal egg counts (FECs) of parasite lines tested in sheep with increased resistance (IRH), decreased resistance (DRH), or unselected control animals (CH). The lines of *H. contortus* were either maintained in IRH hosts (IRH parasite line), DRH hosts (DRH line) or frozen during the experiment and therefore unselected (G0). FECs are expressed on a cube root scale (Source: R.R. Woolaston and S.J. Eady unpublished).

two worm generations occur each year. These results are encouraging, but they should not give rise to complacency, as parasites have been found to adapt eventually in some other host-parasite models.

Feasibility of a Breeding Program

Whether or not it is feasible for a Merino breeder to consider selecting for reduced FEC depends on the relative cost of parasitism to the stud and its clients, the relationships between FEC and other traits and the cost of testing.

Cost of parasitism

The cost of parasitism to the sheep industry is difficult to quantify accurately. It is relatively simple to determine the direct cost of anthelmintics used and to place a value on the labour costs associated with dosing. However, it is a far more difficult task to place a value on the opportunity cost of having restrictions imposed on grazing management because of concerns about pasture contamination; or more importantly, to estimate the cost of production foregone because of the debilitating effects of worms. Obviously these costs will vary considerably, depending on the region of interest.

In an assessment of the cost to the Australian sheep industry of various parasites, Beck et al. (1985) concluded that internal parasites were by far the most economically important, even without taking into consideration probable decreases in fertility, lower birth rates, predisposition to other diseases and costs of management practices that might be employed to reduce their effect. Prevention and treatment costs were estimated to represent only 17% of the total cost of internal parasites, with 83% caused by wool and meat losses and deaths.

Genetic relationships with production

The amount of information on genetic relations between resistance and production in Merinos is not great, with most data coming from one or two experimental flocks. However, more information should be available over the coming year, when production data are available from sheep that were tested for resistance as weaners in the various other research flocks around Australia (described in Eady, this Volume). When assessing such associations, it is important to determine whether the disease is directly affecting production over the measurement period, or whether the association is the consequence of common control at the gene level. In the relationships estimated thus far, most involved relatively short periods of parasite infection and the assumption has been made that this has had only a negligible effect on yearly production. Under such circumstances, associations have been found to be neutral, so that selecting for improved resistance should have only very small effects on productivity when the parasites are absent, and *vice versa.*

Expectations from a breeding program

After about 14 years of single character selection, substantial reductions in FEC have been achieved in the CSIRO *Haemonchus* selection flock and the *Trichostrongylus* lines. Differences between selected and unselected lines are almost invariably found whenever FECs are positive. On a percentage basis, the difference can be as great as 95% or as little as 50%, depending on the time of measurement and other factors yet to be determined. Although no selection pressure has been used on other traits, the lines are relatively small (100 ewes), so a strategy to limit the rate of increase in inbreeding has had to be adopted. This strategy has resulted in a loss of achieved selection intensity, perhaps by 30% of the maximum possible. Thus rates of gain in this flock should not be seen as maximal, and considerably greater rates should theoretically be possible in larger flocks, particularly if information from relatives is used to increase accuracy of selection. A 50% or greater reduction in FECs should be achievable in a multi-trait commercial breeding program over a similar period, depending on how the selection emphasis is apportioned.

After studying the resistance levels of sheep in long-running production selection experiments, workers in New Zealand have recently questioned the virtue of selecting for resistance (Garrick et al. 1992). In general, Romneys bred for high production tended to have higher FECs than their lower-producing cohorts, suggesting that they are less resistant. However, when sheep were treated with slow release capsules to control worms (Captec Extender 100™), the high-producing sheep gained no greater benefit than the low producers. This result was unexpected and gave rise to speculation that the physiological cost of mounting a successful immune response to expel parasites may be sufficiently great to compromise production. From current knowledge of the physiological processes involved, this hypothesis cannot be sustained, as the energy requirements of an immune reaction should in theory at least, be relatively minor. Garrick et al. (1992) also cautioned against diverting selection pressure towards decreasing FEC until more convincing evidence of the benefits is available.

These results from New Zealand point to the need for a proper assessment of the value of resistant sheep and such work is proceeding with the Merino in Australia. However, there is little evidence as yet from the Merino to warrant overcautiousness and the results of calculations shown below indicate that the opportunity cost of placing selection pressure on FEC is modest in comparison with the potential benefits.

Combining genetic and economic data

Woolaston and Piper (unpublished) used available estimates of the relevant genetic associations to predict the effect on production of varying the emphasis on FEC in a breeding program (Fig. 8).

Figure 8 suggests that for flocks in which parasites do not need treatment and are not causing production losses, then making up to about 40% of the maximum possible gain in FEC has little or no detrimental effect on gain in production traits, but about 30% is optimal. If improvements in FEC are also likely to lead to a saving in anthelmintic treatment costs, then about 50% of the possible change in FEC could occur before the net gain is compromised, but about 35% is optimal. In the extreme case, where production losses are considered to represent 83% of the cost of internal parasites (as Beck et al. 1985 claimed was the case in an average Australian situation), then any

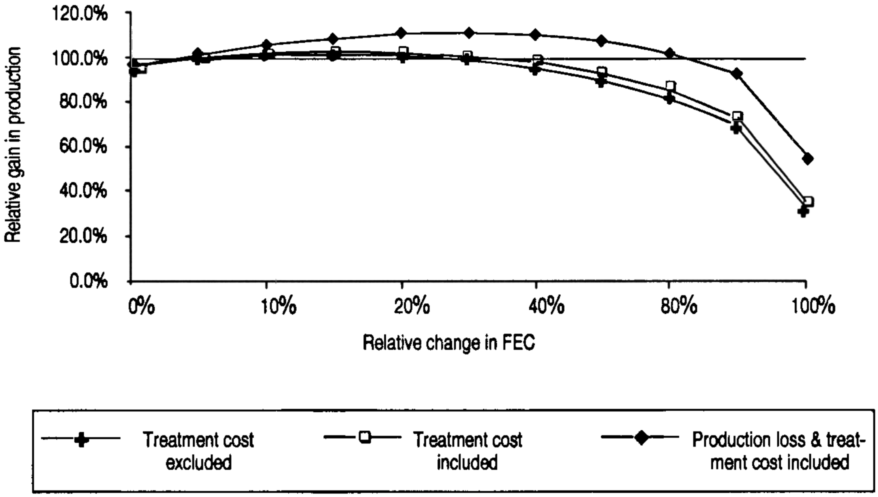

Figure 8 Effect on predicted genetic gain in production (combined value of changes in fleece weight, average fibre diameter, reproduction rate and body weight) as relative gain in FEC is increased to the maximum. The curve with diamond markers refers to unparasitised sheep; the curve with square markers represents a scenario for parasitised sheep where savings in worm treatment costs are added to the value of production; and the curve with crosses is where production loss due to parasitism is valued at about 5 times the cost of treatment in a parasitised environment.

amount of selection pressure on FEC up to 83% of the maximum is better than ignoring it; although about 50–60% is optimal. The true situation will most likely lie somewhere between the two extreme scenarios. A more accurate assessment of the optimal pressure to place on FEC must await better estimates of genetic parameters and measurements of production in selected versus unselected sheep on contaminated pastures. In the meantime however, these calculations suggest that making up to 70% of the maximum possible reduction FEC should not constitute a major risk, as the opportunity cost is not high.

In stud flocks where breeding for reduced FEC has already commenced, the correlations assumed for the above calculations appear to hold. The most resistant rams are typically distributed amongst the highest and lowest producers, so that top-producing rams with a desirable level of resistance can usually be found.

Practicalities of breeding for resistance

A small number of Merino breeders in Australia have commenced measuring FEC in their ram breeding flocks over the past two or three years, and most use this information to aid in their decisions. There have been no set protocols determined for ensuring the animals are adequately challenged, but appropriate procedures are currently under development and being assessed in collaboration with commercial ram breeders. Protocols involving natural infection have been routinely used with success in New Zealand for other breeds and several Australian breeders have chosen to use this method. Others have preferred to use an oral dose of live larvae artificially administered, so that the timetable for FEC determination and termination of the infection is predetermined, and the period of infection can be minimised. It is still not clear which is the most effective method, but in many ram breeding areas, an artificial infection may often be necessary due to unpredictable seasonal conditions. Nor is the optimal age for testing clear, and research is urgently needed on this.

Interactions with other control measures

In a study which simulated, under grazing conditions, a comparison of sheep bred for a 'modest' degree of resistance with normal sheep, Barger (1989) found that the resistant sheep should require little, if any, anthelmintic treatment in most years. During the nine years that Armidale conditions were simulated, the mean worm burden in resistant sheep was lower than that in normal sheep treated three times annually. Parameters used in this study were derived from the CSIRO *Trichostrongylus* selection flock, in which selection commenced in 1976. The assumptions used in this study may be open to question and yet to be proven, but the study was useful for illustrating the interactions that occur between the level of host resistance, the frequency of anthelmintic treatment and the rate of development of drug resistance that occurs in the parasites.

Clearly, an efficient strategy using one method of control cannot be designed without consideration of other factors affecting the worm population. The knowledge base for the role of host resistance is expanding, and management strategies such as strategic use of protein supplementation in weaners are now being evaluated. Meanwhile, the search for an effective vaccine is continuing as are developments with other novel control methods. Internal parasites have proven to be a particularly elusive and adaptable target and effective long-term control methods may well rely on an integrated approach using several methods. Of those available, breeding for improved resistance appears to be one of the more promising alternatives.

Acknowledgments

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References

Albers, G.A.A., Gray, G.D., Piper, L.R., Barker, J.S.F., Le Jambre, L.F. and Barger, I.A. 1987. The genetics of resistance and resilience to *Haemonchus contortus* infections in young Merino sheep. International Journal for Parasitology, 17, 1355–1363.

Barger, I.A. 1989. Genetic resistance of hosts and its influence on epidemiology. Veterinary Parasitology, 32, 21–35.

Barger, I.A. and Sutherst, R.W. 1991. Population biology of host and parasite. In: Gray, G.D. and Woolaston, R.R. ed., Breeding for disease resistance in sheep. Melbourne, Australian Wool Corporation, pp. 51–56.

Beck, A., Moir, B. and Meppem, T. 1985. The cost of parasites to the Australian sheep industry. Quarterly Review of the Rural Economy, 7, 336–343.

Callinan, A.P.L. and Arundel, J.H. 1982. Population dynamics of the parasitic stages of *Ostertagia* spp. in sheep. International Journal for Parasitology, 1, 531.

Cummins, L.J., Thompson, R.L., Yong, W.K., Riffkin, G.G., Goddard, M.E., Callinan, A.P.L. and Saunders, M.J. 1991. Genetics of *Ostertagia* selection lines. In: Gray, G.D. and Woolaston, R.R. ed., Breeding for disease resistance in sheep. Melbourne, Australian Wool Corporation, 11–18.

Garrick, D.J., Blair, H.T. and Bisset, S. 1992. Selection of Romney sheep grazing nematode infected pasture. Proceedings of the Australian Association of Animal Breeding and Genetics, 10, 448.

Gray, G.D., Gill, H.S. and Woolaston, R.R. 1991. Relationships among sheep diseases of commercial importance. In: Breeding for disease resistance in sheep. Gray G.D. and Woolaston R.R. ed., Melbourne, Australian Wool Corporation.

Karlsson, L.J.E., MacLeod, I.M., Leelawardana, D.H., Sissoev, K. and Simmons, J. 1991. Selection for nematode resistance in sheep in the Australian Mediterranean climate zone. In: Gray, G.D. and Woolaston, R.R. ed., Breeding for disease resistance in sheep. Melbourne, Australian Wool Corporation, pp. 131–138.

Overend, D. G., Phillips, M.L., Poulton, A.L. and Foster, Ced. 1994. Anthelmintic resistance in Australian sheep nematode populations. Australian Veterinary Journal, 7, 117–121.

Piper, L.R. 1987. Genetic variation in resistance to internal parasites. In: Merino Improvement Programs in Australia. McGuirk, B.J. ed., Melbourne, Australian Wool Corporation, 351–363.

Symons, L.E.A., Steel, J.W. and Jones, W.O. 1981. Effects of level of larval intake on the productivity and physiological and metabolic responses of lambs infected with *Ostertagia circumcincta*. Australian Journal of Agricultural Research, 32, 139.

Turner, H.N. and Young, S.S.Y. 1969. Quantitative genetics in sheep breeding, Melbourne, Macmillan.

Windon, R. G. 1990. Selective breeding for the control of nematodiasis in sheep. Revue Scientifique et Technique, Office International des Epizooties, 9, 555.

Windon, R.G. and Dineen, J.K. 1984. Parasitological and immunological competence of lambs selected for high and low responsiveness to vaccination with irradiated *Trichostrongylus colubriformis* larvae. In: Dineen, J.K. and Outteridge, P.W. Immunogenetic approaches to the control of endoparasites. Melbourne, CSIRO, 13–28.

Windon, R.G., Dineen, J.K. and Wagland, B.M. 1987. Genetic control of immunological responsiveness against the intestinal nematode Trichostrongylus colubriformis in lambs. In: McGuirk, B.J. ed., Merino improvement programs in Australia. Melbourne, Australian Wool Corporation, 371–375.

Woolaston, R.R. 1992. Selection of Merino sheep for increased and decreased resistance to *Haemonchus contortus*: peri-parturient effects on faecal egg counts. International Journal for Parasitology, 22, 947–953.

——1994. Worms in Merinos: prospects for improved control through breeding. Proceedings of the 4th World Merino Conference, Uruguay, 159.

Woolaston. R.R., Barger. I.A. and Piper. L.R. 1990. Response to helminth infection of sheep selected for resistance to *Haemonchus contortus*. International Journal for Parasitology, 20, 1015.

Woolaston R.R., Elwin R.L and Barger I.A. 1992. No adaptation of *Haemonchus contortus* to genetically resistant sheep. International Journal for Parasitology, 22, 377.

Woolaston, R.R., Windon, R.G. and Gray, G.D. 1991. Genetic variation in resistance to internal parasites in Armidale experimental flocks. In: Gray G.D. and Woolaston R.R. ed., Breeding for disease resistance in sheep. Melbourne, Australian Wool Corporation.

Breeding Sheep in New Zealand for Resistance or Resilience to Nematode Parasites

C.A. MORRIS, T.G. WATSON, S.A. BISSET, A. VLASSOFF AND
P.G.C. DOUCH

ABSTRACT

Breeding sheep for resistance or resilience to internal parasites is being carried out in commercial flocks in New Zealand and is an area of active research. Selection lines have been established in Romney sheep for resistance (low faecal egg count: FEC), or for susceptibility (high FEC) to nematode parasites derived from natural challenge on pasture at two research centres, the Wallaceville Animal Research Centre and the Ruakura Agricultural Centre. After fourteen and eight years of selection, respectively, the divergence between the high and low selection lines, in phenotypic standard deviation units is 1.65 at Wallaceville and 0.86 at Ruakura. These differences in FEC are strongly associated with differences in worm burdens. Exchange of resistant and susceptible rams between these two locations has indicated no interaction between line and location. From nine estimates, the heritability of log FEC in New Zealand has a weighted average of 0.23±0.02. An ELISA assay has been developed at Wallaceville to measure antibody response to antigens from various nematode genera. The heritability of this antibody response in lambs at six months of age is 0.27±0.08, and the response is favourably correlated genetically with log FEC (–0.56±0.18). Screening for FEC is being provided as a commercial service to some ram breeders in New Zealand and the recording scheme (Animalplan) is able to provide breeding values to performance-recording clients for log FEC and dag score. Resilience, or the ability of an animal to grow in spite of a worm challenge, has been measured in various ways, giving heritability estimates ranging from 0.06 to 0.14. Information is presently lacking on the most appropriate way to combine resistance and production traits into a multi-trait selection objective. This is particularly important in view of the recent finding that sheep lines that have been experimentally selected for higher levels of production in New Zealand have higher FEC levels than their controls.

Diseases of importance to sheep farmers in New Zealand include facial eczema, footrot, flystrike, ryegrass staggers and internal parasitism. This review will concentrate on internal parasites but it is noted that significant research is being undertaken in New Zealand on developing breeding strategies for resistance of sheep to facial eczema (Morris et al. 1989, 1991); to footrot (Skerman et al. 1988); and more recently (since 1988) to ryegrass staggers (C.A. Morris and N.R. Towers, unpublished). Flystrike is becoming increasingly troublesome to sheep producers but there has been no research in New Zealand on breeding sheep for resistance to flystrike.

Both stud and commercial sheep farmers in New Zealand must assess the relative importance of these diseases and other production traits (e.g. wool production, meat production, reproduction) when designing their breeding programs and setting their breeding objectives. In many cases, the critical genetic parameters and relative economic values required to design more complete breeding programs are unknown and these deficiencies will be highlighted in this review.

There is considerable difference of opinion about how to include parasitism in sheep breeding objectives. Briefly the issues are:

1. There is a threat to the sheep industry from anthelmintic resistance, suggesting that sheep should be selected for low faecal egg count.
2. There may be some genetic antagonism between production (especially fleece weight) and faecal egg count.
3. It is not clear whether resilience (i.e. resistance to the effects of a parasitic infection) should be included in the objectives.
4. Selection for resilience without concomitant selection for resistance may fail to reduce pasture contamination.

Research in New Zealand on the genetics of resistance to internal parasites in sheep has been reviewed recently by Baker et al. (1990, 1991). This review updates the 1991 paper which summarised and discussed the results of research by the Ministry of Agriculture and Fisheries (now AgResearch) at Ruakura and Wallaceville. It also discusses the application of breeding strategies on both stud and commercial sheep farms, and outlines some of our thinking on future research directions.

In all experimental and progeny test flocks in New Zealand except one (the Perendale flock), resistance has been assessed using faecal egg count (FEC) after natural infection. This is in contrast to most Australian studies which have used artificial challenge with known doses of larvae from different parasitic genera (Woolaston 1990). In New Zealand, the protocol has involved drenching all lambs at weaning (about 3 months of age) and then monitoring a sample of 20–30 lambs on a regular basis, until a mean FEC of 1000–1500 eggs per gram of faeces (epg) is reached. At this time all lambs in the trial are faecal sampled, weighed, recorded for dag score and drenched. After drenching, the procedure is then repeated at least once and in the Wallaceville flocks usually twice. The first faecal sampling takes place in summer (January–February) and the second in early autumn (March–April). Culturing of bulked faecal samples following each sampling has revealed that *Trichostrongylus* and *Ostertagia* are usually the most prevalent parasitic genera.

Genetic Parameters

Heritabilities

Early New Zealand studies established that there was genetic variation between and within strains or breeds of sheep in incidence of dags (Meyer et al. 1983). Dagginess is scored on a 0 to 4 scale with 0 defined by no visual evidence of dags, with 4 extreme levels of dags. The mean heritability of dag score in the 1983 study was 0.31, range 0.13 to 0.60. Since dagginess in sheep is often regarded as an indication of heavy parasite burdens, subsequent research investigated the relationship between dagginess and internal parasite worm burdens assessed through FEC and necropsies (Watson et al. 1986). Heritability estimates for log FEC (Table 1) averaged 0.34±0.19 for total epg excluding *Nematodirus* eggs, and 0.57±0.24 for *Nematodirus* epg.

Since 1986, further data from research and commercial flocks have been analysed, providing further estimates of genetic parameters for FEC and associated traits. These flocks include: the Romney selection and associated progeny testing flocks run from Wallaceville (Douch et al. 1994); the nucleus flock at 'Wairunga' of a large group breeding scheme (Bisset et al. 1992); five flocks on the east coast of North Island (Bisset et al. 1994); and the AgResearch production selection flocks in Southland (McEwan et al. 1992).

Heritability estimates of log FEC for a single measurement made at the first to third sampling ranged from 0.14 to 0.34 with a weighted average of 0.23±0.02 (Table 1). Estimates of the phenotypic correlation between any two successive measurements were of moderate size; repeatabilities for log FEC estimated by Douch et al. (1994) had values of 0.18±0.05, 0.15±0.04 and 0.35±0.02, with a weighted average of 0.30±0.02. (Note that these repeatability results reflect FECs after successive larval challenges, not repeat counts within a challenge period). A genetic correlation estimate from Wallaceville data between log FEC at the first and second sampling was 0.86±0.10 which was not significantly different from unity. If the heritability of a single measurement of FEC is 0.23 and the repeatability is 0.30, then the expectation of the heritability of the mean of 2 measurements is 0.35 and for the mean of 3 measurements is 0.43. A similar finding was reported by Stear et al. (1990) in cattle. There is clearly an advantage in averaging at least two or three FECs but there are diminishing returns after that, especially when the cost of egg counts is taken into account.

Table 1 New Zealand paternal half sib (REML) heritability estimates for faecal egg counts ($\log_e$ FEC+1), liveweight gain (LWG) and dag score.

Trait	Sex of progeny[a]	No. of progeny	No. of sires	h^2±s.e.	References
log FEC	F	363	35	0.33±0.18 (Sample 1) 0.34±0.20 (Sample 2)	Watson et al. (1986)
		1547	64	0.24±0.07 (Sample 1) 0.21±0.07 (Sample 2) 0.29±0.08 (Sample 3)	Douch et al. (1994)
	F	2611	60	0.27±0.07	Bisset et al. (1992)
	F	3395	123	0.21±0.05	Bisset et al. (1994)
	F	2657	104	0.27±0.06	Bisset, S.A. and Morris, C.A. (unpublished; 1992-born lambs)
	M	891	65	0.14±0.07	McEwan et al. (1992)
				0.23±0.02[b]	
LWG	F	363	35	0.36±0.19 (to Sample 1) 0.10±0.13 (Sample 1 to 2)	Watson et al. (1986)
		1547	64	0.20±0.07 (Wng-[c] Sample 2)	Douch et al. (1994)
	F	261	60	0.08±0.04 (Wng-Sample 1)	Bisset et al. (1992)
	F	3395	123	0.16±0.04 (Wng-Sample 1)	Bisset et al. (1994)
	M	891	65	0.39±0.11 (Wng-Sample 1) 0.15±0.03[b]	McEwan et al. (1992)
		363	35	0.50±0.22	Watson et al. (1986)
		1547	64	0.24±0.07	Douch et al. (1994)
		1663	46	0.24±0.08	Bisset et al. (1992)
		3395	123	0.28±0.06	Bisset et al. (1994)
	M	891	65	0.06±0.06 0.20±0.03[b]	McEwan et al. (1992)

[a] F = female; M = male

[b] Weighted means

[c] Wng = weaning

A preliminary estimate was 0.66±0.18 for the heritability of log FEC at the third faecal sampling (FEC3: late autumn) at Wallaceville (Baker et al. 1991). A later estimate using subsequent data from Wallaceville was 0.29±0.08 (Douch et al. 1994). This lower value for log FEC3 (and also for log FEC1 and log FEC2) appears to be the result of fitting source of sire in the analysis, to account for the selection applied to sires used in the progeny test flock.

It has been suggested that it may be effective to select for an increased rate of development of immunity to nematodes and that the change of faecal egg count between samplings may be an appropriate measure. This trait has been used as the selection criterion in the Perendale selection experiment (Watson et al. 1992). In the Wallaceville data the heritabilities were 0.11±0.07 for the difference in FEC between sampling 1 and 2 and 0.29±0.11 for the difference between sampling 2 and 3 (Baker et al. 1991).

Liveweight gain (LWG) over the period when lambs are undrenched and challenged with an infection has been suggested as a measure of 'tolerance' or 'resilience' of an animal to infection (Albers et al. 1987). In the Australian studies of Albers et al. (1987), LWG had a relatively low heritability (0.09±0.07). New Zealand estimates for LWG have been quite variable and ranged from 0.08 to 0.39, with a weighted average of 0.15±0.03 (Table 1). Recent studies of resilience in New Zealand are discussed in more detail below.

Estimates of heritability for dag score (Table 2) had a range of 0.06 to 0.50 and the weighted average of 0.20±0.03. The average of the original estimates of Meyer et al. (1983) was 0.31.

Genetic correlations among traits

Genetic and phenotypic correlation estimates are summarised in Table 2. The phenotypic correlations between LWG and either FEC or dag score are consistently slightly negative (–0.02 to –0.12), as would be expected in lambs that are left undrenched. The genetic correlations, however, are much more variable and in general are not significantly different from zero. The relatively strong negative genetic correlation between FEC and dag score, originally reported by Watson et al. (1986), has since been balanced by three other estimates presented in Table 2, and the average of four is now close to zero.

Recent correlation estimates between log FEC and hogget body weight or hogget fleece weight (Table 2) show inconsistent results which have yet to be explained. Bisset et al. (1992, 1994) refer to data from breeders' flocks which show moderate negative genetic correlations, whereas provisional

Table 2 Estimates of phenotypic (rp) and genetic (rg) correlations among log FEC, liveweight gain (LWG), dag score (DS), hogget (=3D yearling) body weight (HBW) and hogget fleece weight (HFW).

Traits Correlated	Watson et al. (1986)	Bisset et al. (1992)	Douch et al. (1994)	Bisset et al. (1994)
log FEC—LWG				
rp	–0.06	–0.05	–0.12	–0.02
rg	–0.43, 0.49	–0.36±0.23	–0.30	–0.24±0.17
log FEC—DS				
rp	–0.18	0.11	–0.13	–0.12
rg	–0.70	0.44±0.19	–0.03	0.28±0.16
LWG—DS				
rp		–0.09	–0.10	–0.09
rg		–0.27±0.28	–0.04	–0.31±0.17
log FEC—HBW				
rp				–0.08
rg				–0.46±0.13
log FEC—HFW				
rp		–0.02		–0.07
rg		–0.15±0.18		–0.49±0.12

results from an animal model applied to data from the research (selection) flocks described by McEwan et al. (1992) show moderate positive genetic correlations. To date there are no phenotypic or genetic correlation estimates from New Zealand data between the traits in Table 1 and reproductive traits (e.g. number of lambs born or number of lambs weaned).

Ideally, paternal half-sib genetic correlations between disease and production traits should be estimated from sire groups where half of the animals provide the data on the disease trait, whilst the other half are measured for production in the absence of a challenge (Piper and Barger 1988). In the New Zealand experiments, genetic correlation estimates have been obtained where animals of both sexes have generally been drenched at weaning and they have then been challenged under minimal drench conditions. Thus, production traits have been measured under challenge conditions.

Selection Experiments for Faecal Egg Counts

Design

Selection experiments for high and low FEC in Romney sheep were initiated at Wallaceville in 1979 and in 1986. In 1988 these lines were combined into one set of closed selection lines for high and low FEC. No control population was maintained. Analyses are currently being undertaken to estimate selection differentials and realised direct and correlated responses.

Selection lines for high and low FEC were initiated at Ruakura in Romney sheep in 1985. A random-bred control line has been maintained since 1986. The high, control and low flocks were run at Rotomahana until 1989 and at Tokanui until 1992. They have since been merged with the Wallaceville lines and run at Wallaceville. In both the Ruakura and Wallaceville studies with Romneys, parasite infections are acquired naturally from pasture following the protocols described in Section 1. Selection in the Ruakura experiment is based on estimated breeding values (EBVs) calculated each year using BLUP (Best Linear Unbiased Prediction) mixed-model methodology (animal model). Fixed effects in the model include year of birth × sex subclasses, birth-rearing rank and regression on date of birth.

Another smaller study at Ruakura has involved selection of Perendale lambs for resistance or susceptibility following experimental challenge with *Haemonchus contortus* (Watson et al. 1992). The main aim has been to evaluate the outcomes of selecting Perendale lambs on parasitological parameters. The hypothesis has been that animals can be selected for 3 possible objectives, namely an early 'immune' resistance following minimal exposure to parasites, late resistance 'acquired' by 9 to 12 months, and susceptibility to experimental infection. Lambs are exposed to nematodes whilst grazing lightly contaminated pasture. These are the only selection flocks in New Zealand where parasitological responses are being followed after artificial rather than natural challenge.

Direct responses

Averaged over the two most recent lamb crops (1991 and 1992) the difference between the high and low FEC lines, in phenotypic standard deviations, was 0.86 in the Ruakura Romney lines and 1.65 in the Wallaceville lines. The performance of the Ruakura lines is shown in Figure 1. Analyses of responses from the Wallaceville lines are not complete.

Results from the Perendale selection line ewe lambs are given in Figure 2, showing the susceptible and early immune lines. The 'late acquired' line has

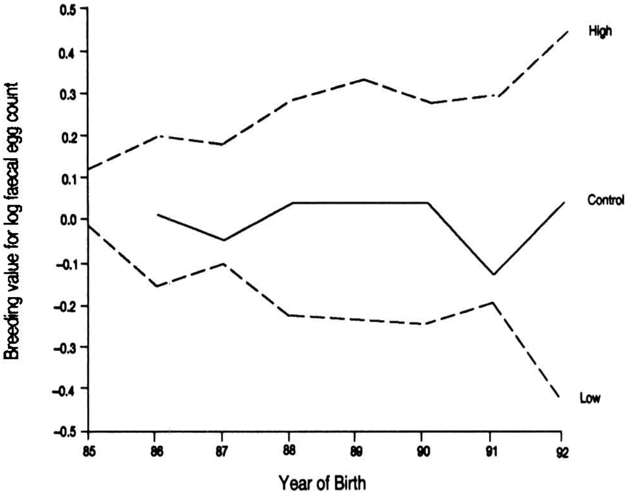

Figure 1 Progress in Ruakura Romney flocks selected for high faecal egg count (FEC), low FEC or controls (flocks originally at Rotomahana, then at Tokanui): average of breeding values for $\log_e$ FEC1 and for $\log_e$ FEC2.

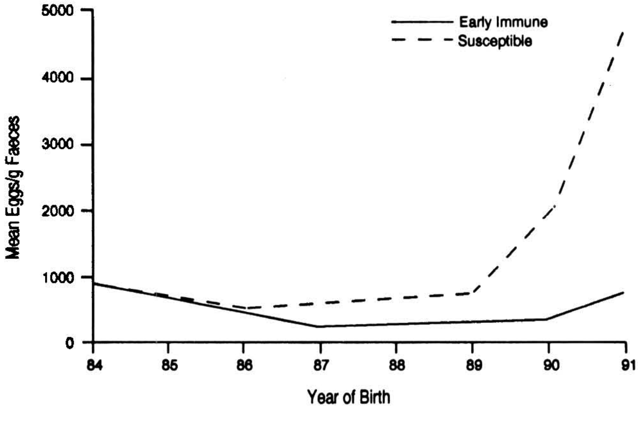

Figure 2 Progress in Perendale flocks selected for early immunity or susceptibility: geometric means of faecal egg counts from ewe lambs.

been subsampled from the 'early immune line' only recently. There were significant line differences in log FEC in lambs on three of five occasions sampled, showing that the late acquired resistance flock and the early immune resistance flocks both had lower FECs than the susceptible flock. Corresponding data from the Perendale selection flock ewes are given in Figure 3, showing pasture contamination may be reduced as a result of selection for immunity.

