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

<table>
<thead>
<tr>
<th>Disease</th>
<th>Comparative disease susceptibility</th>
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<tr>
<td><strong>Sheep Pox</strong></td>
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<tr>
<td>a. Malpura</td>
<td>Low</td>
<td>Low Sharma et al. (1986)</td>
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<tr>
<td>Malpura × Dorset</td>
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<td>Malpura × Suffolk</td>
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<td>Sonadi</td>
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<tr>
<td>Sonadi × Dorset</td>
<td>Low</td>
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<tr>
<td>Sonadi × Suffolk</td>
<td>High</td>
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<tr>
<td>b. Chokla</td>
<td>Low</td>
<td>Low Sharma et al. (1986)</td>
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<tr>
<td>Nali</td>
<td>High</td>
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<td>c. Nali × Rambouillet</td>
<td>Low</td>
<td>Low Sharma et al. (1986)</td>
</tr>
<tr>
<td>Nali × Merino</td>
<td>High</td>
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<tr>
<td>Chokla × Rambouillet</td>
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<tr>
<td>Chokla × Merino</td>
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<tr>
<td>d. Fine Wool Type Sheep</td>
<td>Low</td>
<td>Low Sharma et al. (1986)</td>
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<tr>
<td>(Nali, Chokla and</td>
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<tr>
<td>Nali/Chokla × Rambouillet/Merino)</td>
<td>Medium</td>
<td>Sharma et al. (1986)</td>
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<td>Mutton Type Sheep</td>
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<td>(Malpura, Sonadi and</td>
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<tr>
<td>Malpura/Sonadi × Dorset/Suffolk)</td>
<td>Low</td>
<td>Sharma et al. (1986)</td>
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<td>e. Bikaneri Mandya</td>
<td>Low</td>
<td>Low Murty and Singh (1971)</td>
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<td>High</td>
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<tr>
<td><strong>Blue Tongue</strong></td>
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<tr>
<td>a. Malpura, Marwari, Nali, Sonadi</td>
<td>Low</td>
<td>Low Dubey et al. (1988)</td>
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<tr>
<td>Corriedale, Dorset, Karakul</td>
<td>Medium</td>
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<td>Rambouillet, Merino</td>
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<tr>
<td>b. Nali, Sonadi Rambouillet</td>
<td>Low</td>
<td>Low Mahajan et al. (1991)</td>
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<td>High</td>
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<td><strong>Ovine Adenovirus</strong></td>
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<tr>
<td>a. Malpura, Sonadi, Chokla, Nali Rambouillet, Merino, Dorset, Suffolk</td>
<td>Low</td>
<td>Low Dubey et al. (1985b)</td>
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<tr>
<td><strong>Foot-and-Mouth Disease</strong></td>
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<tr>
<td>a. Malpura Avikalin (Malpura × Rambouillet/Merino)</td>
<td>Low</td>
<td>Low Khurana et al. (1991)</td>
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<tr>
<td>Mutton Synthetic (Malpura/Sonadi × Dorset/Suffolk)</td>
<td>Medium</td>
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<td>b. Mandya Nellore</td>
<td>Low</td>
<td>Low Rao et al. (1993)</td>
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<td>High</td>
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<tr>
<td>d. Chokla lambs Nali lambs</td>
<td>Low</td>
<td>Low Singh et al. (1992c)</td>
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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.
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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 Mal pura 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 Mal pura 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.
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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