Correlated responses

Some significant differences between the high and low lines are beginning to appear for liveweight gain and dag score, which may represent a change from earlier reports (Baker et al. 1990; 1991). However, these need interpreting with caution. In order to be certain that they reflect a genetically correlated trait, rather than a possible founder effect, two criteria need to be met: Ruakura and Wallaceville flocks must show correlated responses in the same direction and the performance of the controls should lie between the high and low lines. These two requirements appear to have been met so far for antibody responses only (Douch et al. 1994).

In addition to correlated antibody responses, significant differences between the lines in periparturient FEC in adult ewes have now been shown at both locations. Periparturient FEC data were collected from the Ruakura Romney selection flock ewes in 1990, with samples being obtained before

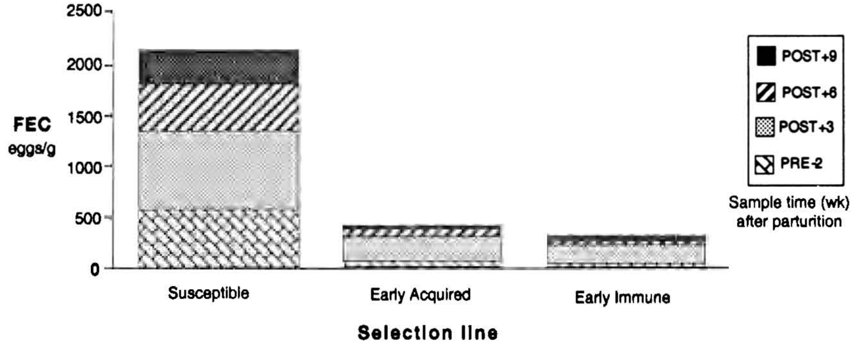

Figure 3 Periparturient faecal egg counts in selection flock Perendale ewes.

lambing, soon after, and at intervals up to weaning (Morris et al. 1993a). A REML repeatability model was fitted to ewe's log FEC, showing a repeatability of 0.50±0.04; selection flock means overall (transforming back from the log scale) were: high flock 349, control 160, low 140 epg, with the high flock having a greater value than the other two ($P<0.001$). From a regression analysis, a 10% increase in dam's FEC was associated with a 4.7% increase in her lambs' FEC at weaning (if no flock differences were accounted for in the analysis). Corresponding data from the Perendale selection flock ewes are given in Figure 3, again showing large differences among lines, presumably leading to differences in pasture contamination.

Measurement of worm burdens

FECs are being used in the selection flocks as an indirect predictor of worm burdens. Samples of lambs from the high and low FEC lines at Ruakura and Wallaceville have been investigated by necropsy to establish actual worm burdens. Results from the Ruakura lines suggest that there are selection-flock differences in the timing of development of immunity to infection and that these may be related to the worm species involved. Experimental infection of hoggets from the high and low FEC lines with both *Haemonchus contortus* and *Trichostrongylus colubriformis* has demonstrated that the low FEC line was infected with 30% fewer worms. This translated into 50% fewer worm eggs being shed per gram of faeces. The differences in worm numbers were due to *T. colubriformis* ($P<0.05$) but not *H. contortus* (Watson et al. 1989; Baker et al. 1990).

The relationship between FEC and post-mortem nematode burdens within and between selected 'resistant' and 'susceptible' sire progeny groups was critically examined in the Wallaceville lines (Bisset et al. 1991). Overall, correlations between FEC and total trichostrongyle burdens during autumn proved to be very high (0.83 and 0.75 respectively, for lambs born in 1988 and 1989). Progeny of the two most resistant rams from the Wallaceville lines were shown to harbour 70% fewer adult trichostrongyle worms and shed 85% fewer worm eggs than their susceptible counterparts. Resistance appeared to be effective against the establishment of adult worm burdens by the majority of important abomasal and small intestinal nematode species which infest lambs in New Zealand. Significant line differences were shown for *Ostertagia circumcincta*, *H. contortus*, *T. colubriformis*, *T. vitrinus*, *Nematodirus spathiger* and *Cooperia curticei*.

Possible mechanisms

Research to establish the parasitological or immunological mechanisms responsible for resistance to parasites in sheep is at a fairly early stage in New

Zealand (Douch 1990). However, some interesting results have become available from immunological studies (Douch et al. 1994). An ELISA assay has been developed to measure antibody response to a number of different parasitic genera including *T. colubriformis* and *H. contortus*. Blood samples were collected from lambs born in 1989–91 at both Ruakura and Wallaceville. Sampling took place at various times from 4 to 10 months of age. In the (larger) Wallaceville progeny test flock, the estimate of heritability for anti-*T colubriformis* antibody response was 0.27±0.08, and the genetic correlation between the antibody response and log FEC in March was −0.56±0.18. Since this ELISA test is relatively quick to process and is only about half the cost of a faecal egg count, it could be a useful indirect predictor of resistance as defined by FEC. Using genetic parameters presently available, the relative genetic progress in FEC expected from indirect (antibody) selection is about 0.5 of the direct FEC response. However, the different costs of antibody versus FEC tests, and the different technical requirements for sample collection, also need to be allowed for. In addition, the antibody difference between lines persists from March (6 months of age) onwards, regardless of week-to-week drenching experience (and thus FEC differences) of the animals. It is implicit in genetic correlations less than unity, that selection for antibody differences may not select for all mechanisms potentially involved in resistance.

Selection for Resistance in Different Environments

A reciprocal exchange of resistant and susceptible rams between Wallaceville and Ruakura was initiated in 1988. Four years of data have been analysed (Morris et al. 1993b). A total of fourteen Ruakura rams (eight high and six low) and twelve Wallaceville rams (seven high and five low) were used in their flock of origin in the mating years 1986–90 and then in the other location in 1988–91. Results were analysed using the BIREML mixed-model computer program (Meyer 1986) to estimate genetic (co)variances, treating records from the two locations as different 'traits'. Genetic source of sire and contemporary group were fitted as fixed effects. The preliminary results indicated a line by environment interaction, with a smaller divergence of estimated breeding values between the lines when progeny tested in a second location than when tested at home (Baker et al. 1991). The full results are now shown in Figure 4, where genetic correlations between performance measures (log FEC) at the two sites were 0.78±0.25 for January samples (average age four months) and 0.86±0.21 for March samples. This indicated that sires used in both sites were quite consistently ranked.

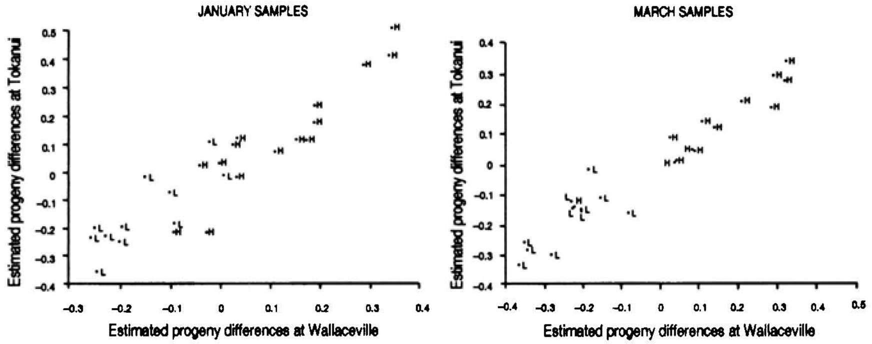

Figure 4 Estimated progeny differences in $\log_e$ faecal egg count (eggs/g) for high (H) and low (L) sires used at both Tokanui and Wallaceville.

Correlated Responses in Flocks Selected for Production

Studies at Ruakura, Massey and Invermay have been carried out to measure FEC levels in research flocks where selection for production was initiated at least twenty years ago alongside a control flock. In each case described below, FEC was analysed on a log transformed scale.

At Massey in 1956, a line of Romneys was established for increased hogget fleece weight (Blair et al. 1985). The 1990 lamb crop of the selected line and unselected controls were recorded for FEC in both worm-free and parasitised conditions. In both ram and ewe lambs, selected lambs were found to be shedding about three times as many faecal eggs as the controls, when undrenched (Howse et al. 1992). For fleece weight there was no interaction between selection flock and drench treatment, so that selected animals produced more wool under worm-free and parasitised conditions. The authors concluded that 'it would be unfortunate if FEC is pursued as a marker of resistance to internal parasitism, at the expense of selection for production traits, if it is only achieving a lower level of pasture contamination with nematode eggs'.

Scientists from AgResearch Invermay and Ruakura have reported on a similar FEC study carried out on the Woodlands flocks of Romney sheep established in 1973 (McEwan et al. 1992). Lines were selected for dam's litter size, 100-day weight, hogget fleece weight, or an index of litter size, body weight and fleece weight. Faecal samples were collected from lambs of various selection lines in 1981, 1982 and 1983. The FECs of 4-month lambs were 31 to 79% greater in the selection lines than in the control ($P<0.001$); largest differences were in the lines selected for 100-day weight or for hogget fleece weight. Because these are production selection flocks, we are presently revising the genetic correlation estimates previously reported, since we now have access to an animal model to take account of ram selection for fleece or body weight.

Faecal egg counts of the Tokanui production selection flocks of Romneys have been investigated (T.G. Watson, C.A. Morris, J.N. Clarke, unpublished), in lambs born in 1990–92. Three sets of selection and control flocks were investigated with the following results:

(i) Both the 100-day weight and hogget fleece weight lines from Woodlands (subsampled and transferred to Tokanui in 1991) had 57% higher FEC1 in January (4 months of age) than the control line ($P<0.001$), and the 100-day weight line (alone) had a significantly higher FEC2 in March than the control ($P<0.05$).

(ii) The Whatawhata hogget body weight, hogget fleece weight and control lines established by G.K. Hight in 1967 and transferred to Tokanui in 1981 (Johnson et al. 1994) had 32 and 47% greater FEC1s in the selection than control animals respectively ($P<0.01$), but only the hogget fleece weight line was significantly greater than the control in FEC2 ($P<0.001$).

(iii) In contrast, hogget body weight and control lines (established at Tokanui in 1973) did not differ significantly from each other in either FEC1 or FEC2.

Overall it must be concluded that there were no favourable correlated responses between hogget body weight or hogget fleece weight and log FEC in our production selection flocks. Most, but not all, of these selection flocks evaluated had significantly higher FECs in selection than control lines.

Studies on Resilience

Clunies-Ross (1932) was among the first to recognise the distinction between 'resistance to infection' and 'resistance to the effects of infection'. Albers et al. (1987) referred to the latter trait as resilience.

Beginning with the 1991 lamb crop, Wallaceville staff have carried out a study with a group of five East Coast, North Island ram breeders to examine the feasibility and implications of testing lambs for resilience to nematode challenge (i.e. those that show minimal symptoms of nematodes despite lack of anthelmintic treatment while grazing infective pasture). Resilience is thus defined as the ability of animals to grow and show minimal dags in spite of a worm challenge. For welfare and economic reasons, less resilient animals received a drench and were 'culled on paper' from the top ranking group (each time when mustered to the yards for drenching), whilst more resilient animals continued without a drench.

For the purposes of the study, resilience was examined in male lambs only, and it was defined in terms of total drenches required. In the first year (Bisset et al. 1994), heritabilities for resilience traits from 123 sire groups were estimated, with results as follows: (a) total drenches (0.13±0.03), (b) standardised age at first drench (0.13±0.03) including a method to account for the most desirable (i.e. undrenched animals), (c) proportion of males in a sire group drenched by the time when half of the flock were drenched ('BY2': 0.14±0.03). The genetic correlations among these three resilience traits were 0.91 or better (disregarding sign), indicating that the three traits were essentially the same.

Productivity and parasitological traits were examined in the corresponding female lambs under a standard minimal drenching regime for each flock. Heritabilities from the same 123 sire groups were: growth rate (0.16±0.04), dag score (0.28±0.06) and log FEC (0.21±0.05). The genetic correlations between standardised age at first drench in males and female traits were: yearling weight (0.43±0.15), yearling fleece weight (0.21±0.16), and of major importance, log FEC (0.16±0.18). In the second year (S.A. Bisset and C.A. Morris, unpublished), heritabilities from 98 sire groups were: standardised age at first drench (0.06±0.03), growth rate in males (0.15±0.04) and dag score in males (0.32±0.07). The genetic correlation between standardised age at first drench in males and log FEC in females was again very low (0.01±0.23). The implications are that:

1. Resilience, measured in terms of drench requirements (or growth under minimal drenching) has a low heritability; selection to increase it could be achieved by progeny testing, but not realistically by performance test selection.

2. The genetic correlation between resilience and resistance (FEC) under our New Zealand conditions appears to be very low and not significantly different from zero, and

3. If improved resilience and resistance are desired, it would be necessary to record both traits and select for both (and for production traits at the same time) in an index.

Facial Eczema

In many regions of the North Island of New Zealand, facial eczema is the major disease problem. In 1988, there was an indication on a farmer's property in Northland that some sire groups identified as having low FEC were also relatively resistant to facial eczema. This observation has been further investigated by measuring gammaglutamyltransferase (GGT) in the FEC lines at Ruakura and by measuring FEC in the flocks at Ruakura being selected for resistance or susceptibility to facial eczema (Morris et al. 1989). GGT is the enzyme presently being used to indicate liver damage from a facial eczema challenge. The accumulated FEC data in the facial eczema flocks still require analysis.

Application in Commercial or Stud Sheep Flocks in New Zealand

Rationale

Ram breeders and commercial producers are being confronted with two significant issues that will change farming systems in the future.

First, resistance to two of the three families of broad-spectrum anthelmintics appears to be developing rapidly in ovine parasites in widely different geographic regions of New Zealand (Watson et al. 1993a): 65% of sheep properties in New Zealand may be developing some form of white drench resistance; in addition, resistance of *O. circumcincta* to ivermectin is already established on goat farms; and both sheep and goats can act as hosts to this species.

Second, there is increasing demand to minimise application of chemicals in animal production.

Reduction in the annual frequency of anthelmintic application is regarded as the most important positive action required to meet these problems. One potentially viable option is to increase natural resistance of our national flock to nematodiasis through identification and use of 'elite' genotypes.

Participation in testing for resistance

A program was initiated on lambs from the 1987 lamb crop on a Romney sheep stud in Northland, screening over 700 ram and ewe lamb progeny from 15 sire groups (Watson et al. 1993b). A study of comparable size was begun at the same time in the nucleus flock (Wairunga) of a large group breeding scheme (Bisset et al. 1992). In both cases FEC was used to measure sire and progeny resistance to infection. Production traits were also recorded through

New Zealand's recording scheme, Animalplan. The aims by both participants were to assess the feasibility of developing 'on-farm' breeding programs for resistance to internal parasites under commercial conditions and to provide their clients, who purchase rams from them, with phenotypic rankings or EBVs of rams for FEC.

From 1988–90 there was an increase in farmer awareness and interest, and the Northland study was expanded to 10 farms and involved over 2700 lambs per year and four sheep breeds (Romney, Perendale, Coopworth and Merino). The clientele has since grown further. Participants have come from loosely bound breeder associations and a group breeding scheme. In most cases, breeders have recorded FEC data on ram lamb progeny only, aiming to evaluate those selected later for progeny FEC. Results from some of the original 10 farms have been published by Watson et al. (1993b), whilst genetic data from the 3-year study at Wairunga (lambs born in 1987–89) were published by Bisset et al. (1992) and general experiences were described by Parker (1991). The Ruakura work has now been expanded to a large-scale evaluation of industry sires by natural mating and artificial insemination at a Northland site (T.G. Watson) and at a Southland site (T.G. Watson and J. McEwan).

Protocol for resilience testing

The protocol for FEC testing is as described above for the experimental Romney flocks. The protocol for resilience testing is still experimental and being refined. In the first year, all ram lambs at each farm were run together for up to 5 drenches (i.e. individual animals were recorded as having received 0 to 5 drenches on specified dates). Overall, 5% of animals had still received no drench by the end of the trial. In the second year, animals were either drafted off when they received a drench or they were 'culled on paper' but not drafted off and they were not included in the later recording. Resilience testing was concluded when 50% of animals overall had received a drench, i.e. at the point where there was the potential for most discrimination among sire groups. Females were treated as described earlier for the routine FEC testing.

Results of resistance and resilience testing

Those farmers involved in FEC testing for resistance have seen that they can undertake the work without too much change to existing management systems and with minimal additional finance and labour input. In most cases the results must be viewed within individual farms. Substantial within- and between-sire variation on each property has served to maintain and expand the breeder interest. More breeders throughout New Zealand are expressing interest and taking the time to find out what is happening. Data from one large property with two breeds and crosses between them have clearly shown that major differences exist in levels of resistance between the Romney and Perendale breeds and their crosses. Selecting for resistance (low FEC) is now established at two locations. At the first, where limited production information is available, FEC is the sole determinant after the farmer has selected for production and conformation. The second property is dedicated to sire referencing and performance recording on Animalplan. Selection is based on EBVs for liveweights and gains, fleece weights, FEC and dag score.

The breeders involved in the study of resilience have large flocks and large progeny group sizes per ram. They thus have the animal resources to establish an effective progeny testing scheme to improve resilience, if they wish, and some are doing so. However, although the trait appears superficially to offer a more direct approach to breeding animals that require less drenching, the progress in productivity is likely to be slow. In addition, research to assess the potential advantages and disadvantages of resistance and resilience as breeding objectives is still in progress, and thus, there is a risk that advice may change with time.

Costs and benefits of FEC testing

Participants in FEC testing for resistance are required to meet direct costs for laboratory services, consumables and disbursements, with a small additional amount for extension built into the charges. Additional costs associated with animal health and welfare, production losses and labour during the program have been slight in relation to the perceived and realised benefits. They have been assessed by the owners generally on a qualitative rather than any quantitative basis as the 'on-farm' management responsibilities of the owner.

The primary expenses of initiating such a genetic recording and selection program lie in the relative commitment that farmers have to other selection traits, both production and disease. Adding another trait to selection objectives established by the breeder will affect rates of gain for both production and disease resistance performance.

The most obvious outcome at this time has been the increased level of interest and awareness that extension is bringing to the drench resistance situation throughout New Zealand. The threat is finally perceived to be real because it is affecting farmers throughout the country. Control measures and options are being revisited and reassessed. Alternatives, however potentially distant or unlikely to succeed, are being considered. Selection for increased resistance to parasites and disease obviously falls into this category.

In many cases breeders involved have been struck by the fact that they have not detected any marked decline in productivity or performance even though stock are left undrenched for a period. This suggests that drenching frequency has been too high. It must be concluded, however, that, without appropriate controls, the effect of subclinical infection in these cases is unknown.

Another important feature of the program is the fact that it is being driven from a number of directions (sire reference schemes, group breeding schemes and individual stud breeders) each of which may have different objectives and levels of interest. Furthermore, there is an awareness in the meat and wool production sectors that the future of their industries will be market and consumer driven. As a consequence, a number of 'environmental' and chemical application issues will have increasing impact on animal production systems; both New Zealand and Australia must be proactive in these areas.

Difficulties

The problems fall into three broad areas: farm/animal management, parasitological and environmental.

The most important animal issue may be the accuracy of FEC as an indirect evaluation of resistance, and its interaction with other factors that may increase the levels of 'noise'. These include such factors as host (age, sex, breed), parasite epidemiology (species, seasonality and abundance), nutrition and concurrent infections and diseases. This is where we believe that our ELISA studies may have potential.

On the farm, a conflict has arisen between research and commercial interests, with breeders trying to superimpose selection for parasite resistance over established production-oriented selection objectives. In spite of the potential benefits of establishing lines for increased resistance, the product and production criteria override the criteria for farmers who are not ram breeders, as these factors generally determine their drafting policy for replacement or culling. To a lesser extent, facilities, topography and farmer ability affect direction or option taken. All or each may alter outcomes significantly.

Unresolved Issues and Possible Future Research Directions

Research

(a) Immunological responses in selection lines, e.g.
    (i) OLA (MHC Class I) and MHC Class II,
    (ii) haemoglobins,

    - (iii) suppression of immune response,
    - (iv) further evaluation of Wallaceville ELISA test across parasite genera.
- (b) Associations with inflammatory responses.
- (c) Relative resistance/susceptibility of different breeds of sheep, especially exotic breeds recently imported from overseas.
- (d) Merits of natural versus artificial infection.
- (e) Assessment of worm burdens in the high and low selection lines following both natural and artificial infection. Relative importance of different parasitic genera.
- (f) Evaluate production performance and level of parasitic infections of the resistant and susceptible selection lines under different management systems and levels of exposure to parasites, e.g.
    - (i) organic farming systems,
    - (ii) non-drenching,
    - (iii) manage selection lines in separate grazing regimes.
- (g) Continued search for DNA markers or associations.
- (h) Continued evaluation of the relationship of parasite infection with other diseases.
- (i) Parasitic adaptation to selection responses by the host.
- (j) Do genetic correlations with FEC change at different levels of infection? Is this a statistical artefact?

Commercial application

- (a) Relative economic values for disease traits.
- (b) Selection indices for disease and production traits (e.g. lack of genetic correlation estimates).
- (c) Usefulness of marker traits (may need a veterinarian to collect blood samples).
- (d) Acquisition of 'elite' genetic material from commercial farmers for research purposes.
- (e) Relationship between FEC and dag score.

References

Albers, G.A.A., Gray, G.D., Piper, L.R., Barker, J.S.F., LeJambre, L.F. and Barger, I.A. 1987. The genetics of resistance and resilience to *Haemonchus contortus* infection in young Merino sheep. International Journal for Parasitology, 17, 1355–1363.

Baker, R.L., Watson, T.G., Bisset, S.A. and Vlassoff, A. 1990. Breeding Romney sheep which are resistant to gastro-intestinal parasites. Proceedings of the Australian Association of Animal Breeding and Genetics, 8, 173–178.

Baker, R.L., Watson, T.G., Bisset, S.A., Vlassoff, A. and Douch, P.G.C. 1991. Breeding sheep in New Zealand for resistance to internal parasites: research results and commercial application. In: Gray, G.D. and Woolaston, R.R. ed., Breeding for disease resistance in sheep. Melbourne, Australian Wool Corporation, 19–32.

Bisset, S.A., Morris, C.A., Squire, D.R., Hickey, S.M. and Wheeler, M. 1994. Genetics of resilience to nematode parasites in sheep. New Zealand Journal of Agricultural Research, 37, 521–534.

Bisset, S.A., Vlassoff, A. and West, C.J. 1991. Progress in selective breeding of sheep for increased natural resistance to infection with nematode parasites. New Zealand Journal of Zoology, 18, 85–86 (Abstract).

Bisset, S.A., Vlassoff, A., Morris, C.A., Southey, B.R., Baker, R.L. and Parker, A.G.H. 1992. Heritability of and genetic correlations among faecal egg counts and productivity traits in Romney sheep. New Zealand Journal of Agricultural Research, 35, 51–58.

Blair, H.T., Garrick, D.J., Rae, A.L. and Wickham, G.A. 1985. Selection responses in New Zealand Romney sheep. 2. Selection for yearling greasy fleece weight. New Zealand Journal of Agricultural Research, 28, 257–264.

Clunies-Ross, I. 1932. Observations on the resistance of sheep to infestations by the stomach worm, *Haemonchus contortus*. Journal of the Council for Scientific and Industrial Research, 5, 73–80.

Douch, P.G.C. 1990. The sheep's immune response to nematode parasites and prospects for its exploitation. Proceedings of the New Zealand Society of Animal Production, 50, 229–236.

Douch, P.G.C., Green, R.S., Morris, C.A., Bisset, S.A., Vlassoff, A., Baker, R.L., Watson, T.G., Hurford, A.P. and Wheeler, M. 1994. Genetic and phenotypic relationships between anti-*Trichostrongylus colubriformis* antibody level, faecal egg count and body weight traits in grazing Romney sheep. Livestock Production Science, 41, 121–132.

Howse, S.W., Blair, H.T., Garrick, D.J. and Pomroy, W.E. 1992. A comparison of internal parasitism in fleeceweight-selected and control Romney sheep. Proceedings of the New Zealand Society of Animal Production, 52, 57–60.

Johnson, D.L., Hight, G.K., Dobbie, J.L., Jones, K.R. and Wrigglesworth, A.L. 1994. Single trait selection for yearling fleece weight or liveweight in Romney sheep—direct responses. New Zealand Journal of Agricultural Research, 38, 115–122.

McEwan, J., Mason, P., Baker, R.L., Clarke, J.N., Hickey, S.M. and Turner, K. 1992. Effect of selection for productive traits on internal parasite resistance in sheep. Proceedings of the New Zealand Society of Animal Production, 52, 53–56.

Meyer, H.H., Harvey, T.G. and Smeaton, J.E. 1983. Genetic variation in incidence of daggy sheep—an indicator of genetic resistance to parasites? Proceedings of the New Zealand Society of Animal Production, 43, 87–89.

Meyer, K. 1986. Restricted maximum likelihood for data with a hierarchical genetic structure. Proceedings of the 3rd World Congress on Genetics Applied to Livestock Production, 12, 397–402.

Morris, C.A., Bisset, S.A., Baker, R.L., Watson, T.G., Johnson, D.L. and Wheeler, M. 1993b. An investigation of sire by location interactions for faecal nematode egg counts in lambs. Proceedings of the New Zealand Society of Animal Production, 53, 231–233.

Morris, C.A., Towers, N.R., Campbell, A.G., Meyer, H.H., Wesselink, C. and Wheeler, M. 1989. Responses achieved in Romney flocks selected for or against susceptibility to facial eczema 1975–1987. New Zealand Journal of Agricultural Research, 32, 379–388.

Morris, C.A., Towers, N.R., Wesselink, C. and Southey, B.R. 1991. Effects of facial eczema on ewe reproduction and postnatal lamb survival in Romney sheep. New Zealand Journal of Agricultural Research, 34, 407–412.

Morris, C.A., Watson, T.G., Baker, R.L., Hurford, A.P. and Hosking, B. 1993a. Repeatability estimates and selection flock effects for faecal nematode egg counts in Romney breeding ewes. Proceedings of the New Zealand Society of Animal Production, 53, 227–229.

Parker, A.G.H. 1991. Selection for resistance to parasites in sheep. Proceedings of the New Zealand Society of Animal Production, 51, 291–294.

Piper, L.R. and Barger, I. A. 1988. Resistance to gastro-intestinal strongyles: feasibility of a breeding programme. Proceedings of the 3rd World Congress on Sheep and Beef Cattle Breeding, Paris. 2, 593–611.

Skerman, T.M., Johnson, D.L., Kane, D.W. and Clarke, J.N. 1988. Clinical footscald and footrot in a New Zealand Romney flock: phenotypic and genetic parameters. Australian Journal of Agricultural Research, 39, 907–916.

Stear, M.J., Baldock, F., Brown, S., Gershwin, L.J., Hetzel, D.J.S., Miller, J.E., Nicholas, F.W., Rudder, T.H. and Tierney, T.J. 1990. The genetic control of gastrointestinal nematode infections in ruminants. Proceedings of the 4th World Congress on Genetics Applied to Livestock Production, 16, 449–452.

Watson, T.G., Baker, R.L. and Harvey, T.G. 1986. Genetic variation in resistance or tolerance to internal nematode parasites in strains of sheep at Rotomahana. Proceedings of the New Zealand Society of Animal Production, 46, 23–26.

Watson, T.G., Baker, R.L., Hosking, B. and Hurford, A.P. 1989. Progress in genetic selection for high or low nematode faecal egg count in Romney sheep. Proceedings of the Australian Society of Parasitology (Townsville, Australia), 75 (Abstract).

Watson, T.G., Hosking, B., Hurford, A.P. and Mather, B. 1992. Developments in breeding Perendale sheep for resistance or susceptibility to internal nematode parasites. Proceedings of the New Zealand Society of Animal Production, 52, 61–64.

Watson, T.G., Hosking, B. and McKee, P.F. 1993a. Stability of ivermectin resistance in a field strain of *Ostertagia* spp. Proceedings of the New Zealand Society of Animal Production, 53, 239–241.

Watson, T.G., Hosking, B, Johnson, D.L. and Hurford, A.P. 1993b. Selection programmes for nematode resistant sheep in commercial flocks. Proceedings of the New Zealand Society of Animal Production, 53, 359–362.

Woolaston, R.R. 1990. Genetic improvement of resistance to internal parasites in sheep. Proceedings of the Australian Association of Animal Breeding and Genetics, 8, 163–171.

Breeding for Resistance to Infectious Diseases of Small Ruminants in Europe

L. GRUNER AND F. LANTIER

ABSTRACT

Recent studies of the susceptibility to helminth infections of sheep and goats have focussed on artificial infections of lambs, kids and adults with several nematode species. Intra-breed studies have been orientated towards the elaboration of methods to investigate resistance acquired by lambs after natural or artificial monospecific or mixed infections with *Teladorsagia circumcincta* and *Haemonchus contortus*. Repeatability, heritability and correlations between types of infection (natural versus experimental) and between resistance to different species have been estimated. Possible use of blood parameters to complement faecal egg counts has also been investigated. Genetic studies on the resistance of sheep against intracellular bacterial diseases have concerned the identification of genes involved in the control of sheep salmonellosis. One of those genes could be the equivalent of the mouse *Ity/Bcg/Lsh* gene(s) that control susceptibility to murine infections with *Salmonella, Mycobacterium* and *Leishmania* respectively. Research in the United Kingdom has increased our knowledge of the role of the PrP protein in the susceptibility of sheep to scrapie and its role in related diseases of other animal species and humans. Research on resistance and immune responses of sheep to infectious and parasitic diseases in Europe is considered important because the sheep is an important livestock species and because it is a model species for ruminants and even for humans.

Europe is characterised by high ecological diversity caused by variable climate: from 'Atlantic' climate in the western part to 'Continental' in the East; and from 'Sub Polar' in the North to 'Mediterranean' in the South. Further diversity is caused by the presence of mountain chains and both humid and dry plains. There is a high diversity of small ruminant breeds which are specialised for meat, milk and wool production. Management systems are also highly diverse.

Small ruminant systems of production commonly are based on pasture and therefore parasitic diseases caused by helminths are of primary importance. Adults are treated with anthelmintic between one and three times per year and up to four times in young animals, to control gastro-intestinal nematodes. Commonly, young animals are treated each year to control cestodes and coccidia. Fascioliosis and dicrocoeliosis are also important; and protostrongylosis occurs in goats and sheep in the Mediterranean areas.

Strains of nematodes that are resistant to anthelmintics have developed in France, Germany, Holland, Switzerland and the United Kingdom. Resistance to the benzimidazoles is predominant, but the true prevalence of resistance in farms is poorly documented. Recent evidence confirms that this phenomenon is increasing in Holland (Borgsteede et al. 1991) and the United Kingdom (Jackson 1993).

The need to reduce the use of drugs has also involved interest in alternative and complementary methods of control such as increasing genetic resistance to nematode parasites (Cabaret and Gruner 1988; Gruner and Cabaret 1988; Gruner 1991; Stear and Murray, 1994). Investigations in Europe on genetic resistance have concerned resistance to two important nematode species, *Teladorsagia circumcincta* and *Haemonchus contortus.*

Intensive production systems for lambs include indoor management where the main parasitosis is coccidiosis, with associated diarrhoea and loss of production. Control measures include management and prophylactic medication (Gregory 1989), but investigations are orientated towards characterisation of common antigens from different species for vaccination. Very little is known about the genetic resistance of small ruminants against these diseases.

In most European countries bacterial diseases caused by intracellular bacteria have probably the highest incidence of all infectious diseases. They induce direct losses through abortion of ewes and does, septicemia and pneumonia in lambs and kids (for example, *Chlamydia*, *Brucella*, *Salmonella* and *Listeria*) or through the more specific lesions induced by *Listeria monocytogenes* (encephalitis), *Corynebacterium pseudotuberculosis* (caseous lymphadenitis), or *Mycobacterium paratuberculosis* (chronic enteritis). Their increasing economic importance stems from their effects on humans, which is linked mainly to their transmissibility through contact with livestock and consumption of milk and meat.

Control of the most important infectious diseases is orientated towards the development of vaccines and efficient preparations are used against brucellosis (Plommet et al. 1987), salmonellosis (Pardon et al. 1990a, 1990b) and chlamydiosis (Souriau et al. 1988). Investigations on the genetic resistance of sheep to intracellular bacteria such as *Salmonella* have been initiated in France, with the objective of finding a major gene for resistance. An additional aim is to increase our knowledge of the immune mechanisms involved in resistance to intracellular bacteria in ruminants and to demonstrate the feasibility of genetic improvement of innate resistance to such pathogens of worldwide importance.

Emerging viral diseases in sheep and goat are Maedi Visna and Caprine Arthritis Encephalitis caused by lentiviruses. Studies have been undertaken in diagnosis research, epidemiology and vaccination.

Scrapie is a widespread disease with genetically determined susceptibility. It has been studied since the sixties in the United Kingdom and more recently in France. A gene for susceptibility has been determined (Hunter 1992) in mice and sheep. The mechanism of transmission of the disease and the nature of the infectious agent are largely unknown. Because of the spread of this kind of disease in Europe (and the Middle East) and the value of the work done by different teams in the United Kingdom, it seemed important to us that a short description of the current investigations should be included here.

Resistance to Parasites

The breed component of resistance to nematode parasites

European sheep breeds have been studied in the United States in comparisons between exotic and local breeds naturally infected while grazing (Stewart et al. 1937; Scrivener 1967; Loggins et al. 1965; Knight et al. 1973). In every case, the local breed was more resistant than the imported one. Comparisons of breeds for their susceptibility to natural infections (Euzeby et al. 1961), or to a single dose of *Trichostrongylus axei* (Ross 1970) or *H. contortus* (Altaif and Dargie 1978) were performed with a small number of animals. Hence it could not be concluded that the observed differences were due to breed or to a sire effect.

More recently, investigations on genetic resistance have been carried out as part of a program to increase the value of poor lands in the south of France by increasing lamb production. Experimental flocks of purebred, highly-prolific Romanov sheep, and Romanov crossbred with the local Lacaune or Mérinos d'Arles breeds, were established. These different genotypes were developed in various ecological situations to collect information on their productivity and adaptability. Animals were infected naturally and, later, experimentally with *T. circumcincta*. Romanov ewes were more susceptible than Lacaune ewes (Gruner et al. 1986) and more susceptible than Mérinos and crossbreds (Gruner et al. 1992a). In this last experiment, individual egg counts of the 250 ewes from the flock were performed at the end of the grazing season for four years to allow for the effects of year of sampling and the age and physiological state of the ewes. From this work, great interest has been shown in crossbred ewes which combine high prolificacy due to Romanov genes and intermediate resistance to adverse conditions including parasitosis due to heterosis (Bouix et al. 1992).

In comparisons of the Saanaen and Alpine dairy goat breeds from north-western France, a significant breed effect was demonstrated for gastrointestinal nematodes and for the small lungworm *Muellerius capillaris* as measured by egg and larval outputs. In these studies faecal egg excretion was found to be lower in Alpine goats (Cabaret and Anjorand 1984; Cabaret et al. 1989; Richard et al. 1990).

Resistance: a dynamic process of regulation of the worm population

The breed effect described above was observed in adult animals after natural infections, but not in young kids less than 3 months old (Richard and Cabaret 1993) or young lambs (Gruner et al. 1994), after a single infection with *T. circumcincta*. This confirms that resistance is not innate. The first manifestation of regulation of the worm population was observed in these young lambs when they received a trickle infection and were slaughtered after a month when most of them had immature worms. Another manifestation of resistance was the lower proportion of worms remaining two months post infection in Merino compared with Romanov lambs. Establishment of worms was, on average, 54% of the larval dose used to infect the animals. By comparison, the establishment in adult ewes 2–7 years old, dewormed before receiving a challenge dose of 20 000 infective larvae of *T. circumcincta*, was 13% with a part of the worm burden staying at the 4th larval stage (Gruner 1991). The distribution of the worms between the animals also changed from a normal in lambs to a negative binomial in adults in which 80% of the total worms were in 20% of the infected animals. In the comparisons between Saanen and Alpine goat breeds, the conclusion was that the egg output after similar infections was greater in the Saanen breed, but the worm burden was similar; the difference was due to the prolificacy of the female worms (Richard et al. 1990).

In conclusion, resistance acts on the establishment of the infective larvae, on the rate and speed of development into the adult stage, on the survival of the adults and on the prolificacy of the female worms.

Measurement of Resistance

Resistance is a dynamic process of parasite regulation by the host and the faecal egg production is one of the variables which reflects this regulation. There is a need to define the type of infection and the most informative faecal egg count (FEC) which will most accurately reflect resistance. Scottish Blackface lambs with high or low FEC after natural exposure to gastrointestinal strongyles had patterns of egg output with or without a rapid peak after a challenge infection with 50 000 L3 of *T. circumcincta*, suggesting different mechanisms of regulation (M.J. Stear, pers. comm.). Since it is not practicable to perform the high number of FECs needed to define such patterns on a large number of animals, the most informative FECs must be selected. For example, after experimental infection of Hungarian Merinos with *H. contortus*, the best time to sample the lambs was around 50 days after a second infection (Kassai et al. 1990). Similar results were observed in Romanov sheep (Luffau et al. 1990).

Genetic parameters

To measure the genetic parameters of repeatability, heritability and, eventually, genetic correlation between two traits, different methods of calculation and of experimental design are available. This is illustrated by two current experiments, one in France and the other in Poland (summarised in Table 1).

Resistance against *T. circumcincta* in Romanov sheep

Heritabilities and their standard deviations (sd) were compared for different experimental designs, with different numbers of animals and for different values of heritability. It was concluded that the least expensive experimental design in time and number of animals necessary was bidirectional selection on one generation (Gruner et al. 1992b). This was chosen in the French experiment, to estimate the parameters of resistance to *T. circumcincta*. The objective was to test the feasibility of a selection for resistance to natural

Table 1 Characteristics of the French and Polish experiments to determine genetic parameters of resistance to gastrointestinal nematodes in sheep.

Characteristic	France	Poland
Breed	Romanov	Polish long wool type
Parasite	*T. circumcincta*	Predominantly *T. circumcincta* and *H. contortus*
Breeding structure	Bidirectional selection	Progeny testing
Number of animals	200 lambs/generation (6–10 months)	200 lambs aged 4–7months (and their dams) each year from 12 sires
Type of infection	Natural on a contaminated pasture Experimental infection with 20000 L3	Natural from May to September
Faecal egg counts	3 x 3 times	Ewes 3 and lambs 2 times

infection by using experimental infections. Two hundred male lambs, representing the maximal diversity of sires (n=21) from the same flock, were divided into two balanced flocks. One flock grazed on pasture contaminated with *T. circumcincta*, whereas the other was experimentally infected with the same strain of *T. circumcincta*—20 000 L3/lamb on three occasions separated by a treatment (fenbendazole) with three weeks of recovery time before the new dose. The lambs were between six and ten months old. Egg counts were performed three times during the 4th week post-infection and simultaneously in the grazing flock. After the last egg count, lambs were classified on the previous six counts and, in each flock, the five with highest and five with lowest index (mean root square of the six last EPG) were selected and mated with non-selected ewes. Fifty offspring of each of these four groups of males were designated the parental generation. Thus, it was possible to estimate the heritability of resistance to natural infection, the heritability to experimental infections and the genetic correlation between these two traits.

Two types of problems were encountered in natural infections. First, parents ingested a total of L3 estimated at 18 000 because of the summer drought in 1990 whereas lambs ingested around 180000 L3 (ten times more), because of the rainy summer in 1992. Second, the difficulty of maintaining a monospecifically infected pasture obliged us to use, for the second year of experiment, a pasture previously grazed by cows the preceding year. Thus, lambs received mixed infection with *Cooperia oncophora* at a low level and eggs and individual cultures needed identifying.

Resistance in Polish long wool type sheep

This work was initiated in a selection flock of a local breed that had exchanges of sires with production flocks in the area (Nowosad et al. 1992). Each year, around 15 sires were tested in the experimental farm for production traits. Their progeny, born in February, grazed from June until the beginning of October. Individual egg counts were performed in August and September for the lambs and in May, July and September for their mothers. On each occasion in the first year, the egg counts were repeated after one week. Repeatabilities between these counts were very high and this second sample was not taken in the second year. Advantage was taken of this reduced work load by doubling the numbers of animals in the second year.

Preliminary results of these experiments (Table 2) demonstrated higher values of repeatability between the two or three egg counts done the same week after natural infection compared with the rapid evolution of the egg production of *T. circumcincta* after artificial infection. Repeatabilities between

Table 2 Preliminary estimates of the genetic parameters of resistance against gastrointestinal parasites in Romanov and Polish long wool sheep.

Breed		**Romanov**		**Polish long wool**	
Type of infection		**Experimental**	**Natural**	**Natural**	
Animals		**Lambs**	**Lambs**	**Ewes**	**Lambs**
Repeatability of FEC within periods	Year 1	0.42	0.64	0.76	0.54
	Year 2	0.69	0.71	–	–
Repeatability of FEC between periods	Year 1	0.26	0.30	0.57	0.50
	Year 2	0.48	0.47	0.44	0.48
Heritability (h^2±S.E.)		0.55[a]		0.28±0.16	
Genetic Correlation		>0.90			

[a] See explanation in text.

periods were lower. The within-period repeatabilities reflected the same worm population; the between-period repeatabilities reflected seasonal variations of worm population after natural infection and the new population established after the challenge dose in experimental infections. The realised heritability after experimental infections was 0.55. Drought during the parental generation in natural conditions of infection did not permit good classification of the sires as resistant or susceptible, but the estimation of the resistance of their offspring in the two types of infection suggests that the genetic correlation is very high. To confirm these preliminary results, a second generation is running with the offspring of sires selected after natural infection. In Polish long wool sheep, a heritability of 0.28±0.16 was calculated with a sire model from data of 336 offspring of 25 sires. This value was close to the estimates of Baker et al. (1991) and Watson et al. (1986) in natural mixed infections. Data from the third year of experiment will permit a more accurate estimate.

One important aspect is the relationship between FEC and worm burden. In the experiments on resistance of Romanov sheep against *T. circumcincta*, 30 lambs were slaughtered in each generation from each of the flocks with natural or experimental infections. In every case, the best correlation was between total worm burdens (or female worm burdens) and the egg counts taken close to time of necropsy, after square-root transformation. In the parental generation, larval intake during natural infection was low and the correlation coefficient was 0.80 indicating a slower turnover of the worms.

Associated parameters

In Scottish Blackface and Finn Dorset, Altaif and Dargie (1978) concluded that homozygous Hb A-type sheep were more resistant to a dose of 10000 L3 of *H. contortus* in terms of FEC and worm burdens, but this was not true with a dose of 50 000 L3. More recently, Kassai et al. (1990) found Hb A-type Merino sheep to be less susceptible and confirmed the relation between Hb type and the severity of anaemia. In an experiment with Romanov sheep constructed to verify the relationship between acquisition of resistance to *H. contortus* and Hb type (Luffau et al. 1986, 1990), it was concluded that faecal egg counts were not related to haemoglobin polymorphism, but might be affected by one or several genes located in the OLA complex. In this work, a statistically significant effect ($P<0.05$) of the haemoglobin allele received from the sire on the packed cell volume was found; it seemed that animals carrying the HbA allele were less anaemic than the others. These differences could be due to differences in oxygen affinity between HbA and HbB animals.

Stear and Murray (1994) found that resistant sheep have high eosinophil, globule leucocyte and IgA plasma cell responses with low worm burdens and that susceptible sheep have high IgG1 responses and high worm burdens. These authors concluded that the three measures of egg counts, plasma pepsinogen and peripheral eosinophilia permitted a better estimate of the worm burden of *T. circumcincta* than egg counts alone, after a challenge dose of 50000 L3.

Stability and specificity of resistance

When estimating acquired resistance it is important to account for both fixed influences on variation such as sex and breed and environmental factors that can also influence resistance. In the comparison of the susceptibility of Romanov and Mérinos d'Arles ewes (Gruner et al. 1992a), the breed effect was significant in dry ewes but disappeared in ewes with one suckling lamb and the hierarchy of resistance was reversed in ewes with twins. This demonstrated the effect of the lactation intensity on the removal of the acquired resistance to gastro-intestinal nematode parasites. A benzimidazole treatment before a challenge dose has been shown to modify the expression of resistance of sheep to *H. contortus* by reducing immunity (Benitez-Usher et al. 1977; Luffau et al. 1990).

Without good knowledge of the mechanism of resistance, it is difficult to know the extent of the protection. In Romanov and Merino ewes naturally infected by grazing irrigated pastures contaminated with numerous helminth species, Merino ewes were less infected with *Nematodirus* spp., *Dictyocaulus* *filaria*, *Chabertia ovina*, the group formed by *T. circumcincta* and *Trichostrongylus colubriformis* and by *Moniezia* spp. than Romanov and crossbred ewes. *Dicrocoelium dentriticum* was similarly present in the three genetic types. On the other hand, Romanov ewes were infected with *Fasciola hepatica* and with the dominant species of the small lungworm *Neostrongylus linearis* (Gruner and Cabaret 1988).

Phenotypic correlations have been estimated in sheep selected against *T. circumcincta* and challenged with *T. colubriformis* (J. Bouix, pers. comm.) and in sheep selected against *H. contortus* and challenged with *T. colubriformis* (Streter and Kassai 1993). No genetic correlations between resistance against these important parasite species have been estimated but, as they often exist in the same area in Europe, with seasonal variations in their predominance, these estimates need to be made.

Genetic resistance to coccidiosis

Very little information is available on the genetic resistance of small ruminants to coccidiosis. In an experiment with 120 three-month-old lambs, faecal oocyst counts were performed over short (4 days) or longer (1 month) periods. Repeatabilities were higher in short periods and it was concluded that the component in variation of oocyst counts was similar to that recorded for trichostrongylid egg counts (Yvore et al. 1992). In a survey on 1100 lambs from 59 sires, using 2 to 3 oocyst counts per lamb, heritability estimates were between 0.10 and 0.20 (Bouix et al. 1992).

Resistance to Infectious Diseases

Resistance criteria

Usefulness of studies on innate resistance to infectious diseases has been discussed by a number of classical veterinary pathologists claiming that selection for resistant flocks might increase the number of infected individuals. In fact, genetic resistance might have more interesting consequences for the population geneticist or the epidemiologist than a 'simple' decrease in the expression of clinical signs of illness. Like good vaccines, natural resistance might also decrease the level of infection of the individuals and the excretion of the infectious agent, limiting the spread of the disease and further contamination of domestic animals and humans. So the criteria of resistance have to be carefully defined and will be preferably quantitative rather than 'death or survival' after an experimental challenge. As in laboratory rodents, the number of organisms colonising the spleen, the liver, or other target organs of ruminants can be such a criterion (Lantier and Fensterbank 1985; Lantier 1987; Pépin et al. 1991).

Moreover, studies on genetic resistance to infectious diseases have focussed on pathogens against which we have imperfect means of control, or no means at all. These include microbial pathogens such as *Brucella*, *Salmonella*, *Mycobacterium*, or *Listeria*, that are able to survive in the environment and to persist for long periods in most wild and domestic mammalian hosts. Limiting the spread of such diseases, for example by increasing the resistance of the small ruminants population by genetic selection, would be of great interest.

Immunology of the sheep

Kinetic studies of the immune response during infection might provide useful immunological correlates of the host susceptibility. By using the now classical procedure developed by Biozzi et al. (1980) in mice, Amlid et al. (1980) have selected for several years in Norway two lines of goats with low and high antibody responses to antigens (heterologous erythrocytes and tetanus toxoid).

In humans, high antibody response to *Mycobacterium leprae* is associated with an increased severity of the disease. We have made similar observations in mice and sheep experimentally infected with *Salmonella abortusovis*, both for the cellular and the humoral components of the immune response (Bernard et al. 1993). Simple measurement of the antibody response after vaccination with a live vaccine might provide a useful tool for developing an experimental selection of lines resistant, or susceptible, to *Salmonella* or other intracellular bacteria.

The breed component of resistance to bacteria

There is breed effect on susceptibility to caseous lymphadenitis provoked in sheep by *Corynebacterium pseudotuberculosis*. The Prealpes breed from south of France was susceptible and the Ile-de-France breed, from the northern part of the country, was resistant. Experimental infection with *C. pseudotuberculosis* of groups of 20 lambs from these two breeds raised with artificial milk in absence of contamination and in the same building provided some evidence of such a breed effect on the severity of the lesions and on persistency of the challenge strain into the host (Pépin et al. 1988). However, neither breed was homogenously resistant or susceptible, and this suggests unequal frequencies of the corresponding alleles in the tested groups. The intermediate level of infection at slaughtering of F1 between Prealpes and Ile-de France (40 sheep) suggested a polygenic control of susceptibility to *C. pseudotuberculosis*. This remains to be tested in a second generation cross between resistant and susceptible animals.

A survey of the susceptibility to *Salmonella abortusovis* of seven French sheep breeds was made by subcutaneous challenge of groups of approximately 20 lambs with a virulent strain (2.5×10^9 *S. abortusovis* per lamb). Lambs were five-month-old males from salmonellosis-free flocks. They were slaughtered at the peak of infection, on day six, after infection and the level of bacterial colonisation were determined in organs and lymph-nodes. A breed effect was observed on a number of clinical and bacteriological parameters and on antibody responses. However, a considerable intra-breed variability was also noticed in all breeds on most measured parameters (Lantier et al. 1989). Such intra-breed variability can be used to measure the genetic parameters of the inheritance of susceptibility to salmonellosis in sheep and/or to look for the role of a major gene (see below).

Genetics of resistance to intracellular bacteria

In the mouse, genetic control of susceptibility to *Salmonella typhimurium* has been well established (review by Wakelin and Blackwell 1988). At least six distinct host genes are presently identified. The early growth of *S. typhimurium* in spleen and liver of infected mice is influenced by one major gene, the gene *Ity* (Plant and Glynn 1979). Gene(s) with the same localisation on mouse chromosome 1 determine the evolution of *Leishmania* (*Lsh*, Bradley et al. 1979) or *Mycobacteria* (*Bcg*, Gros et al. 1981) infections. Such gene(s) should have economic and health importance for domestic animals. Our laboratory has undertaken a series of experiments to study the feasibility of using genetic resistance to control infectious diseases in sheep (Lantier et al. 1989). Genetic control of mouse resistance to *S. abortusovis* infection has been investigated as a first step in our attempt to transpose mouse results to sheep.

S. abortusovis is an ovine adapted serotype which induces abortion and, to a lesser degree, mortality of young animals (Pardon et al. 1990b). *S. abortusovis* is non pathogenic for other domestic animals and humans, although it does multiply in experimentally infected mice (Pardon and Marly 1979).

Although the differences are sometimes less definitive than with *S. typhimurium*, infection of mice with *S. abortusovis* provides an interesting model. In this model, the innate mechanisms of resistance to bacterial multiplication are very likely controlled by genes similar to the ones described earlier with more classical models of *Salmonella* infection. Both humoral and cellular mechanisms are involved in innate or acquired resistance to salmonellosis. They can be investigated with the *S. abortusovis* model (Guilloteau et al. 1993) and, because the mouse experimental infection is close to the one obtained in the natural host (Lantier 1987), transposition of mouse results to sheep should be facilitated.

Comparison of the levels of infection in spleen and liver of mice from various inbred lines suggested that the *Ity* gene also controlled mouse resistance to *S. abortusovis*. This was confirmed by Mendelian analysis, i.e. by testing the co-segregation of various genetic markers and of the susceptibility to *S. abortusovis* in backcross mice from resistant and susceptible mouse lines (Oswald et al. 1992). The availability of strains of mice congenic for the *Ity/Bcg/Lsh* region further allowed to confirm the localisation of the *S. abortusovis* resistance gene close to and very likely identical with, the *Ity* gene on mouse chromosome 1.

This region of mouse chromosome 1 has been shown to be conserved in human and bovine species and we decided to test for its conservation in sheep. By using sheep–hamster somatic hybrid lines, various markers of mouse chromosome 1 and human chromosome 2q were assigned to the sheep synteny group U11 (Tabet-Aoul et al. 1992).

The effects of this gene on the sheep resistance to *S. abortusovis* infection, or to infection with other *Salmonella* serotypes, or other intracellular pathogens of sheep, remain to be investigated. However, the demonstration of the conservation of a large fragment of chromosome (Womack and Moll 1986) raises the possibility of approaches similar to the one described above, that is to investigate similar 'genetic control of host resistance to infection and malignancy' (Skamene 1985) in mouse models of infection and in domestic animal species. The conservation of the NRAMP gene and associated markers in sheep demonstrates the feasibility of such an approach.

Resistance to scrapie

Scrapie is a fatal disease of sheep and goats (Hunter et al. 1992; Wood et al. 1992) involving a progressive degeneration of the central nervous system. The incubation period may last for months or years (Hunter 1992). Scrapie is transmitted by both the horizontal and vertical route by an unconventional organism, the nature of which remains the object of multiple hypotheses and discussions (Bradley and Matthews 1992). Similar diseases affect other species such as cattle, mink and cats, which are supposed to have been contaminated by infected sheep meat used for animal nutrition. Transmission of the disease from animals to humans remains highly speculative. However, progressive spongiform encephalopathy is a common characteristic of the three human diseases, Creutzfeldt-Jacob disease (CJD), Gerstmann-Strausler-Scheinker (GSS) syndrome and Kuru. More recently, fatal insomnia has also been attributed to the accumulation of prion protein (PrP) in the central nervous system (Goldfarb et al. 1992).

The PrP is coded by the PRNP gene on human chromosome 20 and mouse chromosome 2. In cattle, this gene has been recently assigned to the cattle group of synteny U11 (Womack 1993). The PrP can be isolated from the lymphoid organs (lymph-nodes, spleen) and from the nervous system in the normal host, but its role is unknown. PrP accumulates as amyloid fibrils in the organs (essentially in the brain) before clinical signs of the disease appear. Transgenic and 'knock out mice' for the PrP gene have been produced. Knock out mice normally live and are resistant to the disease, affording more evidence for the essential role of the host PrP. The genetics of resistance to scrapie has been reviewed by Hunter (1992).

Transmission of the disease from sheep to sheep, or to laboratory animals is possible by most inoculation routes (intracerebral, parenteral, oral, conjunctival) through the administration of homogenised organs (usually brain). Several 'strains' of scrapie have been differentiated by their origin, clinical signs and duration of the incubation period in inbred lines of mice. Early experimental studies of transmission of scrapie in sheep suggested a breed effect and a large intra-breed variability, in the susceptibility to the disease. Three flocks have been bred in Britain for their susceptibility and/or resistance to scrapie (susceptible and resistant lines from Cheviot and Herdwick breeds, now at NeuroPathogenesis Unit, IAH, AFRC/MRC, Edinburgh; and from a resistant Swaledale flock now at the MAF Experimental Husbandry Farm, Redesdale, Northumberland). Most isolates of the scrapie agent, but not all, produce a faster disease in flocks with the *Sip*^{A} allele of the scrapie Incubation Period (*Sip*) gene. A goat homolog of the *Sip* probably exists, but this has to be proved. A murine equivalent of the *Sip* gene has been identified in inbred strains of mice. As in sheep, it co-localises with the PrP gene and might be identical, but this is controversial.

Various mutations in the sheep PrP gene, as evidenced by means of various molecular biology techniques (RFLP, PCR, DGGE), have been associated with the susceptibility to experimentally induced disease (i.e. the *Sip* alleles), or with the onset of the disease in naturally occurring scrapie (Hunter 1992; Laplanche et al. 1993). Some of them seem to be also present in other species affected by similar encephalopathy, particularly in CJD-affected humans, but a number of other mutations in the PrP gene have been associated with prion disease (Watanabe and Duchen 1993).

Because of the opposite effects of some isolates of the scrapie agent in usually susceptible and resistant lines of sheep (or mice), a marker-assisted selection for susceptibility to scrapie in sheep would probably not ensure an eradication of the disease. However, studies both on DNA polymorphism associated with the occurrence of the disease, and on the diversity of scrapie isolates, might be useful to determine strategies for an efficient prophylaxis. Another very helpful area of research would be on the mechanisms of the vertical transmission of the scrapie agent.

Conclusions: the Main Topics Developed in Europe

Genetic maps of small ruminants, in addition to those for cattle and pigs, are being developed in Europe. Scrapie and salmonellosis-susceptibility genes have now been identified on the ovine genome; and other major genes of resistance to diseases, or involved in other physiological process, may contribute to the development of regional mapping. The primary purpose of such a map is probably to clone a major gene by accumulating markers in its vicinity until one might be sufficiently close to begin the sequencing process. Such a reverse genetic approach (from the phenotype to the gene, which then allows the identification of the relevant protein) is now classical for the identification of genetic deficiencies in humans. This approach has been used in mice for the identification of a candidate gene for mouse genes *Ity/Bcg/Lsh* by the group of P. Gros (Vidal et al. 1993). By allowing the identification of the genomic regions of interest, comparative mapping will probably remain the only possible approach when one ignores the immune mechanisms and/or the protein concerned with the observed phenotype. Furthermore, this approach provides potential genetic markers that could be useful for the identification of resistant or susceptible individuals when performing a familial analysis of any physiological trait, e.g. resistance to infection.

Comparison of the susceptibility of various animal populations (inbred or outbred lines, selected lines, flocks, breeds) is a powerful means of identification of mechanisms of resistance to natural and, more efficiently, experimental infectious or parasitic diseases. This is generally well known in laboratory animals, but multiple examples do exist in farm animals and are described in detail in this volume. Analysing differences between groups of well-identified animals will be conducted to find both new mechanisms and new genes concerned with the regulation of the immune response to pathogens. Moreover, a reasonable hypothesis is that a number of the genetic polymorphisms that are associated with known immune response genes (e.g. immunoglobulin, complement, cytokine genes) are also probably responsible for variations in the efficiency of the response to naturally occurring diseases.

In France, sheep breeding flocks contribute animals to an Individual Control Centre where a number of traits are assessed in a common environment. These traits include a parasitological test and may include other disease traits. It is necessary to have more information on the genetic correlations between resistance to different diseases and between resistance and performance traits.

A good definition of practical selection objectives for resistance to parasitic and infectious diseases is not available. Which of the following outcomes is desirable?

- animals resistant to the establishment of the pathogenic agent?
- resilient animals supporting the presence of the agent?
- low-contaminant animals, which will diminish the general level of infection of the group?

The process of selection could depend on the genetic parameters characterising transmission of susceptibility but could also depend on the pathogenic agent. As an example, selecting animals resistant to scrapie could be dangerous in absence of detection. Animals with this genotype could be infected and, in the absence of a method to detect the agent, contaminate the environment during the incubation period before the first clinical signs appear.

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References

Altaif, K.I. and Dargie, J.D. 1978. Genetic resistance to helminths. The influence of breed and haemoglobin type on the response of sheep to primary infection with *Haemonchus contortus*. Parasitology, 77, 161–175.

Almlid, T., Steine T., Lund, A. and Larsen, H.J. 1980. Selection for high and low immune response in goats. Animal Blood Groups and Biochemical Genetics, 11, Suppl. 1.

Baker, R.L., Watson, T.G., Bisset, S.A., Vlassof, A. and Douch, P.G.C. 1991. Breeding sheep in New Zealand for resistance to internal parasites: research results and commercial application. In: Gray, G.D. and Woolaston, R.R. ed., Breeding for disease resistance in sheep. Melbourne, Australian Wool Corporation, 19–32.

Benitez-Usher, D., Armour, J., Duncan, J.L., Urquhart, G.M. and Gettinby, G. 1977. A study of some factors influencing the immunization of sheep against *Haemonchus contortus* using attenuated larvae. Veterinary Parasitology, 3, 327–342.

Bernard S., Guilloteau L., Buzoni-Gatel D., Pépin M., Bernard F., Lantier I. and Lantier, F. 1993. Mechanisms of acquired immunity induced by the live-attenuated *Salmonella abortusovis* (Rv6) vaccine. NATO Advanced Workshop, The Biology of *Salmonella*. Messine, 2–5 Mai 1992.

Biozzi, G., Mouton, D., Sant-Anna, O.A., Passons, H.C., Gennari, M., Reis, M.H., Ferreira, V.C.A., Heumann, A.M., Bouthillier, Y., Ibanez, O.M., Stiffel, C. and Siqueira, M. 1980. Genetics of immune responsiveness to natural antigens in the mouse. Current Topics in Microbiology and Immunology, 85, 31–98.

Borgsteede, F.H.M., Schavemaker, S., Van der Burg, W.P.J., Gaasenbeek, C.P.H. and Pekelder, J.J. 1991. Increase of anthelmintic resistance in sheep in the Netherlands. Veterinary Record, 129, 430–431.

Bouix, J., Gruner, L., Vu Tien Khang, J., Luffau, G. and Yvoré, P. 1992. Recherches sur la résistance des ovins au parasitisme interne: mise en évidence d'une composante génétique. Bulletin des Groupements Techniques Vétérinaires, 5, 91–99.

Bradley, R. and Matthews, D. 1992. Transmissible spongiform encephalopathies of animals IV. OIE (Office International des Epizootics). Vol. IV, No. 2. Paris, OIE.

Bradley, D.J., Taylor, B.A., Blackwell, J., Evans, E.P. and Freeman, J. 1979. Regulation of *Leishmania* population within the host. III. Mapping of the locus controlling susceptibility to visceral Leishmaniasis in the mouse. Clinical and Experimental Immunology, 37, 7–14.

Cabaret, J. and Anjorand, N. 1984. Comparaison de l'infestation naturelle par les strongles et *Moniezia* spp. chez les races caprines Alpine et Saanen. Bulletin de le Société Française de Parasitologie, 2, 49–52.

Cabaret, J. and Gruner, L. 1988. Genetic variability of resistance to parasites. In: Proceedings of the 3rd World Congress on Sheep and Beef Cattle Breeding 19–23 June 1988, Paris, vol.1, Paris, INRA-Publications. 577–592.

Cabaret, J., Anjorand, N. and Leclerc, C. 1989. Parasitic risk factors on pastures of French dairy goat farms. Small Ruminant Research, 2, 69–78.

Euzeby, J., Bussieras, J., Moraillon, P. and Boccard, R. 1961. Etude de la réceptivité comparée de 4 races ovines à l'infestation par les nématodes de la famille des Trichostrongylidés. Bulletin de la Société des Sciences Vétérinaires et de Médecine Comparée de Lyon, 63, 121–128.

Goldfarb, L.G., Petersen, R.B., Tabaton, M., Brown, P., LeBlanc, A.C., Montagna, P., Cortelli, P., Julien, J., Vital, C. and Pendelburry, W.W. 1992. Fatal familial insomnia and famùilial Creutzfeld-Jacob disease: disease phenotype determined by a DNA polymorphism. Science, 258, 806–808.

Gregory, M.H. 1989. Epidemiology and control of ovine coccidiosis. In: Yvoré, P. ed., Coccidia and intestinal coccidiomorphs, VIth International Coccidiosis Conference, Tours, France, 17–20 October 1989, INRA., 409–418.

Gros, P., Skamene, E. and Forget, A. 1981. Genetic control of natural resistance to *Mycobacterium bovis* (BCG) in mice. Journal of Immunology, 127, 2417–2421.

Gruner, L. 1991. Breeding for helminth resistance in sheep and goats. In: Owen, J.B. and Axford, R.F.E. ed., Breeding for diseases resistance in farm animals, Proceedings of an International Symposium, Bangor, Wales, Sept. 1990. Wallingford, U.K., CAB International, 187–200.

Gruner, L. and Cabaret, J. 1988. Resistance of sheep and goats to helminth infections: a genetic basis. In: Thomson E.F and Thomson, F.S. ed., Increasing small ruminant productivity in semi-arid areas. ICARDA, Aleppo, Syria. Dordrecht, Netherlands, Kluwer Academic Publishers, 257–265.

Gruner, L., Bouix, J., Cabaret, J., Boulard, C., Cortet, J., Sauvé, C., Molénat, G. and Calamel, M. 1992a. Effect of genetic type, lactation and management on helminth infection of ewes in an intensive grazing system on irrigated pasture. International Journal for Parasitology, 22, 919–925.

Gruner, L., Bouix, J., Vu Tien Khang, J., Eychenne, F., Cabaret, J., Cortet, J. and Sauve, C. 1992b. Bidirectional selection of sheep upon their resistance to *Teladorsagia circumcincta* natural or experimental infections: results of the first generation. VIth EMOP, Sept. 7-11 1992, The Hague, Netherlands, 115.

Gruner, L., Cabaret, J., Sauvé, C. and Pailhories, R. 1986. Comparative susceptibility of Romanov and Lacaune sheep to gastro-intestinal nematodes and small lungworms. Veterinary Parasitology, 19, 85–93.

Gruner, L., Mandonnet, N., Bouix, J., Vu Tien Khang, J., Cabaret, J., Hoste, H., Kerboeuf, D. and Barnouin, J. 1994. Worm population characteristics and pathological changes in lambs after a single or a trickle infection with *Teladorsagia circumcincta*. International Journal for Parasitology, 24, 347–356.

Guilloteau, L., Buzoni-Gatel, D., Bernard, F., Lantier, I. and Lantier, F. 1993. *Salmonella abortusovis* infection in susceptible BALB/cby mice: importance of Lyt-2+ and L3T4+ T cells in acquired immunity and granuloma formation., Microbial Pathogenesis, 14, 45–55.

Hunter, N. 1992. Scrapie in sheep and goats. In: Speedy A.W., ed., Progress in sheep and goat research. CAB International, 131–151.

Hunter, N., Foster, J.D. and Hope, J. 1992. Natural scrapie in British sheep: breeds, ages and Prp gene polymorphisms. Veterinary Record, 130, 389–392.

Jackson, F. 1993. Anthelmintic resistance—the state of play. British Veterinary Journal, 149, 123–138.

Kassai, T., Fésüs, L., Hendrikx, W.M.L., Takats, Cs., Fok, E., Redl, P., Takacs, E., Nilsson, Ph.R., van Leeuwen, M.A.W., Jansen, J., Bernadina, W.E. and Frankena, K. 1990. Is there a relationship between haemoglobin genotype and the innate resistance to experimental *Haemonchus contortus* infection in Merino lambs? Veterinary Parasitology, 37, 61–77.

Knight, R.A., Vegors, H.H. and Glimp, H.A. 1973. Effects of breed and date of birth of lambs on gastrointestinal nematode infections. American Journal of Veterinary Research, 34, 323–327.

Lantier, F. 1987. Kinetics of experimental *Salmonella abortusovis* infection in ewes., Annales de Recherches Veterinaires, 18, 393–396.

Lantier, F. and Fensterbank, R. 1985. Kinetics of REV.1 infection in sheep. In: Verger, J.M. and Plommet, M. ed., *Brucella melitensis*, Seminar CEC Programme of Coordination of Research on Animal Pathology, 14–15 Nov. 1984, Dordrecht, Martinus Nijhoff, 247–251

Lantier, F., Vu Tien Khang, J., Bouix, J., Nguyen, T.C., Molénat, I., Pardon, P., Pépin, M. and Boivin, R. 1989. Variability of sheep resistance to *Salmonella abortusovis* infection. 2nd International Veterinary Symposium, July 24–28 1989, Hannover, Germany. Abstracts in Immunobiology, supplément vol. 4.

Laplanche, J.L., Chatelain, J., Westaway, D., Thomas, S., Dussaucy, M., Brugere-Picoux, J. and Launay, J.M. 1993. PrP polymorphisms associated with natural scrapie discovered by denaturing gradient gel electrophoresis. Genomics, 15, 30–37.

Loggins, P.E., Swanson, L.E. and Koger, M. 1965. Parasite levels in sheep as affected by heredity. Journal of Animal Science, 24, 286–287.

Luffau, G., Nguyen,T.C., Cullen, P., Vu Tien Khang, J., Bouix, J. and Ricordeau, G. 1986. Genetic resistance to *Haemonchus contortus* in Romanov sheep. In: Dickerson, G.E. and Johnson, R.K. ed., 3rd World congress on Genetics applied to Livestock Production, Lincoln, Nebraska, July 17–22 1986, vol XI, 683–690.

Luffau, G., Vu Tien Khang, J., Bouix, J., Nguyen, T.C., Cullen, P. and Ricordeau, G. 1990. Resistance to experimental infections with *Haemonchus contortus* in Romanov sheep. Genetics, Selection and Evolution, 22, 205–229.

Nowosad, B., Krupinski, J., Niemczyk, W., Malczewski, A., Gruner, L. and Bouix, J. 1992. Genetic sheep resistance to helminth parasites in Poland: results of the first year in a Polish long-wool type. VIth EMOP, Sept. 7–11 1992, The Hague, Netherlands, p. 117.

Oswald, I.P., Lantier, F., Moutier, R., Bertrand, M.F. and Skamene, E. 1992. Intraperitoneal infection with *Salmonella abortusovis* is partially controlled by a gene closely linked with the Ity gene. Clinical and Experimental Immunology, 87, 373–378.

Pardon, P. and Marly, J. 1979. Experimental *Salmonella abortusovis* infection of normal or primo-infected CD1 mice., Annales de Microbiologie, 130B, 21–28.

Pardon, P., Marly, J., Lantier, F. and Sanchis, R. 1990a. Vaccinal properties of *Salmonella abortusovis* mutants for streptomycin: screening with an ovine model., Annales de Recherches Veterinaires, 21, 57–67.

Pardon, P., Sanchis, R., Marly ,J., Lantier, F., Guilloteau, L., Buzoni-Gatel, D., Oswald, I.P., Pépin, M., Kaeffer, B., Berthon, P. and Popoff, M. 1990b. Experimental ovine salmonellosis (*Salmonella abortusovis*): pathogenesis and vaccination. Research in Microbiology, 141, 945–953.

Pépin M., Lantier F. and Pardon P. 1988. Breed susceptibility to experimental *Corynebacterium pseudotuberculosis* infection in lambs. Proceedings of the 3rd World Congress on Sheep and Beef Cattle Breeding, 19–23 June 1988, Volume 1, Paris, INRA. 646–648.

Pépin, M., Pardon, P., Lantier, F., Marly, J., Levieux, D. and Lamand, M. 1991. Experimental *Corynebacterium pseudotuberculosis* infection in lambs: kinetics of bacterial dissemination and inflammation. Veterinary Microbiology , 26, 381–392.

Plant, J. and Glynn, A.A. 1979. Locating *Salmonella* resistance gene on mouse chromosome 1. Clinical and Experimental Immunology, 37, 1–6.

Plommet , M., Bosseray, N., Lantier, F., Bernard, F., Pardon, P. and Rodolakis, A. 1987. Simultaneous vaccination by three living attenuated strains of *Brucella*, *Salmonella* and *Chlamydia* in mice. Vaccine, 5, 27–32.

Richard, S. and Cabaret, J. 1993. Primary infection of kids with *Teladorsagia circumcincta*: susceptibility and blood constituents. Veterinary Parasitology, 47, 279–287.

Richard, S., Cabaret, J. and Cabourg, C. 1990. Genetic and environmental factors associated with nematode infection of dairy goats in northwestern France. Veterinary Parasitology, 36, 237–243.

Ross, J.G. 1970. Genetic differences in the susceptibility of sheep to infection with *Trichostrongylus axei*. A comparison of Scottish Blackface and Dorset breeds. Research in Veterinary Science, 11, 465–468.

Scrivner, L.H. 1967. Genetic resistance to ostertagiasis and haemonchosis in lambs. Journal of the American Veterinary Medical Association, 151, 1443–1446.

Skamene, E., ed., 1985. Genetic control of host resistance to infection and malignancy. Progress in Leucocyte Biology, Vol. 3. New York, Alan R. Liss.

Souriau, A., Bosseray, N., Rodolakis, A., Lantier, F. and Plommet, M. 1988. Antichlamydial immunity in ewes conferred by vaccination with a combination of three live chlamydia, brucella and salmonella vaccines. Veterinary Record, 123, 12, 29–32.

Stear, M.J. and Murray, M. 1994. Genetic resistance to parasitic disease: particularly of resistance to gastrointestinal nematodes. Veterinary Parasitology, 54, 161–176.

Stewart, M.A., Miller, R.F. and Douglas, J.R. 1937. Resistance of sheep of different breeds to infestation by *Ostertagia circumcincta*. Journal of Agricultural Research, 55, 923–930.

Streter, T. and Kassai, T. 1993. Responder classification of sheep: comparative assessment of distinct *Haemonchus* and *Trichostrongylus* infections. 14th International Conference of the WAAVP, 8th–13th August 1993, Cambridge, U.K., 307.

Tabet-Aoul, K., Pitel, F., Lantier, I., Gros, P., Saidi-Mehtar, N. and Lantier, F. 1992. Mapping of the ovine genome by somatic hybrid cell lines: the IDH1, FN1, VIL1 and CHNRG syntenic group is conserved in sheep. Animal Genetics, 22, p. 96.

Vidal, S., Malo, D., Epstein, D., Skamene, E. and Gros, P. 1993. Natural resistance to infection with intracellular parasites: isolation of a candidate gene for Bcg. Cell, 73, 469–485.

Wakelin, D. and Blackwell, J., ed. 1988. Genetics of resistance to bacterial and parasitic infection. London., Taylor and Francis.

Watanabe, R. and Duchen, L.W. 1993. Cerebral amyloid in human prion disease. Neuropathology and Applied Neurobiology, 19, 253–260.

Watson, T.G., Baker, R.L. and Harvey, T.G. 1986. Genetic variation in resistance or tolerance to internal parasites in strains of sheep at Rotomahana. Proceedings of the New Zealand Society of Animal Production, 46, 23–26.

Womack, J.E. 1993. The goals and status of the bovine gene map. Journal of Dairy Science, 76, 1199–1203.

Womack, J.E. and Moll, Y.D. 1986. Gene map of the cow: conservation of linkage with mouse and man. Journal of Heredity, 77, 2–7.

Wood, J.N., Done, S.H., Pritchard, G.C. and Wooldridge, M.J. 1992. Natural scrapie in goats: case histories and clinical signs. Veterinary Record, 131, 66–68.

Yvore, P., Cabaret, J. and Solon, S. 1992. Repeatability of ovine faecal oocyst counts in natural infections with *Eimeria* spp. International Journal for Parasitology, 22, 515–518.

Genetics of Disease Resistance in Small Ruminants in Africa

R.L. BAKER

ABSTRACT

Disease is one of the most important biological constraints to small ruminant production in the many different agroclimatic zones of Africa. Loss of production, high levels of mortality and the cost of drugs are some of the major concerns. Current control strategies include vaccination, medication, isolation of animals from pathogens and improved sanitation for management systems. In Africa, many control strategies are limited by lack of efficient veterinary services, unavailability or high costs of drugs and vaccines, increasing occurrence of drug resistance by pathogens and limited scope to improve management cost-effectively. An attractive alternative solution is to breed for disease resistance.

There is a large and diverse range of indigenous breeds of sheep and goats in Africa, some of which appear to be genetically resistant or tolerant to disease. The limited data on between- and within-breed genetic variation in resistance to helminthiasis and trypanosomiasis are reviewed and the need for further characterisation is identified. Evidence for the genetic basis of disease resistance in sheep in countries outside Africa, suggests that breeding for disease resistance could be a viable control method. More information on genetic parameters of disease resistance and better assessment of the economic impact of disease is required to develop appropriate breeding strategies.

In Africa, diseases are a substantial constraint on sheep and goat production. They are often a major contributor, along with poor nutrition and poor management, to high annual mortality rates that can range from 30 to 50% in young stock and 10 to 30% in mature animals.

One option for overcoming the impact of infectious disease in small ruminants is the identification and use of disease resistant animals or breeds. This could proceed at the same time as other essential studies on the epidemiology and the costs of disease, development of new vaccines, chemotherapeutic drugs, health management strategies and improvement of animal health delivery systems. This paper will document the evidence in Africa for genetic resistance to diseases in small ruminants and outline some options for breeding for disease resistance.

Why Breed for Disease Resistance?

Conventional approaches to disease control include vaccination, medication, isolation of animals from pathogens, improved sanitation and eradication. Lack of effectiveness of some vaccines and development of resistance of pathogens to drugs and chemicals are becoming increasingly common (e.g. Nicholas 1987; Waller 1991). In Africa, resistance of ticks to acaricides and resistance of trypanosomes to trypanocides is well documented (Young et al. 1988; Peregrine 1994). Similarly, anthelmintic resistance has been reported worldwide across the range of helminth parasites of most domestic livestock (Waller 1991), particularly in gastrointestinal nematode parasites in sheep and goats. Although a reliable assessment of the prevalence of anthelmintic resistance in sub-Saharan Africa is not available, prevalence is believed to be low or non-existent in many cases simply because anthelmintics are used rarely or not at all (Nansen 1991). However, the climate of many tropical and sub-tropical regions of Africa is highly favourable to the development of anthelmintic resistance. Thus, as anthelmintic usage increases, resistance may also increase and this view is supported by recent reports of anthelmintic resistance and multiple anthelmintic resistance in Tanzania (Bjorn et al. 1991), Kenya (Waruiru et al. 1991; Maingi 1991; Mwamachi et al. 1993) and Nigeria (Mbah et al. 1992). In Africa, the development of anthelmintic resistance and drug resistance in general, is further compounded by the use of drug preparations of questionable efficacy.

Resistance to drugs and demand for lower levels of chemical residues in livestock products and in the environment, has stimulated interest in disease control methods which are less reliant on chemotherapy. In Africa the high cost and poor availability of chemicals are further limitations on their use. Thus, there is considerable incentive to use breeds or genotypes that are resistant or tolerant to disease and do not require expensive chemotherapy.

Economic Impact of Disease

Vaccines are available for a few of the many infectious diseases of small ruminants in Africa, for example against peste de petits ruminants. Where comprehensive control campaigns have been mounted, disease prevalence has been markedly reduced. The effects of some acute bacterial and viral diseases are often temporary, and if the animal survives, recovery is usually rapid. In contrast, diseases such as helminthiasis and trypanosomiasis have chronic effects (FAO 1991, 1992). Estimates of the economic impact of the total array of diseases affecting small ruminants in Africa are not available and are difficult to obtain (Ademosun 1988).

Helminthiasis

Given that some important viral diseases can be adequately controlled by vaccination, internal parasitism by nematodes and trematodes is considered to be the most important constraint to sheep and goat production in Africa (Mack 1982; Smith 1988). Information on direct and indirect losses caused by helminth infection is limited. There are few published estimates but they suggest that production losses are generally high. Graber (1965) calculated an annual loss of 11.3% of the total economic value of sheep and goats in Chad due to gastrointestinal nematodes. Schillhorn van Veen (1973) estimated an 11% annual loss of value to that country's sheep and goat industry from helminthiasis in Nigeria. Akerejola et al. (1979) estimated an annual loss of over US$40 million due to gastrointestinal nematodes in the Kano area of northern Nigeria, and annual mortality rates of 60% in lambs and 30% in ewes have been reported (Eysker and Ogunsasi 1980). In Kenya, haemonchosis alone has been estimated to cause an annual loss of US$25 million in sheep and goat production (Preston and Allonby 1979). In Zaire, Brito (1947) estimated an annual mortality rate of 54% due to gastrointestinal helminths alone and an additional 12% due to the combined effects of helminth and coccidial infections.

Ticks and tick-borne diseases

Tick-borne diseases of sheep and goats in Africa include babesiosis, theileriosis, anaplasmosis and cowdriosis. In many areas ticks can be a problem and frequent dipping with acaricides is carried out. Heartwater (*Cowdria ruminantium* infection) is an important disease of both cattle and small ruminants in Africa. It is transmitted by several species of the tick *Amblyomma* of which *A. variegatum* is the most common and can cause high rates of mortality in sheep and goats (Uilenberg 1976, 1983; Arnold and Travassos Santos Dias 1983; Norval et al. 1992a; Camus and Barre 1988). Smith (1988) suggested, however, that tick-borne diseases do not usually cause serious morbidity and mortality of small ruminants.

A number of *Theileria* species occur in sheep and goats in North Africa and some of these are highly pathogenic (Dolan 1989). Integrated control strategies being developed to control *T. parva* include tick control, acaricides, resistant genotypes and immunisation (Norval et al. 1992b).

Trypanosomiasis

Most of the studies of animal African trypanosomiasis have been carried out in cattle. Trypanosomiasis has not been regarded as an important disease of small ruminants and the prevalence of trypanosomiasis appears to be lower in sheep than cattle (Coulibaly et al. 1988; ILCA 1986). Kramer (1966) reported that trypanosomiasis in Nigeria was of little significance in sheep and goats and Finelle (1974) stated that sheep were seldom infected with trypanosomes under natural conditions. However, a more recent survey in tsetse-infected regions in Zaire indicates that trypanosomiasis may be more important in small ruminants than was previously thought (Makumyaviri et al. 1989). Trypanosome infections in small ruminants in East Africa (Zwart et al. 1973; Griffin and Allonby 1979a; Hendy 1988) have been associated with severe economic losses (Griffin and Allonby 1979a; Kanyari et al. 1983). It has also been suggested that small ruminants may be important reservoirs of infection for other livestock (Mahmoud and Elmalik 1977).

Genetic Variation in Disease Resistance

This review will concentrate on the larger body of evidence which is available for genetic variation in small ruminants for resistance or tolerance to helminthiasis and trypanosomiasis. Other diseases for which there is little evidence of genetic variation are discussed elsewhere in this volume.

Breed differences

Helminthiasis. Nearly all the studies reviewed by Gray (1991) and Baker et al. (1992) are characterised by poor experimental design, both in terms of the numbers of animals of each breed tested, and lack of information on how the breeds were sampled. In addition, very few of the studies took account of variation among sires within breeds. The magnitude of the between-sire differences can be of the same order as the largest of the between-breed differences (Gray, et al. 1987). Many of the breed differences reported could just reflect a single sire effect and hence should be interpreted cautiously.

Some breeds of sheep have been identified as resistant in a number of independent studies. These breeds include the Florida Native and St. Croix in the USA (Courtney et al. 1984; Courtney et al. 1985a, b; Knight et al. 1973; Gamble and Zajac 1992) and Red Maasai of East Africa (Preston and Allonby 1978, 1979; Bain et al. 1993; Baker et al. 1993). It is noteworthy that the St. Croix sheep originated in West Africa and are probably related to the Djallonke sheep (Bradford and Fitzhugh 1983), which are believed to be relatively resistant to endoparasites (Osinowo and Abubakar 1988; Smith 1988). Most of the breeds identified as being relatively resistant are native or 'unimproved' breeds. This presumably reflects the fact that these breeds have been under natural selection with little or no treatment with anthelmintics.

Evidence for genetic variation for resistance to endoparasites among goat breeds is limited (Preston and Allonby 1978; Cabaret and Anjorand 1984; Shavulimo et al. 1988; Richard et al. 1990; Rohrer et al. 1991). It is usually the indigenous goat breeds (e.g. the Small East African) that are more resistant than the imported exotic breeds.

Virtually all research on genetic variation to endoparasites in small ruminants has concentrated on nematode parasites. In many areas of Africa and the developing world liver fluke (trematode) infections (*Fasciola hepatica* and *F. gigantica)* are also an important constraint to small ruminant production (FAO 1992). Although it is well documented that sheep can mount an effective immune response (self-cure) to nematode parasites, it has been amply demonstrated that sheep are unable to acquire resistance to liver flukes (e.g. Boyce et al. 1987). This possibly explains why very little research has been undertaken on genetic resistance to liver fluke infections and only two studies have been published. Boyce et al. (1987) found significant breed differences in faecal egg counts and fluke counts following experimental infection of five breeds of sheep with *F. hepatica*. Barbados Blackbelly sheep were the most susceptible to infection while St. Croix and Florida Native sheep were the most resistant. Although none of the breeds demonstrated an ability to resist reinfection with *F. hepatica*, clear breed differences were detected in response to infection. In the other study Wiedosari and Copeman (1990) document relatively high resistance to *F. gigantica* in Javanese thin-tailed sheep, although there was no contemporaneous breed comparison.

Trypanosomiasis. It has been recognised since the beginning of this century that some breeds of cattle, as well as many wild animal species, possess the ability to survive and be productive in tsetse infected areas without the aid of drug treatment, where other breeds rapidly succumb to the disease (Dolan 1987; Murray et al. 1991; Paling and Dwinger 1993). This trait has been termed trypanotolerance.

There has been a considerable research effort on trypanotolerance in cattle but much less is known about trypanotolerance in sheep or goat breeds. The Djallonke sheep and West African Dwarf goats, which are indigenous to the tsetse-infested areas of West and Central Africa and survive without the aid of chemotherapy, have been described as trypanotolerant (ILCA 1979; Toure et al. 1983; Mawuena 1987; Adah et al. 1993; ITC 1992). Studies in East Africa have also shown that the indigenous sheep (Red Maasai and Blackhead Persian) and goats (Small East Africa and Galla) are more resistant to trypanosomiasis than exotic breeds (Griffin and Allonby 1979 a, b; Kanyari et al. 1983; Munyua 1985). Whitelaw et al. (1985) failed to demonstrate any significant differences in resistance of the Small East African, Galla and their crosses with Nubian or Toggenburg goats in Kenya, following challenge with *Trypanosoma congolense*. They attributed this finding to the high virulence of the strain used. Similarly, McGuire et al. (1985) found no significant differences in resistance to trypanosomiasis among four exotic breeds of dairy goats (i.e. Toggenburg, Nubian, Alpine and Saanen). On the other hand, significant differences in trypanotolerance have been reported among strains of East African goats with those sampled from tsetse-endemic areas being more resistant than those from tsetse-free areas (Mutayoba et al. 1989).

Although the prevalence of trypanosomiasis is often higher in cattle than sheep or goats raised in the same environment (e.g. Coulibaly et al. 1988), this does not necessarily indicate that small ruminants are more resistant to trypanosomiasis than cattle. It may just indicate that small ruminants do not graze in heavily tsetse-infested areas or that the tsetse fly finds cattle more attractive than small ruminants. More research on the epidemiology of trypanosome infections in small ruminants is required to resolve these questions.

Within-breed genetic variation

Estimates of heritabilities and repeatabilities of resistance to endoparasites in sheep and goats in Africa are limited but those available were reviewed by Baker et al. (1992). The few heritability estimates range from 0.11 to 0.42 for faecal egg count (FEC) and haematocrit (PCV) (Rohrer et al. 1991; Baker et al. 1993), essentially similar to those found in Australia and New Zealand. Other repeatability estimates available range from 0.05 to 0.42. In some studies the low repeatability estimates for FEC were caused by the egg counting procedure. The improved modified McMaster egg counting technique (MAFF 1977) is recommended and usually gives higher repeatability estimates. It is important that the egg counting technique is standardised in any experimental study on resistance to endoparasites and that the procedure used is clearly documented.

In Africa, there is evidence that resistance to endoparasites (assessed in terms of FEC or PCV) is favourably associated with production, particularly in terms of reproduction and mortality (Baker et al. 1993). If this is found to be true generally then FEC and PCV are likely to be easier and more practical parameters to measure than resilience traits.

Trypanosomiasis. No estimates of within-breed genetic variation for trypanotolerance in sheep and goats have been reported, but the progress made in cattle is reviewed here since it seems likely that similar criteria will also be relevant to small ruminants. For example, the course of *T. congolense* infection and pathophysiology in sheep has been shown to be broadly similar to that observed in cattle (Katunguka-Rwakishaya et al. 1992).

Anaemia can be assessed relatively easily in terms of PCV in infected animals and moderate to high heritabilities (0.35–0.64) have been reported (Murray et al. 1990; Trail et al. 1991 a,b,c; Trail and d'Ieteren 1992; Dolan 1993). Positive phenotypic and genetic correlations between control of anaemia and production traits (i.e. growth, calving interval and cow productivity) have been reported (Trail et al. 1991b), although the genetic correlation estimates have high standard errors and are biased—as discussed in the next section—because production was measured under parasite challenge.

The degree of parasitaemia is not as easily or reliably assessed as PCV, and the most common method used to date is the detection of trypanosomes in blood smears using the dark ground/phase contrast buffy coat microscopic method (Murray et al. 1977; Paris et al. 1982). This technique is highly specific but not very sensitive, thus resulting in low repeatabilities. For example, in Orma Boran cows in Kenya, repeatabilities of number of times cows were classed as parasitaemic within a lactation (parasitaemia recorded at 2-week intervals) were 0.07±0.07 for *T. vivax* infections and 0.24±0.06 for *T. congolense* infections (Dolan 1993).

Recently, antigen-detection enzyme immunoassays (antigen-ELISA) have been developed for the diagnosis of *T. vivax, T. congolense* and *T. brucei* infections (Nantulya and Lindquist 1989; Nantulya 1990). These assays are based on monoclonal antibodies that recognise trypanosome antigens specific for the three trypanosome species. The antigen-ELISA has been shown to be four times more sensitive than the buffy coat technique in monitoring *T. congolense* infections in cattle (Masake and Nantulya 1991). Nantulya (1993) has reported the development of a latex agglutination antigen test for diagnosis of African trypanosomiasis: the presence of specific antigens for different trypanosome genera in the specimen leads to the agglutination of the sensitised latex particles. The results are read within 5 minutes and virtually no equipment is required as the tests can be carried out using heparinised whole blood, plasma, or serum. If field validations demonstrate that this test has a high degree of sensitivity and specificity then it could be a very useful and simple tool for large-scale breeding programs.

Trail et al. (1992a) used the antigen-ELISA for additional assessment of trypanotolerance in N'Dama cattle in Gabon. The antigen test detected trypanosome antigen in 90% of the animals parasitologically positive. More importantly, 40% of the animals that had not been found to be positive using the buffy coat test, were shown to be positive by the antigen-ELISA test. Data from 79 progeny of 21 sires was then analysed for genetic variation in parasitaemia. The approach taken was to consider animals with positive antigen test results, but not positive buffy coat test results to have some ability to limit parasite growth. This parasite control measure had a heritability estimate of 1.08±0.50 and clearly warrants further investigation in larger data sets.

The trials with N'Dama cattle in Gabon using the antigen-ELISA also showed marked differences in the effects of *T. congolense* and *T. vivax* on animal performance. While *T. congolense* infections had significant deleterious effects on animal growth the *T. vivax* infections did not (Trail et al. 1992b). In mixed infections, which are detected more frequently with the antigen-ELISA than the buffy coat test, the significant negative regression of weight gain on the number of *T. congolense* infections was obscured when *T. vivax* data were not deleted. This result illustrates the necessity for accurate trypanosome species identification if infection effects and linkages with other criteria of trypanotolerance (e.g. PCV) are to be clarified and adequately quantified.

Further studies with N'Dama cattle in Zaire (ILCA 1992) and with Orma Boran cattle in Kenya (Dolan 1993) have shown differences in the kinetics of *T. vivax* and *T. congolense* infections, in both cases using the buffy coat test to detect parasitaemia. In both studies it was shown that infection rates with both *T. vivax* and *T. congolense* were lower in calves than their dams. This change in the proportion of *T. vivax* and *T. congolense* infections with age appears to be a common feature in the studies in Gabon and Zaire with N'Dama cattle and with Orma Boran cattle in Kenya. In calves the majority of infections were caused by *T. vivax* (or in Zaire equal proportions of *T. vivax* and *T. congolense*), while *T. congolense* was the predominant trypanosome in cows. These results suggest the ability to acquire some degree of resistance to *T. vivax* infections, and this ability may be more marked in the more trypanotolerant N'Dama cattle.

The new trypanosome antigen-detection techniques, combined with the more traditional microscopic diagnostic techniques offer possibilities for further refining reliable indicators of trypanotolerance. Further recent analyses of N'Dama cattle in Zaire indicate that changes in trypanosome species, length of time parasitaemic, intensity of parasitaemia and average PCV each have approximately equal phenotypic effects on daily liveweight gain (ILCA 1992). What is now required, to evaluate fully the usefulness of each of these traits as selection criteria, are estimates of the heritabilities and phenotypic standard deviations for each of them, the genetic correlations among them and genetic correlations of each selection criterion with production traits.

Genetic resistance to different diseases

The question of whether a breed or population of livestock resistant or tolerant to one disease also shows any resistance or tolerance to other diseases is particularly important in Africa where there is a large range of diseases that constrain production. It has been reported that trypanotolerant N'Dama cattle carry significantly lower tick burdens than Zebu or N'Dama × Zebu crossbred cattle and that N'Dama cattle may possess a degree of tolerance to some tick-associated pathogenic organisms (Mattioli et al. 1993). However, preliminary evidence suggests that N'dama and Boran cattle are equally susceptible to East Coast fever (Dolan et al. 1992).

Combined selection for disease resistance and production traits

In small ruminants in Africa, a critical question will be: what are the genetic correlations between disease resistance and production traits? From between-breed comparisons it is often assumed these may be unfavourable. For example, many of the sheep breeds with high levels of resistance to endoparasites (e.g. Red Maasai, Florida Native, St Croix) are those reputed to have low productivity in terms of reproduction, mortality and growth. However, this negative association between productivity and endoparasite resistance is not supported by within-breed genetic correlation estimates. In addition, these indigenous, 'unimproved' breeds are usually being evaluated in very unfavourable environments. When 'improved breeds' have been evaluated in these environments they have often been shown to be completely unadapted to diseases, with resulting high mortality rates.

Breeding Programs for Disease Resistance

There is a wide variety of small ruminant production systems in Africa, ranging from intensive systems where land size and flocks are very small, to extensive rangelands where larger flocks are run at low stocking rates (Wilson 1982). In these situations, small ruminants are not only kept for meat, milk, fibre and skins, but also contribute manure for crop production. They are also a source of capital investment, are an important way of storing wealth and can play important social and cultural roles. Defining breeding objectives in such systems is likely to be extremely difficult (e.g. Hetzel and Seifert 1986) because of unknown elements such as the relative magnitude of costs and returns, and important socioeconomic factors which can often be of overriding significance (Anteneh 1982). For example, many livestock owners in Africa keep large numbers of animals as a form of risk avoidance with little concern for the efficiency of meat or milk production. Thus the important traits to include in the breeding objective of African production systems may be very different from those in other production systems which seek to improve efficiency and profitability. This is well illustrated by an analysis of economic returns from small ruminant production in South West Nigeria (Upton 1985). In this production system, decreasing mortality and increasing reproduction brought the highest economic returns, while increasing growth rate was of little economic significance.

In Africa one of the first questions is how to utilise breed variation most efficiently. Most breed evaluations carried out to date have compared only purebred populations (e.g. Baker et al. 1992). Although this will provide estimates of additive genetic variation among breeds it does not provide estimates of heterosis and/or epistatic effects which are required to formulate optimum crossbreeding strategies (Dickerson 1969). If, however, some indigenous African breeds are found to be relatively resistant to diseases then one option will be to carry out multi-trait genetic improvement programs within that breed or population. If crossbreeding strategies are indicated (e.g. because the performance levels of the resistant breed are low), then the ranking of resistance in purebred performance is useful in predicting average transmitted effects in crosses (ILCA 1991, 1992). However, the correlation between purebred and crossbred performance is limited by breed differences in level of inbreeding, in epistatic interaction and by sampling errors of estimation of breed means. If crossbreeding strategies are to be employed then it will be important to estimate the appropriate parameters. The possibility of heterosis for disease resistance should not be ignored (Zijpp et al. 1990).

With the evidence that genetic variation in resistance to nematode infections within breeds can be as great as that between breeds, both in sheep (Barger 1989) and cattle (Kaufmann et al. 1990), Pfister (1991) suggested that breeding programs in developing countries should concentrate on genetic improvement of local indigenous breeds. This suggestion is logical but it is important to emphasise that genetic variation among indigenous sheep or goat breeds in Africa is likely to be larger than that found among breeds of sheep in Australasia. Further, there is very limited evidence on the amount of genetic variation within indigenous African sheep and goat breeds for resistance to endoparasites (Baker et al. 1992). It is therefore likely that breeding programs in Africa will utilise both between-breed and within-breed genetic variation for disease resistance.

Pfister (1991) posed a number of questions which need to be answered before breeding programs for resistance to endoparasites in Africa can be implemented successfully. These include socioeconomic issues, profitability and the acceptability of programs by local livestock owners. The breeding program proposed by Pfister did not envisage stopping the use of anthelmintics, but the development of genetically resistant animals which would receive fewer anthelmintic treatments. Pfister's proposal was for on-farm recording and evaluation but his scheme could be increased in scope to include aspects of a group breeding system, including a nucleus flock or herd as suggested by Cummins et al. (1991).

Genetic Markers and Marker-assisted Selection

Recent advances in molecular biology to identify polymorphic genetic markers may be used to improve rates of genetic progress through marker-assisted selection (e.g. Soller 1978; Lande and Thompson 1990; Meuwissen and van Arendonk 1992; Brascamp et al. 1993, Nicholas, this volume). In theory, there is no reason why this technology should not be used in Africa (Teale 1993). For example, there is a major research program at the International Laboratory for Research on Animal Diseases in Nairobi, Kenya, to identify genetic markers for trypanotolerance in families generated by crossing N'Dama and Boran cattle (Teale 1991, 1993).

Use of genetic markers in animal breeding involves a number of important activities as follows:

- Generation of polymorphic DNA markers.
- Establishment of a linkage map of the markers.
- Designing and generating resource families which are segregating for the loci of interest (Quantitative Trait Loci—QTL) and the markers. These can be F_2 families, backcross families or large families from heterozygous F_1 sires.
- Ensuring that the phenotype for the QTLs can be accurately assessed.
- Detection of linkage and estimation of the recombination fraction between markers and QTLs.
- Use of marker–QTL linkage associations in breeding programs (i.e. Marker-assisted Selection-MAS).

A linkage map with sufficient resolution to begin screening the bovine genome for genes (QTLs) which control biologically and economically important characteristics of cattle is now complete (Barendse et al. 1994). It is likely that similar maps will soon become available for small ruminants and there is a need to develop facilities in Africa for the detection of QTLs for disease resistance.

Concluding Comments

Over 95% of Africa's ruminants are of indigenous breeds which provide smallholder rural farmers with protein, income and a secure form of investment (Rege and Baker 1993). Small ruminant breeds have evolved over centuries in diverse African environments and are likely to be adapted to high levels of disease challenge. Disease resistance and other adaptive traits such as heat tolerance, ability to use poor quality feeds and to survive with sporadic supplies of feed and water have enabled small ruminant production in vast areas of the continent where crop production is impractical. They are also an important component of crop–livestock production systems.

Accelerating demands of a growing human population and pressures of economic development are threatening the security and survival of many indigenous African breeds which, until now, have been a stable part of their particular ecosystems for hundreds of years. These breeds are threatened because of an increasing tendency to introduce exotic breeds, to rely on a narrow range of supposedly more profitable breeds and to interbreed among indigenous breeds.

It is essential that this unique genetic diversity is thoroughly characterised and that conservation strategies are implemented (Rege and Baker 1993). Development and utilisation of indigenous breeds may benefit not only Africa, but some of their unique characteristics, such as genetic resistance to disease, could have an important impact on livestock production throughout the world.

References

Adah, M.I., Otesile, E.B. and Joshua, R.A. 1993. Susceptibility of Nigerian West African Dwarf and Red Sokoto goats to a strain of *Trypanosoma congolense.* Veterinary Parasitology, 47, 177–188.

Ademosun, A.A. 1988. Trends in small ruminant production over the last two decades and its future in West and Central Africa. In: Adeneji, K.O., ed., Proceedings of the Workshop on the Improvement of Small Ruminants in West and Central Africa. Nairobi, Kenya, OAU/IBAR, 19–42.

Akerejola, O.O., Schillhorn van Veen, T.W. and Njoku, C.O. 1979. Ovine and caprine diseases in Nigeria: A review of economic losses. Bulletin of Animal Health and Production in Africa, 27, 65–70.

Anteneh, A. 1982. Production objectives and market forces. In: Gatenby, R.M. and Trail, JM., ed., Small ruminant breed productivity in Africa. Proceedings of a seminar held at the International Livestock Centre for Africa, Addis Ababa, Ethiopia, 7–12.

Arnold, R.M. and Travassos Santos Dias, J.A. 1983. Ticks and tickborne haemoparasites of sheep and goats. Seasonal distribution in Mozambique. World Animal Review, 45, 28–35.

Bain, R.K., Wanyangu, S.W., Mugambi, J.M., Ihiga, M.A., Duncan, J.L. and Stear, M.J. 1993. Genetic resistance of Red Maasai sheep to *Haemonchus contortus*. Proceedings of the 11th Scientific Workshop of the Small Ruminant Collaborative Research Support Program (SR-CRSP), 3–4 March 1993, Nairobi, Kenya, 120–126.

Baker, R.L., Lahlou Kassi, A., Rege, J.E.O., Reynolds, L., Bekele, T., Mukassa-Mugerwa, E. and Rey, B. 1992. A review of genetic resistance to endoparasites in small ruminants and an outline of ILCA's research programme in this area. Proceedings of the 11th Scientific Workshop of the Small Ruminant Collaborative Research Support Program (SR-CRSP), 3–4 March 1993, Nairobi, Kenya, 79–104.

Baker, R.L., Reynolds, L., Mwamachi, D.M., Audho, J.O., Magadi, M. and Miller, J.E. 1993. Genetic resistance to gastrointestinal parasites in Dorper and Red Maasai × Dorper lambs in coastal Kenya. Proceedings of the 11th Scientific Workshop of the Small Ruminant Collaborative Research Support Program (SR-CRSP), 3–4 March 1993, Nairobi, Kenya, 228–241.

Barendse, W., Armitage, S.M., Kossarek, L.M., Kirkpatrick, B.W., Ryan, A.M. Shalom, A. Clayton, D., Li, L., Neibergs, H.L., Zhang, N. Grosse, W.M., Weiss, J., Creighton, P., McCarthy, F., Ron, M., Teale, A.J., Fries, R., McGraw, R.A., Moore, S.S., Georges, M., Soller, M., Womack, J.E. and Hetzel, D.J.S. 1994. A genetic map of the bovine genome. Nature Genetics, 6, 227–234.

Barger, I.A. 1989. Genetic resistance of hosts and its influence on epidemiology. Veterinary Parasitology, 32, 21–35.

Bjorn, H., Monrad, J., Kassuku, AA. and Nansen, P. 1991. Resistance to benzimidazoles in *Haemonchus contortus* of sheep in Tanzania. Acta Tropica, 48, 59–67.

Boyce, W.M., Courtney, C.H. and Loggins, P.E. 1987. Resistance to experimental infection with *Fasciola hepatica* in exotic and domestic breeds of sheep. International Journal for Parasitology, 17 ,1233–1237.

Bradford, G.E., Fitzhugh, H.A. 1983. Hair sheep: A general description. In: Fitzhugh, H.A., Bradford, G.E. ed., Hair sheep of Western Africa and the Americas: a genetic resource for the tropics. Boulder, Colorado, Westview Press, 3–22.

Brascamp, E.W., van Arendonk, J.A.M. and Groen, A.F. 1993. Economic appraisal of the utilization of genetic markers in dairy cattle breeding. Journal of Dairy Science, 76, 1204–1213.

Brito, G.J. de 1947. Thesis, Lisbon (cited by E.D. Okon 1988) In: Adeneji, K.O., ed., Proceedings of the Workshop on the Improvement of Small Ruminants in West and Central Africa, OAU/IBAR, Nairobi, Kenya, 191–200.

Cabaret, J. and Anjorand, N. 1984. Comparaison de l'infestation naturelle par les strongyles et *Moniezias* sp. chez les races caprines Alpine et Saanen. Bulletin de la Societe francaise de Parasitologie, 2, 49–52.

Camus, E. and Barre, N. 1988. Heartwater—a review, Office International des Epizooties, Paris, France, 147 p.

Coulibaly, L., Diarrasouba, I., d'Ieteren, G.D.M., Hecker, P., Itty, P., Maehl, J.H.H., Mahamet, B. Nagda, S.M., Paling, R.W., Rarieya, J.M., Schutterle, A., Thorpe, W. and Trail, JM. 1988. Disease interactions in cattle and sheep in northern Cote d'Ivoire. In: Livestock production in tsetse affected areas of Africa (ILCA/ILRAD). Nairobi, Kenya, English Press, 110–118.

Courtney, C.H., Parker, C.F., McLure, K.E. and Herd, R.P. 1984. A comparison of the periparturient rise in faecal egg counts of exotic and domestic ewes. International Journal for Parasitology, 14, 377–381.

——1985a. Resistance of exotic and domestic lambs to experimental infection with *Haemonchus contortus*. International Journal of Parasitology, 15, 101–109.

——1985b. Resistance of nonlambing exotic and domestic ewes to naturally acquired gastrointestinal nematodes. International Journal for Parasitology, 15, 239–243.

Cummins, L.J., Thompson, R.L., Yong, W.K., Riffkin, G.G., Goddard, M.E., Callinan, A.P.L. and Saunders, M.J. 1991. Genetics of *Ostertagia* selection lines. In: Gray, G.D. and Woolaston, R.R. ed., Breeding for disease resistance in sheep. Melbourne, Australian Wool Corporation, 11–18.

Dickerson, G.E. 1969. Experimental approaches in utilizing breed resources. Animal Breeding Abstracts, 37, 191–202.

Dolan, R.B. 1987. Genetics and trypanotolerance. Parasitology Today, 3, 137–143.

——1993. Trypanotolerance in Orma Boran cattle on Galana Ranch in Kenya. Consultancy Report, ILCA, Nairobi, Kenya, October 1993, 124 p.

Dolan, T.T. 1989. Theileriasis: a comprehensive review. Reviews Scientifiques et Technicales de l'Office internationale de Epizooties, 8, 11–36.

Dolan, T.T., Williams, S., Opollo, M. and Kiarie, J. 1992. The susceptibility of N'Dama cattle to East Coast Fever. In: ILRAD 1992. Annual Scientific Report of the International Laboratory for Research on Animal Diseases, Nairobi, Kenya 19-20.

Eysker, M. and Ogunsusi R.A. 1980. Observations on epidemiological and clinical aspects of gastrointestinal helminthiasis of sheep in northern Nigeria during the rainy season. Research in Veterinary Science, 28, 58–62.

FAO 1991. Report of the FAO Expert Consultation on Helminth Infections of Livestock in Developing Countries (AGA -815), 23–27 September 1991, Rome, Italy, p 32 .

——1992. Distribution and Impact of Helminth Diseases of Livestock in Developing Countries. FAO Animal Production and Health paper, No. 96, p 221.

Finelle, P. 1974. African animal trypanosomiasis economic problems. World Animal Review, 10, 15–18.

Gamble, H.R. and Zajac, A.M. 1992. Resistance of St. Croix lambs to *Haemonchus contortus* in experimentally and naturally acquired infections. Veterinary Parasitology, 41, 211–225.

Graber, M. 1965. Helminthes and helminthiasis faisant obstacle a al'ameleration de la production ovine en republique de Chad. Report lab. de Farcha. IEMVT Fort Lamy, Chad. (Cited by Fabiyi 1986). International Journal for Parasitology, 7, 435–42.

Gray, G.D. 1991. Breeding for resistance to trichostrongyle nematodes in sheep. In: Owen, J.B. and Axford, R.F.E. ed., Breeding for diseases resistance in farm animals, Proceedings of an International Symposium, Bangor, Wales, Sept. 1990. Wallingford, U.K., CAB International, 139–161.

Gray, G.D., Presson, B.L., Albers, G.A.A., Le Jambre L.F., Piper, L.R. and Barker J.S.F. 1987. Comparison of within- and between-breed variation in resistance to haemonchosis in sheep. In: McGuirk, B.J., Merino improvement programs in Australia. Proceedings of an Australian Wool Corporation National Symposium, 365–369.

Griffin, L. and Allonby, E.W. 1979a. The economic effects of trypanosomiasis in sheep and goats at a range research station in Kenya. Tropical Animal Health and Production, 11, 127-132.

— -1979b. Trypanotolerance in breeds of sheep and goats with an experimental infection of *Trypanosoma congolense*. Veterinary Parasitology, 5, 97–105.

Hendy, C.R 1988. The effects of trypanosomiasis prophylaxis and anthelmintic treatment in goats under traditional management in Southern Tanzania. In: Livestock production in tsetse affected areas of Africa, ILCA/ILRAD, Nairobi, Kenya, 289–309.

Hetzel, D.J.S. and Seifert, G.W. 1986. Breeding objectives and selection traits for extensive beef cattle production in the tropics. Proceedings of the 3rd World Congress on Genetics Applied to Livestock Production, 9, 244–258.

ILCA (International Livestock Centre for Africa). 1979. Trypanotolerant Livestock in West and Central Africa. Volume 1, General study. Volume 2, Country studies. Addis Ababa, Ethiopia, ILCA, Monograph No.2.

—-1986. The African Trypanotolerant Livestock Network. Indications from Results (1983–85). International Livestock Centre for Africa, Addis Ababa, Ethiopia, December 1986, p 138.

——-1991. Proceedings of the Research Planning Workshop on Resistance to Endoparasites in Small Ruminants, 5–7 February 1991, Addis Ababa, Ethiopia, p78.

——1992. International Livestock Centre for Africa Annual Report and Programme Highlights 1992, Addis Ababa, Ethiopia, p86.

ITC 1992. The International Trypanotolerance Centre Annual Report 1992, Banjul, The Gambia, p 51.

Kanyari, P.W.M., Allonby, E.W., Wilson, A.J. and Munyua, W.K. 1983. Some economic effects of trypanosomiasis in goats. Tropical Animal Health and Production, 15, 153–160.

Katunguka-Rwakishaya, E., Murray, M. and Holmes, P.H. 1992. The pathophysiology of ovine trypanosomis: haematological and blood biochemical changes. Veterinary Parasitology, 45,17–32.

Kaufmann, H., Zuercher, G., Gaye, M., Baldeb, W. and Pfister, K. 1990. University of Berne Helminthiasis Project, Third Progress Report, International Trypanotolerance Centre—University of Berne.

Knight, R.A., Vegors, H.H. and Glimp, H.A. 1973. Effects of breed and date of birth of lambs on gastrointestinal nematode infections. American Journal of Veterinary Research, 34, 323–327.

Kramer, J.W. 1966. Incidence of trypanosomes in the west African dwarf sheep and goats in Nsukka, Eastern Nigeria. Bulletin of Epizootilogical Diseases of Africa 14, 423–428.

Lande, R. and Thompson, R. 1990. Efficiency of marker-assisted selection in the improvement of quantititative traits. Genetics, 124, 743–756.

Mack, S. 1982. Disease as a constraint to productivity. In: Gatenby, R.M. and Trail, JM., ed., Small ruminant breed productivity in Africa. Proceedings of a seminar held at the International Livestock Centre for Africa, Addis Ababa, Ethiopia, 81–83.

MAFF. 1977. Ministry of Agriculture, Fisheries and Food. Manual of veterinary parasitology laboratory technique. Technical Bulletin No. 18, Her Majesty's Stationary Office, London.

Mahmoud, M.M. and Elmalik, K.H. 1977. Trypanosomiasis: Goats as a possible reservoir of *Trypanosoma congolense* in the the Republic of the Sudan. Tropical Animal Health and Production, 9, 167–170.

Maingi, N. 1991. Resistance to thiabendazole, fenbendazole and levamisole in *Haemonchus* and *Trichostrongylus* species in sheep on a Kenyan farm. Veterinary Parasitology, 39, 285–291.

Makumyaviri, A., Mehlitz, D., Kageruka, P., Kazyumba, G.L. and Molisho, D. 1989. La reservoir animal de *Trypanosoma brucei gambiense* au Zaire: Infections trypanosomiennes dans deux foyers du Bas-Zaire, Tropical Medicine and Parasitology, 40, 258–262.

Masake, R. A. and Nantulya, V. M. 1991. Sensitivity of an antigen detection enzyme immunoasays for diagnosis of *Trypanosoma congolense* infections in goats and cattle. Journal of Parasitology, 77, 231–236.

Mattioli, R., Bah, M., Faye, F., Kora, S. and Cassama, M. 1993. A comparison of field tick infestation on N'dama, Zebu and N'dama × Zebu crossbred cattle. Veterinary Parasitology, 47, 139–148.

Mawuena, K. 1987. Trypanosomiasis in sheep and goats of the dwarf Djallonke breed in the south-Guinean regions of Togo (CREAT). In: Proceedings of the International Scientific Council for Trypanosomiasis Research and Control. 19th Meeting, Lome, Togo, OAU/STRC Publication No.114, 321–330.

Mbah, A.H., Ogunrinade, A.F. and Dina, O.A. 1992. Benzimidazole resistance in strongyles of sheep in Ibadan, Nigeria. African Livestock Research, 1, 16–17.

McGuire, T., Carlson, J.L. and Mwamachi, D.M. 1985. Comparison of the effects of African trypanosomiasis in four breeds of dairy goats. Research in Veterinary Science, 39, 352–353.

Meuwissen, T.H.E. and van Arendonk, J.A.M. 1992. Potential improvements in rate of genetic gain from marker-assisted selection in dairy cattle breeding schemes. Journal of Dairy Science, 75, 1651–1659.

Munyua, W.K. 1985. Goat trypanosomiasis: Trypanotolerance and epidemiology among goat breeds in Kenya. In: Proceedings of the International Scientific Council for Trypanosomiasis Research and Control. 18th Meeting, Harare, Zimbabwe, OAU/STRC Publication No.113, 168–175.

Murray, C., Murray, M., Morrison, W.I., Pyne, C. and McIntyre, W.I.M. 1977. Diagnosis of African trypanosomiasis in cattle. Improved parasitological and serological techniques. In: Proceedings of the 15th Meeting of the International Scientific Council for Trypanosomiasis Research and Control, The Gambia, OAU/STRC, Publication No. 110, p. 247.

Murray, M., Stear, M.J., Trail, JM., d'Ieteren, G.D.M., Agyemang, K. and Dwinger, R.H. 1991. Trypanosomiasis in cattle: prospects for control. In: Owen, J.B. and Axford, R.F.E. ed., Breeding for diseases resistance in farm animals, Proceedings of an International Symposium, Bangor, Wales, Sept. 1990. Wallingford, U.K., CAB International, 203–223.

Murray, M., Trail, J.M. and d'Ieteren, G.D.M. 1990. Trypanotolerance in cattle and prospects for the control of trypanosomiasis by selective breeding. Reviews Scientifiques et Technicales de l'Office internationale de Epizooties, 9, 369–386.

Mutayoba, B.M., Gombe, S., Waindi, E.N. and Kaaya, G.P. 1989. Comparative trypanotolerance of the Small East African breed of goats from different localities to *Trypanosoma congolense* infection. Veterinary Parasitology, 31, 95–105.

Mwamachi, D.M., Ouma, J., Magadi, M., Reynolds, L. and Baker, R.L. 1993. Evidence for multiple anthelmintic resistance in gastrointestinal nematodes in sheep in coastal Kenya. Proceedings of the 11th Scientific Workshop of the Small Ruminant Collaborative Research Support Programme 3–4 March 1993, Nairobi, Kenya.

Nansen, P. 1991. Strategies for the development and establishment of cost-efficient and sustainable control programmes for helminth infections in the developing countries. Paper presented at the FAO Expert Consultaton on Helminth Infections of Livestock in Developing Countries (AGA/HIL/91/14), FAO, Rome, 17 p.

Nantulya, V.M. 1990. Trypanosomiasis in domestic animals: the problems of diagnosis. Reviews Scientifiques et Technicales de l'Office internationale de Epizooties, 9 (2), 357–367.

——1993. The development of latex agglutination antigen tests for diagnosis of African trypanosomiasis. In: Programme Abstracts of the International Scientific Council for Trypanosomiasis Research and Control, 22nd Meeting, Kampala, Uganda.

Nantulya, V.M. and Lindquist, K.J. 1989. Antigen-detection enzyme immunoassay for the diagnosis of *Trypanosoma vivax*, *T. congolense* and *T. brucei* infections in cattle. Tropical Medicine and Parasitology, 40, 267–272.

Nicholas, F.W. 1987. Veterinary Genetics. Oxford, Clarendon Press, 580 p.

Norval, R.A.I., Meltzer, M.I. and Burridge, M.J. 1992a. Distribution, economic importance and control measures for *Cowdria ruminantium*. In: Dolan, T.T., ed., Recent developments in the control of anaplasmosis, babesiosis and cowdriosis. Proceedings of a workshop held at ILRAD, 13–15 May 1991, Nairobi, Kenya, 13–27.

Norval, R.A.I., Perry, R.D. and Young, A.S. 1992b. The epidemiology of theileriosis in Africa. London, Academic Press, 481 p.

Osinowo, O.A. and Abubakar, B.Y. 1988. Appropriate breeding strategies for small ruminant production in West and Central Africa. In: Adeniji, K.O., ed., Proceedings of the Workshop on the Improvement of Small Ruminants in West and Central Africa, OAU/IBAR, Nairobi, Kenya, 71–84.

Paling, R.W. and Dwinger, R.H. 1993. Potential of trypanotolerance as a contribution to sustainable livestock production in tsetse affected Africa. The Veterinary Quarterly, 15, 60–67.

Paris, J., Murray, M. and McOdimba, F. 1982. An evaluation of the sensitivity of current parasitological techniques for the diagnosis of bovine African trypanosomiasis. Acta Tropica, 39, 307–316.

Peregrine, A.S. 1994. Chemotheraphy and delivery systems: haemoparasites. Veterinary Parasitology, 54, 225–248.

Pfister, K. 1991. Genetic resistance to helminth infections in indigenous breeds of livestock. How could this be exploited? Paper prepared for the FAO Expert Consultation on Helminth Infections of Livestock in Developing Countries (AGA/HIL/91/17), FAO, Rome, 28 p.

Preston, J.M. and Allonby, E.W. 1978. The influence of breed on the susceptibility of sheep and goats to a single experimental infection with *Haemonchus contortus*. Veterinary Record, 103, 509–512.

——1979. The influence of breed on the susceptibility of sheep to *Haemonchus contortus*. American Journal of Veterinary Research, 33, 817–823.

Rege, J.E.O. and Baker, R.L. 1993. Conservation of indigenous African breeds: Issues and options. Paper presented at the International Conference of the Convention on Biological Diversity: National Interests and Global Imperatives, 26–29 January 1993, Nairobi, Kenya.

Richard, S., Cabaret, J. and Cabourg, C. 1990. Genetic and environmental factors associated with nematode infection of dairy goats in Northwestern France. Veterinary Parasitology, 36, 237–243.

Rohrer, G.A., Taylor, J.F., Davis, S.K., Waruiru, R.M., Ruvuna, F., Mwandotto, B.A.J., McGuire, T. and Rurangirwa F. 1991. The use of randomly amplified polymorphic DNA markers in analysis of susceptibility to *Haemonchus* and Coccidia. Proceedings of the 9th Scientific Workshop of the Small Ruminant Collaborative Research Support Program, 71–85.

Schillhorn van Veen, T.W. 1973. Small ruminant health problems in northern Nigeria with emphasis on the helminthiasis. Nigerian Veterinary Journal, 2, 26–31.

Shavulimo, R.S., Rurangirwa, F., Ruvuna, F., James, A.D., Ellis, P.R. and McGuire, T. 1988. Genetic resistance to gastrointestinal nematodes, with special reference to *Haemonchus contortus*, in three breeds of goats in Kenya. Bulletin of Animal Health and Production in Africa, 36, 233–241.

Smith, O.B. 1988. Health packages for the smallholder farmer in West and Central Africa. In Adeneji, K.O., ed., Proceedings of the Workshop on the Improvement of Small Ruminants in West and Central Africa OAU/IBAR, Nairobi, Kenya, 211–221.

Soller, M. 1978. The use of loci associated with quantitative effects in dairy cattle improvement. Animal Production, 27, 133–139.

Teale, A.J., ed. 1991. Bovine Genome Mapping and Trypanotolerance. Proceedings of a workshop held at the International Laboratory for Research on Animal Diseases, Nairobi, Kenya, 9–11 April 1991, 72p.

Teale, A.J. 1993. Improving control of livestock diseases. Animal biotechnology in the Consultative Group on International Agricultural Research. Bioscience, 43, 475–483.

T

Wilson, R.T. 1982. Husbandry, nutrition and productivity of goats and sheep in tropical Africa. In: Gatenby, R.M. and Trail, JM., ed., Small ruminant breed productivity in Africa. Proceedings of a seminar held at the International Livestock Centre for Africa, Addis Ababa, Ethiopia, 61–75.

Young, A.S., Groocock, C.M. and Kariuki, D.P. 1988. Integrated control of ticks and tick-borne diseases of cattle in Africa. Parasitology, 96, 403–432.

Zijpp, A.J. van der, Pinard, M.H. and Blankert, J.J. 1990. Heterosis, immune response and disease in poultry. Proceedings of the 4th World Congress on Genetics Applied to Livestock Production, 16, 31–38.

Zwart, D., Perie, N.M., Keppler, A. and Goedbloed, E. 1973. A comparison of methods for the diagosis of trypanosomiasis in East African domestic ruminants. Tropical Animal Health and Production, 5, 79–87.

Genetic Variation in Resistance to Infectious Disease in Small Ruminants in India

C. NIMBKAR AND B.V. NIMBKAR

ABSTRACT

Disease incidence among small ruminants in India is reviewed with a focus on comparisons between breeds. Few breeds and diseases are represented in the available literature. In the absence of well-designed experiments or studies, there is no conclusive evidence for genetic variation in resistance to disease between or within Indian breeds of small ruminants. Resistant genetic material may exist in India as a consequence of natural selection over centuries in an environment with a wide range of endemic diseases and parasites and efforts need to be made to identify it.

The scientific community in the field of small ruminants in India has not looked seriously at genetic variation in disease resistance in sheep and goats. Certainly, no efforts have been made so far anywhere in India to breed small ruminants for resistance to infectious diseases. Forty breeds of sheep and twenty breeds of goats are recognised in India (Acharya 1982). However, there are much larger and biologically diverse populations of nondescript sheep and goats which have not gained the status of 'breeds' but which contribute most to small ruminant production. All these sheep and goats have evolved in different geographical areas—mainly in low-input subsistence systems of rearing. India can be divided into four major geographical regions.

1. Northern temperate and hilly region.
2. Northwestern arid and semi-arid region.
3. Southern peninsular region (semi-arid in the central peninsula and hot and humid along the coast).
4. Northeastern region (mostly hot and humid).

In each region, there are sheep and goats adapted to the typical environmental conditions of that region. Sheep are mainly concentrated in the arid and semi-arid parts of the country but goats are more or less uniformly distributed. Sheep and goat rearing is an occupation of great socioeconomic importance throughout rural India. Stationary as well as migratory flocks are found.

There are a wide range of diseases and parasites in India and preventive health care facilities for small ruminants are inadequate. Even in Maharashtra, which is one of the more developed states in India, only about 25–30% of the total sheep and goat population is protected by vaccination against enterotoxaemia, rinderpest, anthrax, sheep pox, foot-and-mouth disease and haemorrhagic septicaemia (Department of Animal Husbandry, Maharashtra State 1992). Consequently, infectious diseases constitute a major constraint to sheep and goat production in India.

Evidence for disease among small ruminants in India is scanty and mainly based on data collected in small flocks maintained at experimental stations in government research institutes or universities. These flocks are reared usually under management and environmental conditions that are widely different from rearing practices of sheep and goat owners. The conclusions derived from such studies, therefore, may not be directly relevant to field situations. The limited number of studies that are available have been predominantly on breed differences in susceptibility following natural exposure to diseases and on ranking of causes of morbidity and mortality. Since most of the studies are not aimed at assessing the genetic variation in resistance to infectious diseases between and within breeds, they do not take into account important factors such as whether the compared groups were at the same location and whether they were reared under the same nutrition and management conditions. Care must be taken, therefore, while interpreting the results of these studies. There are few studies on the large numbers of animals that do not belong to any 'recognised' breed.

There have been many studies to compare lamb and kid mortality between different breeds and genotypes. Most of these studies are not relevant to genetic resistance to disease since they do not take into consideration many factors such as environment, nutrition, litter size, pre- and post-parturition management which can have huge influences on lamb and kid mortality.

Sheep

The source of most of the available information on differences among breeds of sheep in susceptibility to certain diseases is the All India Coordinated Research Project (AICRP) on sheep conducted at the Central Sheep and Wool Research Institute (CSWRI), Avikanagar, Rajasthan; a dry, arid part of India. The indigenous breeds from Rajasthan, i.e. Malpura, Sonadi, Chokla and Nali and their crosses with Rambouillet, Merino, Dorset and Suffolk have high representation in the available literature compared to other breeds.

Some reports were also found on the Mandya and Nellore breeds from South India.

No reports were found of sheep affected by footrot or fleece rot. At the Arid Region Campus of the CSWRI at Bikaner, Rajasthan, the incidence of listeriosis has been recorded from time to time in Marwari sheep but this infection has never been found in the exotic Karakul sheep at the same farm (Bohra 1988).

Sheep are reared mainly in the dry, arid and semi-arid regions of India. But there is at least one breed of sheep, the Garole (Ghalsasi and Nimbkar 1993), that thrives in the hot and humid delta of the Ganges river known as the Sunderbans in West Bengal state. There are also some sheep breeds in the temperate humid areas of Kashmir state in the north and the Nilgiri hills of Tamil Nadu state in the south. These sheep may have superior genetic resistance and they need to be studied.

Under the Transfer of Technology project of the CSWRI in six villages in Rajasthan, the principal causes of mortality in village sheep were recorded (Ayub et al. 1988). They were, in descending order of importance, diseases of the respiratory system, alimentary system and general systemic states. Among specific diseases were foot-and-mouth disease, enterotoxaemia and sheep pox. This pattern was constantly observed from 1985 to 1987. Some other important diseases that cause substantial morbidity and mortality and consequent loss of sheep production in India are (not necessarily in their order of importance) blue tongue, Johne's disease, rinderpest, brucellosis, haemorrhagic septicaemia, contagious ecthyma, gastrointestinal nematodiasis, paramphistomiasis and fascioliasis. Reports of breed differences in susceptibility to infectious diseases in sheep are summarised in Table 1.

Sheep pox

Murty and Singh (1971) have reported that in an outbreak of sheep pox in an organised mixed flock in Uttar Pradesh from May to July 1969, the morbidity among Mandya sheep (28%) was only slightly higher than that in Bikaneri sheep (24%). But the case fatality in the Mandya breed was 76% compared to 51% in the Bikaneri breed.

A sheep pox outbreak (despite vaccination) in 1980–81 among 1492 mutton type (Malpura and Sonadi breeds and their crosses with Dorset and Suffolk) and 1457 fine wool type (Nali and Chokla breeds and their crosses with Rambouillet and Merino) sheep in the All India Coordinated Research Project on Fine Wool and Mutton at CSWRI is reported by Sharma et al. (1986). The reported overall morbidity of 13% and mortality of 8% is, however, very low compared to the morbidity of 70% and mortality of 20% in

Table 1 **Summary of studies (a, b, c...) on breed differences in susceptibility to infectious diseases in sheep.**

Disease — Breed	Comparative disease susceptibility	References
SHEEP POX		
a. Malpura	Low	Sharma et al. (1986)
Malpura × Dorset		
Malpura × Suffolk		
Sonadi	High	
Sonadi × Dorset		
Sonadi × Suffolk		
b. Chokla	Low	Sharma et al. (1986)
Nali	High	
c. Nali × Rambouillet	Low	Sharma et al. (1986)
Nali × Merino		
Chokla × Rambouillet	High	
Chokla × Merino		
d. Fine Wool Type Sheep (Nali, Chokla and Nali/Chokla × Rambouillet/Merino)	Low	Sharma et al. (1986)
Mutton Type Sheep (Malpura, Sonadi and Malpura/Sonadi × Dorset/Suffolk)	High	
e. Bikaneri	Low	Murty and Singh (1971)
Mandya	High	
BLUE TONGUE		
a. Malpura, Marwari, Nali, Sonadi	Low	
Corriedale, Dorset, Karakul	Medium	Dubey et al. (1988)
Rambouillet, Merino	High	
b. Nali, Sonadi	Low	Mahajan et al. (1991)
Rambouillet	High	
OVINE ADENOVIRUS		
a. Malpura, Sonadi, Chokla, Nali	Low	Dubey et al. (1985b)
Rambouillet, Merino, Dorset, Suffolk	High	
FOOT-AND-MOUTH DISEASE		
a. Malpura	Low	Khurana et al. (1991)
Avikalin (Malpura × Rambouillet/Merino)	Medium	
Mutton Synthetic (Malpura/Sonadi × Dorset/Suffolk)	High	
b. Mandya	Low	Rao et al. (1993)
Nellore	High	
c. Bellary, Nilgiri, Chokla, Magra	Low	Sriraman and Rao (1980)
Nellore, Mandya, Bikaneri	High	
d. Chokla lambs	Low	Singh et al.(1992c)
Nali lambs	High	

Table 1 continued.

Disease — Breed	Comparative disease susceptibility	References
HAEMONCHOSIS		
a. Malpura	Low	Pachlag and Kumar (1974)
Sonadi	High	
b. Munjal (Nali × Lohi) lambs	Low	Yadav et al.(1993)
Hisardale (Nali × Corriedale) lambs	High	

a typical outbreak in a village. The duration of the outbreak was about one year in the mutton type sheep and only about six months in the fine wool type sheep. The morbidity and mortality due to sheep pox among the fine wool sheep were reportedly much lower than those among the mutton type sheep. Mahajan (1979) also found the mutton breeds at CSWRI to be more susceptible to almost all diseases compared to the fine wool breeds. But while making any such comparisons, it must be considered that the staff, grazing areas and locations of these two types of sheep were well separated (Sharma et al. 1986). Among the mutton type sheep, Sharma et al. (1986) found the Sonadi breed to be more susceptible than the Malpura breed and among the fine wool type sheep, the Nali breed to be more susceptible than the Chokla breed. But the statistical significance of these comparisons is not mentioned.

Bluetongue

In a study done over a period of 4 years from 1985 at an organised sheep breeding farm near Hissar in Haryana state, Mahajan et al. (1991) did not detect any frank clinical cases of blue tongue in indigenous sheep (i.e. Nali and Sonadi) or in their crosses with Rambouillet and Corriedale. However, antibodies against blue tongue were detected in the serum of 21% to 36% of about 20 Nali and Sonadi sheep tested compared to 44% to 57% of about 100 Rambouillet sheep tested between 1985 and 1988. The seroprevalence of blue tongue disease in sheep in Rajasthan was studied by Dubey et al. (1988). The indigenous breeds tested were Malpura, Marwari, Nali and Sonadi. The exotic breeds Merino, Rambouillet, Corriedale, Dorset and Karakul and their crosses with the native breeds were also tested. The higher seroprevalence of the disease was in exotic sheep with 34% of the 76 tested Rambouillet and 33% of the 114 tested Merino sheep found to be positive. Among the native sheep, only 0.6% of the 335 tested sheep were positive.

This lack of antibody response was attributed by the authors to the resistance of the native sheep to blue tongue.

A mortality of 33% was reported among 123625 affected Deccani sheep in Maharashtra in blue tongue outbreaks over the years 1985 to 1990 (Department of Animal Husbandry, Maharashtra State 1992).

Ovine adenovirus (OAV)

Rao and Singh (1975) reported the results of a search for the presence of OAV infection in sheep around Agra in the state of Uttar Pradesh. They reported that none of the 39 sheep sera tested was positive for OAV antibodies.

Dubey et al. (1985a) found that 4% of the sheep tested in Punjab were seropositive for OAV but there was no major variation in the percentage of seropositive sheep of different breeds.

Dubey et al. (1985b) report the results of the screening of sera of the flocks at CSWRI, Avikanagar against OAV antigen. They state that the indigenous sheep (i.e. Malpura, Sonadi, Chokla and Nali) had no antibodies whereas 50% of the tested exotics and 33% of the tested higher crosses (with more than 74% exotic blood) were found to be positive.

Foot-and-mouth disease (FMD)

Shankar et al. (1992) report the occurrence of FMD during the year 1990–91 in sheep flocks in the villages around the Central Goat Research Institute (CIRG) near Mathura in the state of Uttar Pradesh. Sixty nine percent of the village sheep were found to be affected and the case fatality rate was 6%. Breeds were found to be affected equally.

In an outbreak of FMD at the CSWRI, the prevalence among crosses with exotic breeds was reported to be higher compared to the indigenous Malpura breed. Among the crosses, the mutton type crosses (with Dorset and Suffolk) were more affected than the fine wool type crosses (with Rambouillet and Merino) (Khurana et al. 1991). It should, however, be noted that different breed types are maintained separately at CSWRI.

Pneumonia

The conclusions of two studies in Andhra Pradesh (Rao et al. 1993 and Sriraman and Rao 1980) appear to conflict. Rao et al. (1993) have reported post mortem findings of 1685 sheep that died at the All India Coordinated Research Project for Mutton at Palamaner in Andhra Pradesh state over a period of 10 years. They found that the Mandya breed was found to have significantly higher resistance to pneumonia compared to the Nellore breed and to the Mandya and Nellore Synthetics. Sriraman and Rao (1980) analysed the causes of mortality of sheep from organised sheep farms in Andhra

Pradesh state. The native sheep studied were of the breeds Nellore, Mandya, Bikaneri, Bellary, Nilgiri, Chokla and Magra. They found the Nellore, Mandya and Bikaneri breeds together with exotics to be more susceptible to pneumonia compared to other breeds. They also found the Nellore and Mandya breeds to be more susceptible to enteritis. The sheep included in both these studies were from different farms, maintained possibly under different management conditions. Therefore, the differences in susceptibility among them cannot be considered to be wholly genetic as there may be other factors such as environmental variation, prior exposure to disease or variations in nutrition influencing these differences.

Gastrointestinal helminthiasis

Male lambs of Malpura and Sonadi breeds maintained at three energy levels were studied by Pachlag and Kumar (1974). They found differences in the eggs per gram of faeces between the two breeds at the low and medium energy levels. The egg count in Malpura lambs (327±102) was substantially lower than that in Sonadi lambs (837±193),at the medium energy level. The statistical significance of this difference is not reported. It is also stated that deworming prior to introduction into a feedlot did not prevent reinfection by *Haemonchus contortus* in either breed.

Yadav et al., (1993) investigated the differences in susceptibility to *H. contortus* infection between seven lambs each of two different crossbreeds: Nali × Lohi (Munjal) and Nali × Corriedale (Hisardale). They found the body weight gain, haemoglobin and packed cell volume after artificial infection with *H. contortus* to be significantly lower in Hisardale lambs and the peripheral eosinophil count to be significantly higher in Munjal lambs. They conclude that Hisardale lambs have significantly greater susceptibility to experimental *H. contortus* infection than Munjal lambs and suggest that these genetic differences in susceptibility should be investigated with an appropriate experimental design.

Goats

Most of the available literature on genetic variation in disease resistance in Indian goats has originated at the Central Institute for Research on Goats (CIRG), Makhdoom, near Agra in the state of Uttar Pradesh and at CIRG's Western Regional Research Centre (WRRC) located at Avikanagar in the state of Rajasthan. The breeds on which at least some information is available are the Jamunapari, Barbari, Black Bengal, Sirohi, Jhakrana, Beetal, Marwari and Kutchi. Goats are reared throughout India albeit under different systems of management which are integrated with the agricultural production system of each region. Goats are kept mainly by landless labourers and marginal farmers in small flocks of two to three adult does. But in some states like Rajasthan, large flocks of more than 20 goats can be found. Some of these flocks also migrate.

Some common diseases among goats in India are, goat pox, brucellosis, enterotoxaemia, contagious caprine pleuropneumonia, Johne's disease, rinderpest, foot-and-mouth disease, haemorrhagic septicaemia, contagious ecthyma, contagious pustular dermatitis, gastrointestinal nematodiasis, fascioliasis and paramphistomiasis. Reported breed differences in resistance to infectious diseases of goats are listed in Table 2.

Goat pox

An outbreak of goat pox was recorded in November–December 1987 in Sirohi, Marwari and Kutchi breeds of goats at the WRRC (CIRG) Avikanagar, Rajasthan where goats of all three breeds are reared together (Nagpal et al. 1990). At this farm, there were 79 adults and 123 kids of the Sirohi breed, 53

Table 2 Summary of reported breed differences in resistance in infectious diseases in goats.

Disease — Breed	Comparative disease susceptibility	References
Goat pox		
a. Sirohi	Low	
Kutchi	Medium	Nagpal et al. (1990)
Marwari	High	
b. Sirohi	Low	ISGP (1988)
Sirohi × Toggenburg	Medium	
Sirohi × Alpine	High	
Foot-and-mouth disease		
a. Barbari	Low	Shankar et al. (1992)
Jamunapari	Medium	
Jhakrana	High	
Johne's disease		
a. Jamunapari	Low	Singh et al. (1990)
Barbari	High	
b. Jhakrana, Sirohi	Low	Singh et al. (1992a)
Jamunapari	Medium	
Barbari	High	
Colibacillosis		
a. Jamunapari kids	Low	Vihan and Singh (1988)
	Vihan (1991)	
Barbari kids	High	Singh et al. (1992b)

adults and 72 kids of the Marwari breed and 55 adults and 92 kids of the Kutchi breed. The morbidity among Kutchi goats was the highest (45%) followed by Sirohi (39%) and Marwari (30%). Mortality was the highest in the Marwari breed (3%) followed by Kutchi (2%) and Sirohi (0.5%).

The Indo-Swiss Goat Project report (1988) reports an outbreak of goat pox at their farm near Ajmer, Rajasthan from February to May 1987. The mortality in the Sirohi breed was negligible (0.6%) compared to 6% in the crossbreds of Sirohi with Alpine and Toggenburg. The mortality among affected animals was 58% in Sirohi-Alpine crosses, 24% in Sirohi-Toggenburg crosses and a mere 3% in the Sirohi animals.

Foot-and-mouth disease (FMD)

Outbreaks of foot and mouth disease during the year 1990–91 were monitored in organised goat flocks as well as in villages (Singh et al. 1992c). The prevalence rates in organised flocks were, 52% in the Jhakrana breed, 12% in the Jamunapari breed and 3% in the Barbari breed. There was no mortality. It is not mentioned whether these three breeds were kept at the same farm. In the village goats, the prevalence rate was 30% and the case fatality was 8%.

Johne's disease

Singh et al. (1990) estimated the genetic component of variance of susceptibility to Johne's disease among Jamunapari and Barbari goats by considering the progeny data of goats above one year of age. A regular check-up was conducted on natural infection in 708 and 535 half-sib progenies of 21 Barbari and 16 Jamunapari sires respectively. The mean proportion of animals affected by Johne's disease was lower in Jamunapari (8%) than in Barbari (17%) goats. The average difference from the population mean was 1.405 and 0.95 standard deviation units in Jamunapari and Barbari goats respectively. The estimate of heritability of susceptibility to Johne's disease was 0.02 in Jamunapari and 0.15 in Barbari goats. Standard errors of the heritability estimates were not reported.

Singh et al. (1992a) also found that the prevalence of Johne's disease from 1985 to 1990 was significantly higher in Barbari goats (7%) and in Jamunapari goats (4%) as compared to that in Jhakrana and Sirohi goats. But these differences in susceptibility are not necessarily genetic since the different breeds were grazed and housed separately.

Caprine mycoplasma

Disease syndromes like contagious caprine pleuropneumonia (CCPP) have been reported from many parts of India. In the state of Tripura in the northeastern region, 135 goat sera samples were collected to test the seroprevalence of caprine mycoplasma. The overall percentage of positive reactors to spot agglutination test (against *M. mycoides* subspecies *capri*) was 26% and it was the highest in the Black Bengal breed (Ghosh 1989).

Gastrointestinal nematodiasis

Parasitic gastroenteritis due to gastrointestinal helminthiasis is a widely prevalent pathological condition among goats in India, mainly affecting growing kids. *H. contortus* is the most commonly occurring gastrointestinal nematode (Chattopadhyay et al. 1992). Ghosh et al. (1976) reported that all but six of the 125 goats of the local Mizoram type purchased in April 1975 died from heavy infestation of *Haemonchus* by February 1976. Mortality due to parasitic infestation in goats of the Barbari, Jamunapari and Jhakrana breeds was found to be 10% over the years 1985 to 1990 (Sharma et al. 1992). These deaths occurred despite a regular deworming regime. Paramphistomiasis is reported to have caused 44 to 69% morbidity and 45 to 88% mortality in goats (Chattopadhyay et al. 1992).

Colibacillosis in kids

Diarrhoea is one of the primary causes of kid mortality in Indian goats. Colibacillosis is highly prevalent in kids throughout the country (Chattopadhyay et al. 1992). At the livestock farm of CIRG, 180 clinical cases of colibacillosis in Barbari and Jamunapari kids were observed during March–April 1985 (Vihan and Singh 1988). The incidence of *E. coli* infection was greater in the age group 0–10 days in Barbari and 11–20 days in Jamunapari kids. The mortality was higher in Barbari kids (46%) than in Jamunapari kids (22%).

The mortality due to colibacillosis was also found to be higher in Barbari than in Jamunapari kids by Vihan (1991) after a study of the kid mortality at CIRG from 1985 to 1989. A similar study of the prevalence of *E. coli* infection among Barbari and Jamunapari kids born at CIRG during 1985–1988 indicated that mortality was higher in the Barbari breed in 1987 and it was higher in the Jamunapari breed in 1985 and 1988 (Vihan et al. 1990). But this difference in mortality between years and breeds was not statistically significant. Singh et al. (1992b) also found the mortality due to *E. coli* infection among neonates of Barbari to be significantly higher (12%) as compared to that in Jamunapari kids (6%). While evaluating these results, it must be borne in mind that the Jamunapari and Barbari breeds are kept at separate locations on the CIRG campus.

Conclusions

Research in genetic variation in disease resistance between- and within-breeds of small ruminants in India is sporadic, inadequate and largely the incidental outcome of other studies on small ruminant production. Almost no studies have been done with the intention of assessing such genetic variation with a view to exploiting it for improving disease resistance of indigenous breeds. The majority of reports are based on observations taken after natural infection. The possible effects of prior exposure to the disease, environmental variation and variation in nutrition, management practices and behavioural traits of the compared breeds have not been taken into account in such studies. Consequently, it is impossible to arrive at a firm conclusion about the genetic resistance of a particular small ruminant breed or strain. But the variation in disease incidence among breeds found in these studies suggests that resistant genotypes may exist in India. Most Indian breeds are well adapted to the harsh climate, long migrations, tropical diseases, poor nutrition, shortage of drinking water and poor water quality (Acharya 1992). Systematic trials need to be conducted to verify the existence of such genetic material.

Many kinds of diseases and parasites are rampant in India and preventive health care is available to only a very small proportion of the small ruminant population. Hence disease is a major constraint to small ruminant production in India and it is important to look for sustainable low-cost methods for controlling disease. The use of resistant breeds and genetic improvement within these breeds may contribute towards such control. It is, therefore, important that well-designed studies are undertaken to evaluate this approach.

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References

Acharya, R.M. 1982. Sheep and goat breeds of India. FAO Animal Production and Health Paper No. 30. FAO, Rome.

——1992. Goat genetic resources and their management. In: Research in goats Indian experience. Bhattacharyya, N.K. and Singh, K. ed., Makhdoom, Uttar Pradesh, Central Institute for Research on Goats, 1–21.

Ayub, M., Maru, A. and Singh, N.P. 1988. Morbidity, mortality and disease profile in sheep under field conditions of semi-arid Rajasthan. In: Proceedings of the Second National Seminar on Sheep and Goat Diseases. Avikanagar India, Central Sheep and Wool Research Institute, Makhdoom, India, Central Institute for Research on Goats, 83–86.

Bohra, S.D.J. 1988. Genetic resistance to diseases and parasites in sheep. In: Proceedings of the Second National Seminar on Sheep and Goat Diseases. Avikanagar India, Central Sheep and Wool Research Institute, Makhdoom, India, Central Institute for Research on Goats, 16–22.

Chattopadhyay, S.K., Vihan, V.S. and Singh, N. 1992. Kid diarrhoea and its prevention in India. In: Research in goats Indian experience. Bhattacharyya, N.K. and Singh, K. ed., Makhdoom, Uttar Pradesh, Central Institute for Research on Goats, 159–163.

Department of Animal Husbandry (DAH), Maharashtra State. 1992. Final Report of the Sheep and Goat Commission to look into the problems of sheep and goat production in the State of Maharashtra. Government of Maharashtra, 81–83.

Dubey, S., Joshi, D.V. and Sharma, S.N. 1985a. Serological evidence for ovine adenovirus antibodies in sheep, goats and bovine in Punjab. Indian Journal of Animal Sciences, 55, 652–653.

Dubey, S., Srivastava, C.P., Lonkar, P.S. and Maru, A. 1985b. Prevalence of ovine adenovirus antibodies in sheep and goats of semi-arid Rajasthan. Indian Journal of Comparative Microbiology, Immunology and Infectious Diseases, 6, 167–169.

Dubey, S., Rao, T.R.M., Srivastava, C.P., Lonkar, P.S. and Maru, A. 1988. Seroprevalence of blue tongue disease in Rajasthan. Indian Journal of Animal Sciences, 58, 68–70.

Ghalsasi, P.M. and Nimbkar, B.V. 1993. The 'Garole' microsheep of Bengal, India. Animal Genetic Resources, 12, 73–79.

Ghosh, S.S. 1989. Seroprevalence of caprine mycoplasma in Tripura. Indian Veterinary Journal, 66, 577.

Ghosh, S.S., Roy, D. J., Kwatra, M.S. and Kapthuama, R. 1976. Heavy mortality in a goat farm in Mizoram due to haemonchosis. Indian Veterinary Journal, 53, 681–684.

Indo-Swiss Goat Development and Fodder Production Project (ISGP). 1988. Biennial Report (1986–88), Department of Animal Husbandry, Rajasthan.

Khurana, K.L., Maru, A., Bhagwan, P.S.K., Dubey, S. and Srivastava, C.P. 1991. An outbreak of foot and mouth disease in crossbred and indigenous sheep at an organised farm. In: Recent advances in the control of diseases of crossbred and companion animals. Proceedings of the Decennial Convention of the Indian Society for Veterinary Medicine, Goregaon, Bombay.

Kulkarni, D.D., Bannalikar, A.S., Karpe, A..G, Gujar, M.B. and Kulkarni, M.N. 1993. In: Walton, T.E. Osburn, B.I. ed., Bluetongue, African horse sickness and related orbiviruses. Proceedings of the Second International Symposium, Baton Rouge, CRC Press, 193–196.

Mahajan, J.M. 1979. Study on factors affecting preweaning survivability in lambs. Ph.D. thesis, Kurukshetra University, Kurukshetra, Haryana, India.

Mahajan, N.K., Prasad, G., Jain, N., Dhanda, J.S. and Gupta, Y. 1991. Epizootiological studies on blue tongue at an organised sheep breeding farm near Hissar, Haryana. Indian Journal of Animal Sciences, 61, 1–5.

Murty, D.K. and Singh, P.P. 1971. Epidemiological studies on an outbreak of sheep pox in a mixed flock in Uttar Pradesh. Indian Journal of Animal Sciences, 41, 1072–1079.

Nagpal, A.K., Vihan, V.S., Singh, D., Singh, S.V. and Singh, N. 1990. Epidemiological study of an outbreak of goat pox and its effect on the performance of kids. Indian Journal of Animal Sciences, 60, 544–546.

Pachlag, S.V. and Kumar, P.N. 1974. Studies on the gastro-intestinal helminthiasis in sheep. In: Annual Report of the Central Sheep and Wool Research Institute, Avikanagar, Rajasthan, India.

Rao, M.V.S. and Singh, G. 1975. A note on search for the serologic evidence of adenovirus infection in goats and sheep in Agra. Indian Journal of Animal Sciences, 45, 976–977.

Rao, T.M., Charyulu, E.K., Prasad, R.D.D., Srinivasulu, D. and Munirathnam, D. 1993. Some observations on incidence and mortality of pneumonia in sheep. Indian Journal of Animal Health, 32, 77–78.

Shankar, H., Singh, S.V., Singh, N. and Vihan, V.S. 1992. Occurrence of foot and mouth disease in small ruminants. In: Lokeshwar, R.R. ed., Pre-conference Proceedings, Abstracts of Contributory Papers, Fifth International Conference on Goats. New Delhi, India. Vol. 1, p .504.

Sharma, D.K., Singh, N., Singh, S.V., Vihan, V.S. and Tiwari, H.A. 1992. Mortality in goats due to parasitic infestation. In: Lokeshwar, R.R. ed., Pre-conference Proceedings, Abstracts of Contributory Papers, Fifth International Conference on Goats. New Delhi, India. Vol. 1, p. 505.

Sharma, M.M., Uppal, P.K., Lonkar, P.S. and Mathur, P.B. 1986. Epidemiology of a sheep pox outbreak in mutton and fine wool type sheep at an organised farm. Indian Journal of Animal Sciences, 56, 1183–1186.

Singh, N., Kala, S.N., Vihan, V.S. and Singh, V. 1990. Genetic study on the susceptibility to Johne's disease in goats. Indian Journal of Animal Sciences, 60, 1163–1165.

Singh, N., Vihan, V.S., Singh, S.V. and Gupta, V.K. 1992a. Prevalence of Johne's disease in organised goat flocks. In: Lokeshwar, R.R. ed., Pre-conference Proceedings, Abstracts of Contributory Papers, Fifth International Conference on Goats. New Delhi, India. Vol. 1, 1813–1817.

Singh, N., Vihan, V.S., Singh, S.V. and Tiwari, H.A. 1992b. Prevalence and pathology of *Escherichia coli* infection in neonatal kids. In: Lokeshwar, R.R. ed., Pre-conference Proceedings, Abstracts of Contributory Papers, Fifth International Conference on Goats. New Delhi, India. Vol. 1, p. 512.

Singh, S.V., Shankar, H., Singh, N., Sharma, S.K. and Sinha, N.K. 1992c. Outbreak of foot and mouth disease causing heavy mortality in small ruminants. In: Lokeshwar, R.R. ed., Recent advances in goat production. Proceedings of the Fifth International Conference on Goats, New Delhi, India. 1818–1823.

Sriraman, P.K. and Rao, P.R. 1980. A survey of disease conditions in adult sheep of Andhra Pradesh. Indian Veterinary Journal, 57, 971–978.

Vihan, V.S. 1991. Studies on various factors affecting neonatal mortality due to enteropathogenic colibacillosis. In: Recent advances in the control of diseases of crossbred and companion animals. Proceedings of the Decennial Convention of the Indian Society for Veterinary Medicine, Goregaon, Bombay.

Vihan, V.S. and Singh, N. 1988. Epidemiological and clinicopathological studies on colibacillosis in kids. Indian Journal of Animal Sciences, 58, 233–236.

Vihan, V.S., Singh, S.V. and Singh, N. 1990. Prevalence, pathogenicity and serotypes of *Escherichia coli* associated with diarrhoea in newborn kids. Indian Journal of Animal Sciences, 60, 793–795.

Yadav, C.L., Grewal, H.S. and Banerjee, D.P. 1993. Susceptibility of two crossbreeds of sheep to *Haemonchus contortus*. International Journal for Parasitology, 23, 819–822.

Genetic Resistance to Infectious Disease in Small Ruminants: North America and the Caribbean

A.M. ZAJAC

ABSTRACT

Early studies in the United States stimulated considerable interest in the prospect of developing sheep with genetic resistance to helminth parasites. More recently, research has been more fragmented yet there is clear evidence that some North American breeds, particularly those of Carribean origin, are more resistant to infection. European breeds and Merino crosses are more susceptible to nematode infections than Florida Native, Barbados Blackbelly and St. Croix. Some studies have indicated that prior exposure enhances genetic differences and that resistance is also expressed in adult sheep, particularly around the time of lambing. There is little information on genetic variation in goats. Limited studies on genetic resistance of sheep to other diseases suggest that there are breed differences in Maedi/Visna, footrot and mastitis.

Some of the earliest work describing genetic resistance to infectious diseases in small ruminants originated in the United States, but there has been little recent progress in the field. This is due primarily to the relative unimportance of sheep and goats in North American agriculture which has severely limited the availability of research funding for these species. Investigations of disease resistance in Caribbean sheep and goats are also limited and have been conducted principally in the United States with some of the indigenous hair sheep breeds. Furthermore, experimental data from the United States and the Caribbean region have often been obtained from small numbers of animals in single generations and none of the studies has equalled the technological sophistication of work currently being conducted in other parts of the world. Consequently, only a fragmentary picture of genetic resistance to infectious disease can be assembled from this region.

Genetic Resistance to Gastrointestinal Nematodes

Genetic resistance to parasites in sheep has received much greater attention than other infectious diseases. Investigations of breed variation in resistance are predominant, with only a few reports examining differences between individuals within breeds.

European breeds

In the earliest work on genetic resistance from North America, Stewart et al. (1937) followed faecal egg counts in grazing Rambouillet, Hampshire, Shropshire, Southdown and Romney sheep from 6 to 20 months of age and found that Romney lambs were most resistant to *Ostertagia circumcincta*. Gregory et al. (1940) found that faecal egg counts differed between ewes sired by 2 Hampshire rams.

In a series of papers, Whitlock (1955, 1958a,b) examined the resistance to gastrointestinal trichostrongyles in the offspring of 6 Suffolk rams. Lambs sired by one ram (code-named 'Violet') had lower faecal egg counts and higher hematocrit levels than lambs from the other 5 sires. This 'Violet factor,' was followed in his progeny and the author concluded that it behaved as a simple dominant factor.

Although animal numbers were small and analysis limited in some of these studies, the evidence provided by them led the authors to conclude that sheep can inherit enhanced resistance to trichostrongyle infections. Subsequent studies were based on these early observations.

Scrivener (1964a, 1964b, 1967) compared several European breeds with some of the European cross breeds that have been developed in the western United States. These latter breeds include Targhee (developed in 1924 from Lincoln, Rambouillet and Corriedale sheep), Columbia (Lincoln × Rambouillet) and Panama (Rambouillet × Lincoln) (Briggs and Briggs 1980). In a comparison over a 3-year period of natural (primarily *O. circumcincta*) infections in Rambouillet, Suffolk, Hampshire and Targhee, the Targhee lambs had lower faecal egg counts and worm burdens than other breeds. In the final year of the study, Panama lambs were also included and these showed the same level of parasitism as the Targhee lambs.

Resistant Targhee rams were also selected and faecal egg counts in their lambs compared to faecal egg counts in lambs from a susceptible Suffolk ram. Progeny of the Targhee rams had significantly lower faecal egg counts during experimental *O. circumcincta* and subsequent *Haemonchus contortus* infection. In natural infections, *Nematodirus* numbers were also lower in lambs with greater resistance to *O. circumcincta.*

In other studies using these western breeds, crossbred Columbia ewes showed lower faecal egg counts than crossbred Suffolk ewes (Norman and Hohenboken 1979) and Targhee lambs had lower blood packed cell volumes (PCV) than Merino lambs (Colgazier et al. 1968). As with earlier studies, establishing a hierarchy of parasite resistance amongst breeds based on these results is not justified because they represent largely isolated studies, performed in different parts of the United States under varying management conditions.

Native American and Caribbean breeds

Since 1970, the focus of experiments on genetic resistance to helminths has shifted to comparisons between European (including the western stabilised crosses) and Caribbean or native American breeds. Although these latter breeds have often been referred as to 'exotic' in experimental reports, it is probably more accurate to consider them indigenous to this region. Under conditions of natural infection, these breeds have consistently shown enhanced parasite resistance when compared to common domestic breeds. Consequently, they have been proposed as a potential resource for crossbreeding for genetic resistance (Courtney et al. 1984; Zajac et al. 1990). Investigators have also attempted to use these breeds to identify mechanisms of immunity to trichostrongyle parasitism which might be deficient in more parasite susceptible breeds (Zajac et al. 1990; Gamble and Zajac 1992).

In a single experiment conducted over two years a small number of Navajo sheep showed evidence of lower levels of parasitism than European breeds (Knight et al. 1973). All other studies on breed resistance with indigenous breeds have used Florida Native, Barbados Blackbelly and St. Croix sheep (Tables 1 and 2).

The Florida Native is a small, wool sheep developed in Florida by crossbreeding over many years (Courtney 1982). Its origins probably include both Spanish and Northern European breeds. Florida Native sheep used in parasite studies in the United States have been derived from a flock established at the University of Florida in the 1950s, from animals acquired locally. These sheep were initially selected for their resistance to parasites and subsequently received little or no anthelmintic treatment (Loggins et al. 1965; Courtney 1982). Some individuals from this flock were later sent to the Ohio State University, where additional experiments were performed.

St. Croix and Barbados Blackbelly sheep have been introduced in small numbers into the United States from the Caribbean. These hair breeds originated largely from African sheep imported into the region during the colonial era. They are relatively small, prolific sheep (Bradford and Fitzhugh 1983).

The St. Croix sheep used in parasite studies were derived from a group brought into the United States from the island of St. Croix in 1975 (Foote 1983). Although parasite research on this breed has subsequently been conducted at several different locations in the United States, the animals represent only a few lines of related sheep.

Barbados Blackbelly sheep were probably introduced into the United States in about 1904 and crossbreeding with a number of breeds has occurred in this country. The Barbados Blackbelly in the United States has also been crossbred with Moufflon sheep in an effort to produce a game animal

(Shelton 1983). The breed in the United States is sometimes referred to as 'Barbado' to distinguish it from the original Caribbean sheep (Courtney 1982). The United States Barbados Blackbelly consequently is composed of a more diverse population of animals than the other indigenous breeds used in parasite resistance studies.

Natural infections

Increased parasite resistance was first reported in these indigenous breeds in the Florida Native. Loggins et al. (1965) observed decreased faecal egg counts and increased hematocrit levels in pastured Florida Native ewes and lambs compared to Rambouillet and Hampshire animals. Subsequently, natural trichostrongyle infections of Florida Native, Barbados Blackbelly and St. Croix sheep have been followed in several studies (Table 1) and both lambs and ewes of the Florida Native and St. Croix breeds regularly show lower faecal egg counts than domestic breeds.

The differences observed in faecal egg counts between exotic and domestic breeds are often striking. Courtney et al. (1984) followed faecal egg counts (composed primarily of *H. contortus*) in Florida Native, Barbados Blackbelly, St. Croix and Dorset × Rambouillet spring lambing ewes. When their parasite burdens were composed only of worms acquired in the previous grazing season, faecal egg counts of Florida Native and Caribbean sheep did not rise above 100 eggs per gram (epg) and they showed no periparturient rise (PPR), that is, the increase in parasite eggs in faeces associated with lambing and early lactation. In contrast, faecal egg counts of lambing domestic ewes peaked at greater than 2000 epg. This difference was lower if the sheep acquired their parasite burden by grazing after lambing. Then, the PPR was absent only in Florida Native and St. Croix ewes. Crossbred exotic ewes showed an intermediate level of resistance in both portions of the study.

The PPR is epidemiologically important because it ensures that large numbers of infective larvae will be present at the time when fully susceptible lambs begin grazing. Selective crossbreeding to eliminate the PPR could be of significant practical value in controlling trichostrongyle populations.

The consistent differences in faecal egg counts found in ewes were not always paralleled by differences in adult parasite numbers. Although non-lactating Florida Native and St. Croix ewes showed lower faecal egg counts than domestic ewes in another study (Courtney et al. 1985a,b), no significant differences were seen among breeds in total worm counts. However, when winter-housed, pregnant Florida Native and Dorset × Rambouillet ewes

Table 1 Evidence of breed resistance in natural infections of Caribbean and native American sheep breeds.

Breed	Compared with	Age	Result	References
Navajo	Suffolk, Targhee, Rambouillet, Corriedale	4 months	Reduced *Haemonchus* numbers	Knight et al. 1973
Barbados Blackbelly, Blackbelly × Dorset	Dorset and domestic crosses	Ewes and lambs	Reduced FEC[a]	Yazwinski et al. 1979
Florida Native	Rambouillet, Hampshire	Ewes and lambs	Reduced FEC and *Haemonchus* numbers; reduced haemoglobin	Loggins et al. 1965
Florida Native	Rambouillet	Ewes	Reduced FEC Reduced PCV[b], haemoglobin	Jilek and Bradley, 1969
Florida Native, St. Croix, Barbados Blackbelly	Rambouillet, Finn-Dorset × Rambouillet	Ewes	Reduced or absent PPR, less evident in Barbados Blackbelly	Courtney et al. 1984
Florida Native, St. Croix	Finn-Dorset × Rambouillet, Barbados Blackbelly	Ewes	Reduced FEC and no difference in worm burden	Courtney et al. 1985a,b
Florida Native	Dorset × Rambouillet	Ewes	Reduced FEC and worm burdens throughout pregnancy	Zajac et al.1988
St. Croix	Dorset	2 months	Reduced FEC and *Haemonchus* numbers; reduced globule leukocytes	Gamble and Zajac 1992
St. Croix	Dorset	2 months	Reduced FEC and *Haemonchus* numbers	M.E Mansfield and H.R. Gamble, pers. comm.

Faecal Egg Count
Packed Cell Volume

were followed through pregnancy and parturition, both faecal egg counts and total worm counts were significantly lower in the Florida Natives. Breed differences were apparent in numbers of *H. contortus, O. circumcincta* and *Trichostrongylus axei* (Zajac et al. 1988).

In these ewe studies, sheep containing only residual worm populations from the preceding grazing season appeared to show more distinct breed resistance than comparisons of grazing ewes. One cause of the increased resistance occurring in Florida Natives and St. Croix may be a more rapid loss of adult parasites after grazing and a smaller persistent residual population than that maintained by more susceptible breeds.

St. Croix lambs, like St. Croix ewes, have also produced significantly lower faecal egg counts and developed lower total worm burdens when grazed with Dorset lambs on naturally infected pasture (Gamble and Zajac 1992; Mansfield and Gamble, submitted for publication). After initial infection and treatment, grazing St. Croix lambs became infected with 99% fewer *H. contortus* than Dorset lambs (Gamble and Zajac 1992).

Barbados Blackbelly sheep have been less consistent in manifesting enhanced parasite resistance (Yazwinski et al. 1979; Todd et al. 1978; Courtney et al. 1984; Courtney et al. 1985a, b) and they have not been used to study parasite resistance in recent years. Because the Barbados Blackbelly has undergone considerable crossbreeding in the United States, it probably cannot be expected to show the same uniformity of resistance seen in the smaller populations of St. Croix and Florida Natives.

Experimental infections

H. contortus infection has been followed in several experiments comparing these indigenous breeds with domestic breed sheep, usually Dorset, Rambouillet or their crosses (Table 2). As observed in natural infections, Florida Native and St. Croix sheep dependably show decreased faecal egg counts when compared to domestic breeds, with more variable differences in worm burdens. Greater differences in parasite numbers are seen when young lambs are used (Radhakrishnan et al. 1972; Bradley et al. 1973; Courtney et al. 1985b). In older lambs (9–10 months), differences in some studies were not significant (Courtney et al. 1985a, b; Zajac et al. 1990).

If lambs of these resistant breeds have been naturally selected over time to develop immunity to parasites at an earlier age than domestic breeds, exaggerated breed differences would be expected in younger animals. However, like the studies comparing natural infections in ewes, it is also possible that some of the inconsistencies in experimental infections result from variation in the interval after infection when worm burden is

Table 2 Evidence of breed resistance in experimental trichostrongyle infections of Caribbean and native American sheep breeds.

Breed	Compared with	Age	Result	Reference
Barbados Blackbelly, Barbados × Dorset	Dorset	8 months, ewes	Lambs: Reduced FEC[a] and eggs produced/worm Ewes: no significant differences	Yazwinski et al. 1979
Targhee × Barbados, Blackbelly	Targhee	4 months	No difference in FEC and worm burden, PCV[b], wt. gain	Todd et al. 1978
Florida Native	Rambouillet	5 months	Reduced FEC and fewer and smaller adult *Haemonchus* numbers Reduced PPP[c], PCV, larvae	Radhakrishnan et al. 1972
Florida Native	Rambouillet	5 ½–6 months	Reduced FEC and *Haemonchus* numbers Reduced PPP, larvae numbers, weight gain, abomasal eosinophils, PCV	Bradley et al. 1973
Florida Native, St. Croix, Barbados Blackbelly	Domestic Crossbred	6-40 weeks	Reduced FEC and *Haemonchus* numbers, but difference reduced with lamb age	Courtney et al. 1985a
Florida Native, St. Croix	Dorset × Rambouillet	9-10 months	Reduced FEC, reduced PCV and total protein	Zajac et al. 1990
St. Croix	Dorset	2 months	Reduced FEC	Gamble and Zajac 1992

[a] FEC = faecal egg count
[b] PCV = packed cell volume
[c] PPP = prepatent period

determined. Regardless of these experimental differences, St. Croix and Florida Native sheep, when compared with domestic breeds have shown significant evidence of increased resistance to trichostrongyle infection which may affect both the magnitude and pathogenicity of *H. contortus* infection.

Differences in prepatent period, adult worm size, proportion of larval parasites in the abomasum and eggs produced per worm between these indigenous and domestic breeds have also been reported (Radhakrishnan et al. 1972; Bradley et al. 1973). In addition, resistant breeds have shown increased packed cell volumes (PCV), haemoglobin levels and weight gains in experimental *H. contortus* infection (Radhakrishnan et al. 1972, Bradley et al. 1973; Zajac et al. 1990). Haemoglobin type was examined in several experiments. Jilek and Bradley (1969), Radhakrishnan et al. (1972) and Bradley et al. (1973) found a high rate of haemoglobin A in Florida Native sheep and associated type A and type AB with increased resistance compared to type B. Courtney et al. (1985b) did not find haemoglobin type to be useful in predicting resistance in Florida Native, St. Croix and Barbados Blackbelly sheep. Yazwinski et al. (1979) also did not find an association between haemoglobin type and resistance in Barbados Blackbelly and domestic breed sheep.

The time required for breed differences to become evident has been variable. There was no difference in parasite numbers amongst Florida Native, St. Croix or Dorset × Rambouillet lambs 1 week after experimental infections (Zajac et al. 1990). However, breed differences have been seen in the length of the prepatent period and faecal egg counts within the first month of a primary infection in some studies (Bradley et al. 1973; Zajac et al. 1990; Radhakrishnan et al. 1972). In other experiments, breed differences in faecal egg counts have only been evident in challenge infections (Courtney et al. 1985b; Gamble and Zajac 1992).

Three-quarter St. Croix lambs showed a similar level of resistance to the full St. Croix lambs in experimental *H. contortus* infection. In the same study, Courtney et al. (1985b) found that gender had a significant influence on parasite resistance independent of breed. Combined female lambs of all breeds showed lower *H. contortus* burdens and higher PCVs than male lambs of all breeds.

The consistent level of parasite resistance shown by the Florida Native and St. Croix breeds suggested that comparisons with domestic breeds might identify critical components of immunity to trichostrongyles, particularly *H. contortus*. However, there is no evidence from natural or experimental infections that exotic breeds differ in any unique way in the expression of immunity to parasites. When trichostrongyle populations in pregnant Florida

Native and Dorset × Rambouillet ewes were followed, lambing ewes of both breeds had higher numbers of adults and a lower proportion of arrested parasites than non-lambing ewes of both breeds (Zajac et al. 1988). Although the total number of parasites was lower in the Florida Natives, these results indicate that host factors influencing parasite population changes were similar in both breeds.

In one of the earlier studies comparing experimental *H. contortus* infection, the extent of eosinophil infiltration in the abomasum was greater in Florida Native lambs than Rambouillet lambs (Bradley et al. 1973). However, no attempts were made to quantify the local eosinophil response.

No differences were seen among Florida Native, St. Croix and Dorset × Rambouillet sheep in lymphocyte reactivity to *H. contortus* antigen, levels of parasite specific mucosal or serum antibody, number of abomasal mast cells (including globule leukocytes) or histamine level during primary and challenge infection (Zajac et al. 1990). In another study, naturally infected St. Croix lambs were shown to have significantly increased levels of globule leukocytes compared with Dorset lambs, although antibody levels, leukocyte reactivity, and inhibition of larval migration were not different. An increase in globule leukocyte numbers has previously been associated with decreased worm burdens in studies of genetic resistance to trichostrongyle infection in Merino sheep (Dineen et al. 1978; Dineen and Windon 1980).

Stability of resistance and use in crossbreeding

Persistent reduction in faecal egg counts and PPR and minimal effects on hematologic parameters observed in infected St. Croix and Florida Native sheep suggest that they could be used effectively with common domestic breeds to produce crossbred sheep with enhanced parasite resistance. St. Croix sheep offer the additional advantages of prolificacy and out-of-season breeding (Bradford and Fitzhugh 1983).

Use of the St. Croix, Florida Native or other indigenous breeds in commercial production would be easier to promote if it could be established that the degree of parasite resistance conferred by crossbreeding for resistance is greater or more stable than selection within other breeds. However, the increased resistance of Navajo sheep to trichostrongyle infection was not present in a wet year when parasite numbers were high (Knight et al. 1973). Moreover, helminthiasis is one of the most important health problems in the Virgin Islands, even in the St. Croix breed, which shows such striking resistance to parasites in experimental settings (Hupp and Deller 1983). These observations suggest that high parasite challenge may overwhelm the ability of these breeds to control infection.

The finding of Courtney et al. (1984) that PPR was greater in a line of Florida Native sheep which had received greater exposure to anthelmintic that the University of Florida flock, also indicates that parasite resistance in these breeds is as susceptible to selection pressures as in any other breed. Moreover, St. Croix and Florida Native sheep are small compared to common meat breeds used most often in North America and it is unlikely that producers would accept any reduction in live lamb and carcass weights in return for only a partial improvement in parasite resistance. Crossbreeding with hair sheep, like the St. Croix, will also affect wool production, although with the elimination of the federal wool incentive in the United States, this factor might be of less importance.

Nonetheless, it appears that use of St. Croix or Florida Native sheep in North America does not provide any advantages over the selection within breeds which results in much lower, if any, production loss. These breeds, especially the St. Croix, will probably be of greatest use in the type of tropical or subtropical environment in which they were produced. In those production systems their potential parasite resistance could be selected without the associated economic loss that might be seen in North America.

Other Parasites

Very little work has been performed in the United States on disease resistance to other small ruminant parasites. Boyce et al. (1987) found that Florida Native lambs showed the greatest degree of resistance to experimental *Fasciola hepatica* infection measured by faecal egg counts and fluke numbers. St. Croix and Targhee lambs were also more resistant than Finn × Rambouillet and Barbados Blackbelly lambs. Since none of the sheep breeds appeared to acquire immunity to challenge infection, it is unclear whether these differences in resistance to liver flukes are related to breed variation in resistance to gastrointestinal trichostrongyle infection. Fewer St. Croix than Dorset lambs became infected with the lungworm *Protostrongylus rufescens*, but infection rates were too low to determine if this difference was significant (M.E. Mansfield and H.R. Gamble, pers. comm.).

Other Diseases

Only a handful of studies have been published in this region on genetic resistance in sheep to non-parasitic diseases. Lesions and clinical signs associated with ovine progressive pneumonia (Maedi/Visna) were greater in Border Leicester than Columbia sheep (Cutlip et al. 1986). A significantly lower prevalence of infection in Rambouillet sheep and greatest prevalence in Finn sheep crosses were found, compared with several other breeds, in a serological survey for antiviral antibodies in western range sheep (Gates et al. 1978). In another serologic survey, the infection rate of ovine progressive pneumonia was found to be greatest in North Country Cheviots, followed by Columbia, Rambouillet, Suffolk, and Hampshire ewes (Light et al. 1979).

Transmission of resistance to footrot has also been examined. Several Targhee rams were identified as footrot resistant. These rams were bred to western white-faced ewes susceptible to footrot or of unknown susceptibility. Lambs sired by the resistant rams showed a lower prevalence of footrot compared with offspring of susceptible sheep or sheep of unknown susceptibility. The resistance to the disease could largely be overwhelmed by direct exposure of macerated skin to a heavy dose of *Dichelobacter nodosus*, suggesting that skin integrity is critical to disease resistance (Bulgin et al. 1988).

Finally, in a study examining genetic effects on milk production and mastitis, Finn sheep and Romney crossbreds showed a lower rate of mastitis than Dorset and Cheviot crossbreds. This effect was unrelated to the number of lambs suckled but tended to reflect the milk production rank of the sire breed (Torres-Hernandez and Hohenboken 1978).

Goats

There has been little interest in genetic resistance to disease in goats in this region. In one study of selective breeding for resistance to trichostrongyle parasites, progeny of resistant males and unselected females showed a 71% survival rate following *H. contortus* infection compared with a 33% rate in controls. If both parents were resistant there was an 83% survival rate compared with 31% in controls (Hutt 1958).

Future Directions

Sheep production in the United States has been hampered by the restricted availability of approved chemicals and low rate of new chemical approvals. Resistance has been detected in *H. contortus* to all the modern anthelmintics available for sheep in North America (Zajac and Moore 1993). Public concern is also mounting over the issue of chemical residues in meat. Under these circumstances, continued characterisation of genetic resistance to disease and production of resistant lines of sheep should be an active area of research. However, the size of the national sheep flock in the United States is not expected to exceed 8 to 10 million animals in the near future and lamb comprises only 0.6% of all meat and poultry consumed in this country (Stillman et al. 1990). There is little incentive or opportunity to pursue the field of genetic resistance in North America and limited resources for work in the Caribbean. Consequently, substantial advances in this area will continue to come from other parts of the world small ruminant production is more important in national agricultural programs.

References

Boyce, W.M., Courtney, C.H. and Loggins, P.E. 1987. Resistance to experimental infection with *Fasciola hepatica* in exotic and domestic breeds of sheep. International Journal for Parasitology, 17, 1233–1237.

Bradford, G.E. and Fitzhugh, H.A. 1983. Hair sheep: A general description. In: Fitzhugh, H.A. and Bradford, G.E. ed., Hair sheep of western Africa and the Americas: A genetic resource for the tropics. Boulder, Colorado, Westview Press, 3–22.

Bradley, R.E., Radhakrishnan, C.V., Patil-Kulkarni, V.G. and Loggins, P.E. 1973. Responses in Florida Native and Rambouillet lambs exposed to one and two oral doses of *Haemonchus contortus*. American Journal of Veterinary Research, 34, 729–735.

Briggs, H.M. and Briggs, D.M. 1980. Modern Breeds of Livestock. New York, Macmillan, 415–581.

Bulgin, M.S., Lincoln, S.D., Parker, C.E., South, P.J., Dahmen, J.J. and Lane, M.L. 1988. Genetic-associated resistance to foot rot in selected Targhee sheep. Journal of the American Veterinary Medical Association, 192, 512–515.

Colgazier, M. L., Lindahl, I.J., Wilson G.I., Whitmore, G.E. and Wilson, R.L. 1968. Effect of management systems on the growth of lambs and development of internal parasitism. II. Field trials involving medication with national formulary and purified grades of phenothiazine. Journal of Parasitology, 54, 89–97.

Courtney, C.H. 1982. Resistance of three exotic breeds of sheep to gastrointestinal nematodes. PhD Dissertation. The Ohio State University. Columbus, Ohio, 167 pp.

Courtney, C.H., Parker, C.F., McClure, K.E. and Herd, R.P. 1984. A comparison of the periparturient rise in faecal egg counts of exotic and domestic ewes. International Journal for Parasitology, 14, 377–381.

-1985a. Resistance of exotic and domestic lambs to experimental infection with *Haemonchus contortus*. International Journal for Parasitology, 15, 101–109.

-1985b. Resistance of nonlambing exotic and domestic ewes to naturally acquired gastrointestinal nematodes. International Journal for Parasitology, 15, 239–243.

Courtney, C.H., Gessner, R., Sholz, S.R. and Loggins, P.E. 1985c. The periparturient rise in faecal egg counts in three strains of Florida Native ewes and its value in predicting resistance of lambs to *Haemonchus contortus*. International Journal for Parasitology, 16, 185–189.

Cutlip, R.C., Lehmkuhl, H.D., Brogden, K.A. and Sacks, J.M. 1986. Breed susceptibility to ovine progressive pneumonia (Maedi/Visna) virus. Veterinary Microbiology, 12, 283–288.

Dineen, J.K. and Windon, R.G. 1980. The effect of sire selection on the response of lambs to vaccination with irradiated *Trichostrongylus colubriformis* larvae. International Journal for Parasitology, 10, 189–196.

Dineen, J.K., Gregg, P. and Lascelles, A.K. 1978. The response of lambs to vaccination at weaning with irradiated *Trichostrongylus colubriformis* larvae: segregation into 'responders' and 'nonresponders'. International Journal for Parasitology, 8, 59–63.

Foote, W.C. 1983. The St. Croix sheep in the United States. In: Fitzhugh, H.A. and Bradford, G.E. ed., Hair sheep of western Africa and the Americas: A genetic resource for the tropics. Boulder, Colorado, Westview Press, 275–287.

Gamble, H.R. and Zajac, A.M. 1992. Resistance of St. Croix lambs to *Haemonchus contortus* in experimentally and naturally acquired infections. Veterinary Parasitology, 41, 211–225.

Gates, N.L., Winward, L.D., Gorham, J.R. and Shen, D.T. 1978. Serologic survey of prevalence of ovine progressive pneumonia in Idaho range sheep. Journal of the American Veterinary Medical Association, 173, 1575–1577.

Gregory, P.W., Miller, R.F. and Stewart, M.A. 1940. An analysis of environmental and genetic factors influencing stomach-worm infestation in sheep. Journal of Genetics, 39, 391–400.

Hupp, H. and Deller, D. 1983. Virgin Islands white hair sheep. In: Fitzhugh, H.A. and Bradford, G.E. ed., Hair sheep of western Africa and the Americas: a genetic resource for the tropics. Boulder, Colorado, Westview Press, 171–178.

Hutt, F.B. 1958. Genetic Resistance to Disease in Domestic Animals. Ithaca, New York, Comstock Publishing Associates, 198 p.

Jilek, A.F. and Bradley, R.E. 1969. Haemoglobin types and resistance to *Haemonchus contortus* in sheep. American Journal of Veterinary Research, 30, 1773–1778.

Knight, R.A., Vegors, H.H. and Glimp, H.A. 1973. Effects of breed and date of birth of lambs on gastrointestinal nematode infections. American Journal of Veterinary Research, 34, 323–327.

Light, M.R., Schipper, I.A., Molitor, T.W., Tilton, J.E. and Slanger, W.D. 1979. Progressive pneumonia in sheep: incidence of natural infection and establishment of clean flocks. Journal of Animal Science, 49, 1156–1160.

Loggins, P.E., Swanson, L.E. and Koger, M. 1965. Parasite levels in sheep as affected by heredity. Journal of Animal Science, 24, 286–287.

Norman, L.M. and Hohenboken, W. 1979. Genetic and environmental effects on internal parasites, foot soundness and attrition in crossbred ewes. Journal of Animal Science, 48, 1329–1337.

Radhakrishnan, C.V., Bradley, R.E. and Loggins, P.E. 1972. Host responses of worm-free Florida Native and Rambouillet lambs experimentally infected with *Haemonchus contortus*. American Journal of Veterinary Research, 33, 817–823.

Scrivener, L.H. 1964a. Breed resistance to *Ostertagia* in sheep. Journal of the American Veterinary Medical Association, 144, 883–887.

——1964b. Transmission of resistance to ovine ostertagiasis. Journal of the American Veterinary Medical Association, 144, 1024–1027.

——1967. Genetic resistance to ostertagiasis and haemonchosis in lambs. Journal of the American Veterinary Medical Association, 151, 1443–1446.

Shelton, M. 1983. The Barbados Blackbelly ('Barbado') breed in Texas. In: Fitzhugh, H.A. and Bradford, G.E. ed., Hair sheep of western Africa and the Americas: a genetic resource for the tropics. Boulder, Colorado, Westview Press, 289–291.

Stewart, M.A., Miller, R.F. and Douglas, J.R. 1937. Resistance of sheep of different breeds to infestation by *Ostertagia circumcincta.* Journal of Agricultural Research, 55, 923–930.

Stillman, R., Crawford, T. and Aldrich, L. 1990. The United States Sheep Industry. Economic Research Service, United States Department of Agriculture. Staff Report No. AGES 9048.

Todd, K.S., Mansfield, M.E. and Levine, N.D. 1978. *Haemonchus contortus* infections in Targhee and Targhee-Barbados Blackbelly cross lambs. American Journal of Veterinary Research, 39, 865–866.

Torres-Hernandez, G. and Hohenboken, W. 1978. Genetic and environmental effects on milk production, milk composition and mastitis incidence in crossbred ewes. Journal of Animal Science, 49, 410–417.

Whitlock, J.H. 1955. A study of the inheritance of resistance to trichostrongyloidosis in sheep. Cornell Veterinarian, 45, 422–439.

——1958a. The inheritance of resistance to trichostrongylidosis in sheep. II. Observations on the genetic mechanism in trichostrongylidosis. Cornell Veterinarian, 48, 135–145.

——1958b. The inheritance of resistance to trichostrongylidosis in sheep. III. Preliminary studies using a gastric pouch. Cornell Veterinarian, 48, 145–163.

Yazwinski, T.A., Goode, L., Moncol, D.J., Morgan, G.W. and Linnerud, A.C. 1979. Parasite resistance in straightbred and crossbred Barbado Blackbelly sheep. Journal of Animal Science, 49, 919–926.

Zajac, A.M. and Moore, G.W. 1993. Treatment and control of gastrointestinal nematodes in sheep. Compendium on Continuing Education for the Practicing Veterinarian, 15, 999–1013.

Zajac, A.M., Herd, R.P. and McClure, K.E. 1988. Trichostrongylid parasite populations in pregnant or lactating and unmated Florida Native and Dorset/Rambouillet Ewes. International Journal for Parasitology, 18, 981–985.

Zajac, A.M., Krakowka, S., Herd, R.P. and McClure, K.E. 1990. Experimental *Haemonchus contortus* infection in three breeds of sheep. Veterinary Parasitology, 36, 221–235.

Helminth Infections of Sheep in Rubber Plantations in Sumatra

R.M. GATENBY, A.J. WILSON, E. ROMJALI, V.S. PANDEY,
L.P. BATUBARA AND G.E. BRADFORD

ABSTRACT

In Indonesia there is much interest in the integration of sheep production with the cultivation of rubber in plantations. One of the major limitations on the development of this industry is the impact of helminth parasites, mainly gastrointestinal nematodes and pancreatic fluke. A major research program in North Sumatra has been investigating the differences between indigenous and imported sheep breeds to determine if any of these breeds is more resistant to parasites. All the breeds being studied—Sumatra, Javanese Thin-Tail, Virgin Island and Barbados Blackbelly—originate in the tropics where some degree of genetic resistance may have developed by selection. This may explain why no major breed differences have been detected. Programs for selective breeding of Sumatra/Virgin Island crosses are described.

In Indonesia there are about 3 million hectares of rubber and 1 million hectares of oil palm plantations, most of which are located in Sumatra. Until now, little of the surplus vegetation growing in these plantations has been used, but with the growing market demand for meat and the need of smallholder rubber farmers to supplement their income, there is considerable interest in integrating sheep in plantations.

Since 1984, the Small Ruminant Collaborative Research Support Program (SR-CRSP) has been working with the Research Station for Animal Production (SBPT) in Sei Putih to develop sheep production in North Sumatra. Work has focused on developing a suitable system of sheep management and the most appropriate sheep genotype. Since 1989, staff of the Research Institute for Veterinary Science, Bogor and the Indonesia-International Animal Science Research and Development Foundation (INI ANSREDEF) have collaborated with scientists at Sei Putih to study the disease constraints on sheep in rubber plantations.

It was soon established that one of the main constraints to sheep production in this hot humid climate is parasitism, particularly gastrointestinal nematodes and pancreatic fluke. Degree of helminthiasis is at least as important as nutrition in determining levels of production (Handayani and Gatenby 1988). Control of internal parasites by rotational grazing is impracticable.

Control solely by anthelmintics is expensive and unwise, and at present, anthelmintics are sold only in urban centres distant from areas of sheep production. The development of animals that are resistant to parasites would be a valuable contribution to a control strategy (Gray 1991).

The work described in this paper was carried out at the Research Station for Animal Production, Sei Putih in North Sumatra (3°N, 99°E). Altitude is about 50 m above sea level and annual rainfall about 1800 mm with rain in every month. Mean maximum and minimum temperatures are 32°C and 23°C respectively, with little seasonal variation.

Sheep and Management

Local sheep in North Sumatra are small and mature ewe weight averages 22 kg. Adult sheep have coarse wool which is not utilised; coat colour varies, with the majority of animals being light brown or white. A characteristic feature is that the tail is short and thin and this breed is now known as 'Sumatra'. Sumatra sheep are similar to the Malin (Malaysian Indigenous) and probably have common ancestry with the Java Thin-tail, but are smaller with a shorter tail and less variety in colour pattern. Virgin Island sheep (also known as the St. Croix), Barbados Blackbelly and the Java Fat-tail from other parts of the humid tropics have been introduced to Sei Putih for crossbreeding with the Sumatra. Both first and second generation crosses of these breeds have been assessed for resistance to parasites.

Sheep are housed at night in group pens in sheep houses with a raised slatted floor. Ewes and suckling lambs are grazed during the day on natural vegetation in rubber plantations. Grazing animals are treated with an anthelmintic every three months. Lambs are stall fed from weaning until they are 6 months of age. Rams are maintained separately to avoid unplanned matings.

Worm Burdens in Purebred and Crossbred Ewes

From April 1992 to April 1993 faecal samples were collected from twenty-six ewes every two weeks (Wilson et al. 1993). Means for each breed are shown in Table 1. These values suggest that Virgin Island ewes can maintain lower egg counts than Sumatra ewes. The number of ewes representing each breed was small and egg counts were highly variable within each breed.

A second study of 3 younger ewes from these breeds and their crosses was started in April 1993. Faecal samples were collected for a three-month period. Overall there was a significant difference between breeds (Batabura et al. 1993) although egg counts were low [range 27–187 (epg)] with Virgin Island ones the most resistant.

Table 1 Means of egg counts on faeces collected every two weeks from purebred and crossbred ewes.

Breed (n)	Faecal Egg Count (epg)±sem
Sumatra (43)	2470±660
Java Fat-tail (34)	837±340
Virgin Island (50)	382±110
Virgin Island x Sumatra (65)	976±200

n = number of egg counts

Total Worm Counts of Rams

Sixteen weaned ram lambs of each genotype were exposed to parasite-contaminated pastures in each of three years and slaughtered after a further month indoors without exposure to parasites (Wilson et al. 1993; Gatenby et al. 1993). Barbados × Sumatra, Virgin Island × Sumatra (F_1) and Virgin Island × Sumatra (F_2) had geometric means (4030 epg) similar to or slightly lower than the indigenous animals (4140 epg), showing that crossbreeding Sumatra with Barbados Blackbelly or Virgin Island sheep does not increase susceptibility to worm infection. The Virgin Island × Sumatra (F_2) had similar worm burdens to the Virgin Island × Sumatra (F_1). Java Fat-tail × Sumatra (F_1) ranked highest or second highest in each year (5624 epg), suggesting that this genotype is the most susceptible to worm infection. In all seasons there was significant variation between animals within breed groups. There were no consistent effects of breed type on the numbers of worms and flukes at slaughter.

Discussion

The introduction of a new breed of sheep is often followed by the exacerbation of disease problems. However, the introduction of Virgin Island and Barbados Blackbelly sheep into Sumatra does not seem to have increased the worm problem. Indeed, animals of these breeds seem to be slightly more resistant to internal parasites than local Sumatra sheep. Conversely, Java Fat-tail may be more susceptible. These breed differences result from the environment of origin of these sheep. The Virgin Island and Barbados Blackbelly breeds are from the Caribbean where the climate is hot and humid and the density of sheep per unit area is relatively high and there is a constant challenge of internal parasites which may lead to the development of some degree of genetic resistance. Java Fat-tail sheep are from Eastern Indonesia, where the climate is drier, and the selection pressure for increased resistance to worms is expected to be lower. From the results presented here, there is an indication that there is between-breed variation in resistance to nematodes. Some sheep maintain low worm numbers.

It is planned to develop resistant and susceptible lines of sheep in Sumatra, and to initiate these lines, we have selected 21 Virgin Island × Sumatra (F_2) ewes classified as resistant (on the basis of faecal egg count) and 14 classified as susceptible. Among Sumatra ewes, 3 resistant and 6 susceptible have been selected.

Identification of resistant and susceptible sires is based on a single assessment of faecal egg count at 3 months of age. Using only this limited information, we have provisionally selected one resistant and one susceptible young ram in each of our Virgin Island × Sumatra (F_2) and Sumatra populations, and will use these four animals to mate with the selected ewes. In the future we will experimentally infect potential sires to better characterise resistance to worms.

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References

Batubara, A., Mirza, I., Hutauruk, M., Gatenby, R. and Wilson, A.J. 1993. Effect of breed of sheep on levels of gastro-intestinal nematodes at Sungai Putih. In Annual Report 1992–1993, SR-CRSP Sei Putih, P.O. Box 1, Galang 20585, North Sumatra, Indonesia. 45–48.

Gatenby, R.M., Adiwinata, G., Wilson A.J.H., Mirza, I., Batubara, A., Hutauruk, M. and Immanyanto. 1993. Effect of genotype of sheep on levels of worms and fluke. In Annual Report 1992–1993, SR-CRSP Sei Putih, P.O. Box 1, Galang 20585, North Sumatra, Indonesia. 49–52

Gray, G.D. 1991. Breeding for resistance to trichostrongyle nematodes in sheep. In: Owen, J.B. and Axford, R.F.E. ed., Breeding for diseases resistance in farm animals, Proceedings of an International Symposium, Bangor, Wales, Sept. 1990. Wallingford, U.K., CAB International, 139–161.

Handayani, S. W. and Gatenby, R.M. 1988. Effects of management system, legume feeding and anthelmintic treatment on the performance of lambs in North Sumatra. Tropical Animal and Production, 20, 122–128.

Wilson, A.J., Beriajaya and Adiwinata, G. 1993. Studies on the epidemiology and control of important disease constraints of sheep at Sungei Putih, North Sumatra 1992–1993. Consultants report 27/93. INI ANSREDEF and RIVS, P.O. Box 1093 BOO, Bogor 16010, Indonesia.

Studies on Genetic Resistance to Infectious Diseases of Small Ruminants in Southeast Asia

V.S. PANDEY

ABSTRACT

Disease caused by helminths is a constraint on production of sheep and goats in Southeast Asia. Lost production and increasing resistance to anthelmintics have resulted in the initiation of several research programs, in Indonesia, Thailand and the Philippines, to investigate breeding approaches to helminth control. These programs are focussing on differences in worm numbers between breeds and on the potential for humoral and cellular immune responses to be used as alternative selection criteria. The major problems encountered in this work are firstly, the reluctance of scientists to accept that breeding has a role in worm control and secondly, in assembling the relatively large flocks required for genetic studies.

Southeast Asia, including China, with a human population of about 1.6 billion has 120 million sheep and 114 million goats (Table 1) (FAO 1992). The region possesses various indigenous breeds of small ruminants. Several exotic breeds have been imported for improving the local stock. Disease resistance has not been included in breeding programs and few reports on disease

Table 1 **Sheep and goat (in thousands) and human population (in millions) in Southeast Asian countries (FAO 1992).**

Country	Sheep	Goat	Human
Philippines	30	2132	62
Indonesia	5900	11250	184
Malaysia	206	332	17
Thailand	162	121	
Cambodia	NA	NA	
Laos	NA	139	
Vietnam	NA	413	
Burma (Myanmar)	276	1036	
China	113508	98313	1153
Total	120082	113736	1589
% of world population	10.1%	19.1%	30%

NA=Not available.

resistance in small ruminants in Southeast Asia exist. Recently, some work has been initiated in Malaysia, Indonesia, Thailand and the Philippines to study aspects of general resistance, or resistance to specific disease agents, of small ruminants. This paper reports some of the activities of these programs. Most of the research is targeted towards helminths as they cause major problems in the hot humid climate of the region.

Malaysia

A research program to develop a synthetic hair sheep by crossbreeding wool sheep with hair sheep started in Malaysia in 1990. The hair sheep used is the 'Cameroon', which belongs to Djallonke breed of West Africa. Preliminary studies indicate that cross-breeds perform better and have some reproductive advantage over local wool sheep (Horst et al. 1992). Disease resistance is one aspect of this program.

Effect of breed on natural infections with nematodes and coccidia

Gastrointestinal nematodes, mainly *Haemonchus contortus*, are major constraints in all age groups of sheep. In young animals, especially those in a zero grazing system, coccidia are also common but their real impact on health and production has not been investigated in detail.

Weaned lambs of local longtail wool sheep and their crosses with Cameroon were monitored for nematode eggs and coccidia oocysts in faeces over a period of 9 months (Pandey and Sivaraj 1992). Analysis of data showed that crossbreds were more resistant to *H. contortus*, the predominant nematode species present, than the local wool sheep lambs. However, oocyst counts in crossbred sheep were higher than in local sheep. Coccidia is a self-limiting infection and within a few weeks their numbers were reduced to a very low level of insignificant importance. Further studies are under way to confirm these preliminary findings.

Immune response of different breeds/genotypes of sheep

Phenotypic markers of general disease resistance have proved useful in a selection index to breed pigs for disease resistance (Mallard et al. 1993). Humoral and cellular immune responses and complement have been studied in different breeds/genotypes of sheep in Malaysia to assess their suitability as markers for disease resistance.

Humoral immune response

Humoral immune responsiveness of three genotypes of sheep, namely local longtail wool sheep (LL), Cameroon (C) and C × LL, was assessed by measuring the haemagglutinating antibodies after two intravenous injection of chicken red blood cells (CRBC), on day 0 and day 14. Although the titres of antibodies of three genotypes were not significantly different, there were big variations in the titres of individuals within a genotype. This suggests genetic variation in the response to CRBC.

Cellular immune response

Five genotypes of sheep were examined for *in vivo* response to the mitogen, phytohaemagglutinin-P (PHA-P) by intradermal injection and measurement of double skinfold thickness before and 24 hours after injection. The effect of genotype on skin thickness was highly significant ($p<0.001$). The genotypes could be classified in ascending order of response as follows (Pandey and Sivaraj 1992): local longtail (LL), Cameroon × LL, Cameroon (C), Dorsimal (DM) (a cross of Poll Dorset Horn × Malaysian indigenous sheep), C × DM.

Complement

Complement is a non specific element in the defence mechanism against infections and therefore is of interest in disease resistance studies. Complement levels measured by classical pathway (CPW), alternative pathway (Pandey and Sivaraj 1993) and C_3 molecules, as well as C_3 activity, were examined from 12 genotypes of sheep in Malaysia. There were significant differences ($0.005<P<0.05$) between genotypes. The significance of such differences needs to be evaluated in relation to disease resistance. It may be postulated that animals with higher levels of complement would be able to respond better to infections.

The practical implications of the differences in immune response or complement level in breeding for disease resistance merit investigation through selection and challenge infections.

Indonesia

Javanese thin-tailed sheep were experimentally infected with *Fasciola gigantica* and their response studied for up to 16 weeks post infection by Wiedosari and Copeman (1990). Based on the susceptibility to infection, as indicated by percentage take of metacercaria, and the severity of pathological changes, these authors concluded that Javanese thin-tailed sheep have a higher innate resistance to *F. gigantica* than other breeds studied elsewhere such as Merino, Corriedale, Sudanese desert sheep and African dwarf sheep.

Recently, a research program has been initiated in Sumatra, Indonesia in which breeding of sheep for disease resistance is one of the objectives. Sumatra (a breed similar to Malaysian indigenous breed), Java fat-tail and two exotic hair sheep, Virgin Island (St. Croix) and Barbados Blackbelly are being used. Some of the results obtained so far are presented in this monograph (Gatenby, this volume).

Thailand and the Philippines

As gastrointestinal nematodes are one of the major constraints in small ruminant production in Southeast Asia, a study was initiated in 1993 to evaluate the breeds or genotypes of goats in the Philippines and Thailand.

In southern Thailand, local indigenous goats and their crosses with Anglo Nubian goats with 25%, 50% and 75% Anglo Nubian blood, are initially being studied under natural infection on pastures. These studies would permit comparison of different genotypes and the identification of individuals with high or low susceptibility to nematodes. At a later stage, it is hoped to establish lines of resistant and susceptible goats since this would allow the detailed study of mechanisms involved in helminth resistance; and the subjective breeding of goats resistant to helminths.

In northern Philippines, studies with objectives similar to those of Thailand are being made on local, indigenous goats.

General Remarks

The main difficulty in such studies is the availability of large numbers of animals for initial studies from which nucleus flocks of resistant or susceptible animals can be created. Furthermore, such breeding studies require a relatively long time frame, which implies the creation of suitable infrastructure and qualified manpower committed to these programs for long periods. Another problem is the reluctance of the scientific community and decision makers to invest in long term activities for breeding of genetic resistance to diseases. Recently, anthelmintic resistance in sheep and goats has been recognised to be a serious problem in Malaysia (Pandey and Sivaraj 1993, 1994; Sivaraj et al. 1993, 1994; Dorny et al. 1993; Sivaraj and Pandey 1994). Similar problems may be encountered in other Southeast Asian countries especially in the hot, humid climates prevailing in the region. Research on breeding for disease resistance needs to be encouraged. Vigorous scientific and public relations activities need to be undertaken with regional and international collaboration.

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References

Dorny, P., Claerebout, E., Vercruysse, J., Jalila, A. and Sani, R. 1993. Benzimidazole resistance of *Haemonchus contortus* in goats in Malaysia. Veterinary Record, 133, 423–424.

F.A.O. 1992. Animal Health Year Book 1992. FAO/OIE/WHO, FAO, Rome, 271 p.

Horst, P., Mathur, P.K., Mukherjee, T.K., Antongiovanni, M. and Pandey, V.S. 1992. Development of a synthetic hair sheep with improved performance in sheep-hevea integration in humid tropics of Southeast Asia (Malaysia) by crossbreeding local sheep with hair sheep. In: Proceedings of EEC contractant workshops on resistance or tolerance of animals to disease and veterinary epidemiology and diagnostic methods, November 1992, Rethymno, Crete, Greece. Commission of the European Communities, p. 13.

Mallard, B.A., Wilkie, B.N., Kennedy, B.W. and Magnusson, U. 1993. Use of estimated breeding values in selection index to breed Yorkshire pigs for high and low immune and innate resistance factors. Veterinary Immunology and Immunopathology, 38, 392–393.

Pandey, V.S. and Sivaraj, S. 1992. Development of a synthetic hair sheep with improved performance in sheep-hevea integration in the humid tropics (Malaysia) by cross-breeding local sheep with hair sheep: Preliminary report on disease resistance aspects. In: Proceedings of EEC contractant workshops on resistance or tolerance of animals to disease and Veterinary epidemiology and diagnostic methods, November 1992, Rethymno, Crete, Greece. Commission of European Communities, p. 14.

Pandey, V.S. and Sivaraj, S. 1993. Benzimidazole resistance in *Haemonchus contortus* from sheep in Malaysia. In: Proceedings of 14th International Conference of World Association for Advancement of Veterinary Parasitology (WAAVP), August 1993, Cambridge, U.K., p. 377.

Pandey, V.S. and Sivaraj, S. 1994. Anthelmintic resistance in *Haemonchus contortus* from sheep in Malaysia. Veterinary Parasitology (in press).

Sivaraj, S. and Pandey, V.S. 1994. Isolation of an ivermectin resistant strain of *Haemonchus contortus* from sheep in Malaysia. Veterinary Record, 135, 307–308.

Sivaraj, S., Dorny, P., Vercruysse, J. and Pandey, V.S. 1993. Multiple drug resistance of *Haemonchus contortus* of sheep in Malaysia and the efficacy of moxidectin. In: Proceedings of the 14th International Conference of WAAVP, August 1993, Cambridge, U.K., p. 64.

Sivaraj, S., Dorny, P., Vercruysse, J. and Pandey, V.S. 1994. Multiple and multigeneric anthelmintic resistance on a sheep farm in Malaysia. Veterinary Parasitology, 55, 159–165.

Wiedosari, E. and Copeman, D.B. 1990. High resistance to experimental infection with *Fasciola gigantica* in Javanese thin-tailed sheep. Veterinary Parasitology, 37, 101–111.

Breeding to Assist Control of Gastrointestinal Parasites of Small Ruminants in the Pacific Islands

R.R. WOOLASTON, P. MANUELI, R. SINGH, N. TABUNAKAWAI
AND L.F. LE JAMBRE

ABSTRACT

Internal parasites are a major impediment to sheep and goat production in the Pacific Islands. Investigations were carried out in Fiji to determine whether host resistance was heritable for either goats or sheep. Faecal egg counts (FEC) were determined after natural infection in goats and under the conditions of this study, the trait was found to be neither heritable nor repeatable. There was no significant genetic variation detected in measures of blood haemoglobin content or packed cell volume during infection. Selectively eliminating *Haemonchus contortus* with closantel, leaving mainly *Trichostrongylus colubriformis*, did not appear to improve heritability of FEC. In contrast, FEC in sheep under these conditions was heritable (0.23±0.07). There was, however, no evidence of genetic variation in eosinophilia during infection, nor was the trait correlated with FEC (–0.03). Breeding strategies involving two-stage selection were investigated. One promising option involved a preliminary culling of animals based on their production, then two or three FEC measurements on those remaining.

Over recent years, governments in Fiji, Papua New Guinea, Solomon Islands, Western Samoa, Tonga and Vanuatu have encouraged an expansion of their sheep and goat populations in an attempt to increase domestic meat production (Banks et al. 1990). Efforts to intensify production, however, have been seriously impeded by losses due to gastrointestinal parasites, particularly *Haemonchus contortus* and *Trichostrongylus colubriformis*. For example, it has been estimated that up to 25% of Fiji's goat herd dies annually as a result of infection with these parasites (ACIAR 1991). Outbreaks of haemonchosis kill up to 50% of animals in some goat farming projects. Control of these parasites often relies on anthelmintic treatment every three to four weeks. The suppressive use of chemicals has increased the cost of production and more importantly, has lead to the selection of resistant strains of parasites. Anthelmintic resistance is widespread in Fiji and several farms are now dependent on ivermectin, the one remaining chemical to which resistance has not been detected. This problem, together with the high cost of chemicals, has led to a thrust for the small ruminant industries to move away from total dependence on chemicals for worm control (Walkden-Brown and Singh 1986).

Collaborative research sponsored by ACIAR was commenced in 1986 to refine and test practical methods of parasite control that do not rely exclusively on the suppressive use of chemicals. Several Pacific Island countries have been involved in the research effort, but much of the work has centred in Fiji. The need for a broad approach to the problem was recognised, and the possibility of developing parasite-resistant lines of livestock was considered. If genetic progress in resistance is possible, then the sheep and goat industries are well-placed to undertake appropriate improvement programs, as Government-run research stations are the main seedstock suppliers for both industries.

By 1987, it was clear from Australian studies that faecal egg count (FEC) was a heritable trait in sheep under many circumstances, but there had been no comparable studies for goats. L.R. Piper (1987, unpublished) found evidence of sire effects in FEC data from goats in Fiji, but more comprehensive studies were required before the feasibility of within-herd improvement in worm resistance of goats could be determined with any confidence. Thus larger-scale investigations were undertaken during 1988–92, using goat herds run on research stations run by the Fijian Government. Parallel studies were conducted in the Fijian sheep population, which for much of this time, was in the process of assimilating genes from exotic breeds under quarantine on the island of Makogai.

Resistance in Goats

The goat breeding program run by the Fijian Ministry for Agriculture, Fisheries and Forests, is directed towards producing an improved, tropically-adapted meat goat (Hussain et al. 1983). Genetic improvement is disseminated to the islands' stock-owners through the sale of improved bucks from the Government's two research stations. Breed effects on FECs in goats have been reported in Kenya (Preston and Allonby 1978) and France (Richard et al. 1990), indicating that genetic variation exists among hosts in their resistance to nematode infections. Early evidence from Fiji, however, suggested that age-acquired immunity in goats was either non-existent or a much less pronounced phenomenon than was commonly found in sheep (ACIAR 1990) so it was not clear whether the same degree of within-population genetic variation was likely to be found in goats. An account of the heritability study in Fijian goats was reported by Woolaston et al. (1992) and only a summary is reported here.

FEC data were collected from 1513 weaner and 951 adult Fijian goats over the period 1988–1992. Of the adults, 162 were repeat sampled, in successive years. Data were available from two herds—one at Sigatoka Research Station in the south-west of Viti Levu (average rainfall 1800 mm) and the other at Seaqaqa Research Station on the north-western side of Vanua Levu (also 1800 mm). Management of the herds was similar at both stations.

Faecal samples were collected in December of 1988 and 1989 and February of 1991 and 1992 from goats grazing infected pastures. The mean age of weaner goats (defined as <365 days old) was 185 days, with a considerable range (S.D. = 52 days). Most adult goats (defined as >365 days old) sampled were does (n = 749), but 40 bucks were also included in the study. The mean age of adult goats sampled was 3.0 years (range 1–7 years). In all years, existing parasite burdens were terminated with ivermectin at the start of the observation period, then FECs allowed to build up over 4–6 weeks. In order to minimise the number of zero FECs, sampling was deferred until it was considered that allowing infection to continue would compromise the welfare of the goats. However, because samples were sent to a distant laboratory, the inevitable delay in obtaining results tended to precipitate a conservative approach, and FECs were often lower than considered optimal for detecting genetic differences. Approximately one month prior to sampling in 1991 and 1992, goats were also drenched with closantel, to selectively remove *H. contortus* during the monitoring and sampling periods. This was to remove possible variation due to between-animal differences in the ratio of *H. contortus* to *T. colubriformis*, which are known to differ considerably in their egg output (Reinecke 1983).

The arithmetic mean (±S.D.) FEC of weaners was 1385±1922 eggs/g (epg), compared with 508±893 epg in adults. Using least squares, preliminary statistical analyses were carried out on various sub-sets of the data to determine significant sources of variation in log-transformed FEC. Effects tested for weaners included sex/paddock, birth status, dam age, interactions and age at testing. For adults, effects tested were sex/paddock, management group and age in years. In all contemporary comparisons of weaners and adults, weaner FECs were higher, but they were always grazed separately. Although not conclusive, this was suggestive of a degree of age-acquired immunity (a phenomenon which has since been confirmed in trials with goats in Australia, (L.F. LeJambre and R.G. Windon, unpublished). Sire effects were significant among one small group of weaners, but in no other case. In only two instances were the estimates of the sire component of variance positive. Sex/paddock significantly affected log-transformed FEC in five of the groups of contemporary weaners studied, but there was no consistency of ranking. The effects of dam age and age at testing failed to reach significance in any instance, but birth status was significant in one instance, when twins and triplets had higher FECs than singles. None of the effects tested in adults were a significant source of variation, but sex/paddock effects approached significance (bucks higher than does, $P = 0.07$).

Genetic analyses were carried out using the program DFREML (Meyer 1989), by fitting a full animal model and any fixed effects identified as potentially important by the least squares analyses. Heritability estimates were not significantly different from zero in weaners ($h^2 = 0.04 \pm 0.03$) or adults (0.08±0.06). In adult goats, the estimate of a permanent environmental effect was zero (0.00±0.11), indicating the repeatability of log-FECs between years to be no greater than the heritability. Different groupings of animals were made, according to age. For 981 goats aged 6–18 months, the heritability estimate was the same as that for weaners. For 188 goats aged 12–24 months, the estimate was 0.25±0.38. Combining data from goats of all ages utilised repeat records on 361 animals, which resulted in a heritability estimate of 0.04±0.02, and again, a permanent environmental effect of zero (0.00±0.05).

Unpublished studies of haematological parameters conducted in 1988 and 1989 (ACIAR 1990) when *Haemonchus* were present, did not suggest that packed cell volume (PCV) or haemoglobin (HB) measures were any more useful as indicators of resistance. Sire effects were small and phenotypic correlations with FEC were poor. The average correlation between FEC and PCV was –0.17, compared with –0.42 to –0.74 found in infected sheep in the CSIRO *Haemonchus* lines (R.R. Woolaston, unpublished data). The average correlation between FEC and HB was –0.13, but as might be expected, the correlation between HB and PCV was higher, at 0.75. Genetic correlations were generally inestimable.

Treating the sheep to control *H. contortus* in 1991 and 1992 did not increase the magnitude of sire effects on FECs, but as the species were not differentiated in earlier years, it is unclear the extent to which differences in composition of the worm populations were important. It is however, worth noting that Baker et al. (1991) reported significant sire effects in New Zealand Romneys when mixed infections of *T. colubriformis* and *H. contortus* were present.

These results indicate very little scope for within-herd genetic improvement in resistance of goats to nematode parasites in the humid tropics, using FEC as a selection criterion. Unlike sheep in Australia and New Zealand, very little significant genetic variation in FEC could be found. Furthermore, the low repeatability of FEC offers little promise for the use of repeated measures as an aid to selection.

Resistance in Sheep

The sheep flock on Makogai Island is controlled by the Fijian Ministry for Agriculture, Fisheries and Forests and serves the dual purposes of a research flock and a source of improved meat sires for use by commercial farmers. Sheep of the Barbados Blackbelly (BB) breed were introduced to Fiji from the USA in 1980 and until 1990 were quarantined on Makogai. During the decade of quarantine, various crosses were generated using the BB, Wiltshire Horn, Poll Dorset and Corriedale breeds, with the aim of developing a tropically-adapted breed of sheep. At present the two most clearly identifiable breeds are the BB and a new synthetic based on mainly a Wiltshire-Barbados cross (referred to here as the WB breed). The WB is essentially a hair sheep but is permitted to have some wool cover along the midline of the back. Since the release of these animals from quarantine in 1990, a second breeding flock has been established at Naiwacoba Research Station, on the western side of Viti Levu.

Studies of the 1988- and 1989-born sheep in this flock (ACIAR 1991) were similar to those described above for the same period in the goat herds. Weaners were drenched with an effective broad spectrum anthelmintic, then faecal egg counts allowed to build up until most animals had positive counts. Mean ages of the three groups of cohorts measured were 227, 130 and 161 days and mean FECs of 2505, 1292 and 136 epg, respectively. There was a significant tendency for older animals to have lower FEC and higher PCV measures than younger animals measured on the same day. Weaners of the WB breed had significantly higher PCV values than BB weaners ($P<0.05$, 26.6% *vs* 24.8%) but breed effects were not significant for FEC or HB. The estimated heritability of FEC was negative (sire degrees of freedom = 62, error degrees of freedom = 618), while the heritability of HB was estimated at 0.18±0.09 and for PCV was 0.09±0.08. Because of the negative estimate of sire variance for FEC, the only estimable genetic correlation was between HB and PCV, at 0.02±0.58. The phenotypic correlation between FEC and HB was –0.17, between FEC and PCV was –0.14 and between HB and PCV was 0.66.

For animals born 1991–1993, weaners were treated with closantel 4–6 weeks before sampling, to remove *H. contortus*. Although faecal samples were not generally cultured, it is likely that most worms present were *T. colubriformis*. The mean age of the 1826 weaners analysed was 124 days and the mean FEC was 983 epg. When data were pooled across years, breed effects were not significant, but there was a highly significant sire effect, resulting in a heritability estimate for cube-transformed FEC of 0.23±0.07. Also highly significant were sex effects (female<entire male), year effects and age effects

(older<younger). Circulating eosinophil counts were also recorded on blood samples collected from over 900 weaners at the time of FEC measurement. Significant sex effects (males>females) and age effects (older>younger) were found for eosinophilia, but neither breed effects nor sire effects could be detected. The phenotypic correlation between FEC and circulating eosinophils was –0.03, suggesting that under these conditions, the latter trait is of little or no value in indicating resistance.

Unlike goats, its appears that FEC in sheep under tropical conditions can be heritable. The development of optimal breeding strategies that include resistance will require a clearer definition of breeding objectives and the estimation of covariances among traits of importance. Given the appropriate information, it is possible to compare the efficiency of alternative strategies. Assume for example, a simple breeding objective that aims to improve growth rate and resistance and that a standard deviation of improvement in hogget liveweight (HW) is assigned equal importance to a standard deviation of improvement in resistance. Table 1 gives examples of the gains expected with these and other typical assumptions (heritabilities: HW 0.4, FEC 0.25; coefficients of variation: HW 12.5%, FEC 100%; repeatability of FEC 0.3; selection efficiency 60%; generation length 3 years). The phenotypic and genetic correlations are those assumed by Piper and Barger (1988) for a parasitised environment.

Options 2, 3, 4, 5 and 7 of Table 1 are equally expensive in terms of the total number of FEC determinations, but they differ considerably in the expected rates of gain in resistance. With the difficulties associated with processing of a large number of faecal samples and the risks associated with

Table 1 **Expected annual rates of gain in sheep breeding flocks assuming measurements are only made on rams and that a final proportion of 5% is required. (HW = Hogget Weight, FEC = Faecal Egg Count). For assumptions, see text.**

Option	Stage	Stage II	Annual gain in:	
			HW	FEC
	Best 5% on HW	–	1.0%	–1.3%
2	Best 5% on HW & FEC	–	0.9%	–3.3%
3	Lowest 50% on FEC	Heaviest 10% on HW	0.9%	–3.6%
4	Heaviest 50% on HW	Lowest 10% on FEC (1 count)	0.9%	–3.6%
5	Heaviest 50% on HW	Lowest 10% on FEC (2 counts)	0.9%	–4.5%
6	Heaviest 30% on HW	Lowest 17% on FEC (2 counts)	0.9%	–4.4%
7	Heaviest 30% on HW	Lowest 17% on FEC (3 counts)	0.9%	–4.9%

delays in treating animals in tropical conditions, two stage selection procedures appear to offer advantages. Option 7, for example, involves culling 70% of the candidates on the basis of inexpensive body weight measurements, then measuring FECs three times in the remaining animals. This option gives the most gain in resistance with only a small compromise in the rate of gain in body weight. Such an option would lend itself readily to conditions in Fiji where the ram breeding flock could be monitored locally, then measured and treated at relatively short notice. With three measures, the importance of errors in measurement will be diminished. The parameters assumed in these calculations should be the subject of further research, but in the interim a two-stage selection procedure is likely to be the most practical option for those breeders interested in improving resistance.

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References

ACIAR 1990. ACIAR Project 8414 'The epidemiology and control of gastrointestinal nematodes of small ruminants in the Pacific Islands' 4th Annual Report, ed. L.F. LeJambre.

-1991. ACIAR Project 8913 'Ecological and host-genetic control of internal parasites of small ruminants in the Pacific Islands' 1st Annual Report, ed. L.F. LeJambre.

Baker, R.L., Watson, T.G., Bisset, S.A., Vlassof, A. and Douch, P.G.C. 1991. Breeding sheep in New Zealand for resistance to internal parasites: research results and commercial application. In: Gray, G.D. and Woolaston, R.R. ed., Breeding for disease resistance in sheep. Melbourne, Australian Wool Corporation, 19–32.

Banks, D.J.B., Singh, R., Barger, I.A., Pratap, B. and Le Jambre, L.F. 1990. Development and survival of infective larvae of *Haemonchus contortus* and *Trichostrongylus colubriformis* on pasture in a tropical environment. International Journal for Parasitology, 20, 155.

Hussain, M.Z., Naidu, R., Tuvuka, I. and Singh, R. 1983. Goat production and development in Fiji. World Animal Review, 48, 25–32.

Meyer, K. 1989. Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. Genetics, Selection, Evolution, 21, 317.

Piper, L.R. and Barger, I. A. 1988. Resistance to gastro-intestinal strongyles: feasibility of a breeding programme. Proceedings of the 3rd World Congress on Sheep and Beef Cattle Breeding, Paris. 2, 593–611.

Preston, J.M. and Allonby, E.W. 1978. The influence of breed on the susceptibility of sheep and goats to a single experimental infection with *Haemonchus contortus*. Veterinary Record, 103, 509.

Reinecke, R.K. 1983. Veterinary Helminthology, Butterworths, Durban.

Richard, S., Cabaret, J. and Cabourg, C. 1990. Genetic and environmental factors associated with nematode infection of dairy goats in north-western France. Veterinary Parasitology, 36, 237.

Walkden-Brown, S.W. and Singh, R. 1986. A review of goat (meat) research in Fiji 1950–1986. Fiji Agricultural Journal, 48, 35.

Woolaston, R.R., Singh, R., Tabunakawai, N., Le Jambre, L.F., Banks, D.J.D. and Barger I.A. 1992. Genetic and environmental influences on worm egg counts of goats in the humid tropics. Proceedings of the Australian Association of Animal Breeding and Genetics, 10, 147.