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<tr>
<th>Disease</th>
<th>Breed</th>
<th>Comparative disease susceptibility</th>
<th>References</th>
</tr>
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<tbody>
<tr>
<td>GOAT POX</td>
<td>a. Sirohi</td>
<td>Low</td>
<td>Nagpal et al. (1990)</td>
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<tr>
<td></td>
<td>Kutchi</td>
<td>Medium</td>
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<td></td>
<td>Marwari</td>
<td>High</td>
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<td></td>
<td>b. Sirohi</td>
<td>Low</td>
<td>ISGP (1988)</td>
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<td></td>
<td>Sirohi × Toggenburg</td>
<td>Medium</td>
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<td></td>
<td>Sirohi × Alpine</td>
<td>High</td>
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<tr>
<td>FOOT-AND-MOUTH DISEASE</td>
<td>a. Barbari</td>
<td>Low</td>
<td>Shankar et al. (1992)</td>
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<tr>
<td></td>
<td>Jamunapari</td>
<td>Medium</td>
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<td></td>
<td>Jhakrana</td>
<td>High</td>
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<tr>
<td>JOHNE'S DISEASE</td>
<td>a. Jamunapari</td>
<td>Low</td>
<td>Singh et al. (1990)</td>
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<td></td>
<td>Barbari</td>
<td>High</td>
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<td></td>
<td>b. Jhakrana, Sirohi</td>
<td>Low</td>
<td>Singh et al. (1992a)</td>
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<td></td>
<td>Jamunapari</td>
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<td></td>
<td>Barbari</td>
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<td></td>
<td>Barbari kids</td>
<td>High</td>
<td>Singh et al. (1992b)</td>
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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 north-
eastern 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.

Acknowledgments

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References

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Breeding for Resistance to Infectious Diseases in Small Ruminants


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 Caribbean 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 to as '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 cross-breeding 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.
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(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.

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

Faecal Egg Count
Packed Cell Volume
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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.

<table>
<thead>
<tr>
<th>Breed</th>
<th>Compared with</th>
<th>Age</th>
<th>Result</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barbados Blackbelly,</td>
<td>Dorset</td>
<td>8 months,</td>
<td>Lambs: Reduced FEC(^a) and eggs produced/worm</td>
<td>Yazwinski et al. 1979</td>
</tr>
<tr>
<td>Barbados × Dorset</td>
<td></td>
<td>ewes</td>
<td>Ewes: no significant differences</td>
<td></td>
</tr>
<tr>
<td>Targhee × Barbados,</td>
<td>Targhee</td>
<td>4 months</td>
<td>No difference in FEC and worm burden, PCV(^b), wt. gain</td>
<td>Todd et al. 1978</td>
</tr>
<tr>
<td>Blackbelly</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florida Native</td>
<td>Rambouillet</td>
<td>5 months</td>
<td>Reduced FEC and fewer and smaller adult <em>Haemonchus</em> numbers</td>
<td>Radhakrishnan et al. 1972</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Reduced PPP(^c), PCV, larvae</td>
<td></td>
</tr>
<tr>
<td>Florida Native</td>
<td>Rambouillet</td>
<td>5 (\frac{1}{2})-6 months</td>
<td>Reduced FEC and <em>Haemonchus</em> numbers Reduced PPP, larvae numbers, weight gain, abomasal eosinophils, PCV</td>
<td>Bradley et al. 1973</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florida Native,</td>
<td>Domestic Crossbred</td>
<td>6-40 weeks</td>
<td>Reduced FEC and <em>Haemonchus</em> numbers, but difference reduced with lamb age</td>
<td>Courtney et al. 1985a</td>
</tr>
<tr>
<td>St. Croix, Barbados Blackbelly</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florida Native,</td>
<td>Dorset × Rambouillet</td>
<td>9-10 months</td>
<td>Reduced FEC, reduced PCV and total protein</td>
<td>Zajac et al. 1990</td>
</tr>
<tr>
<td>St. Croix</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dorset</td>
<td>2 months</td>
<td>Reduced FEC</td>
<td>Gamble and Zajac 1992</td>
</tr>
</tbody>
</table>

\(^{a}\) FEC = faecal egg count  
\(^{b}\) PCV = packed cell volume  
\(^{c}\) PPP = prepatent period
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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.
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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


Breeding for Resistance to Infectious Diseases in Small Ruminants


Helminth Infections of Sheep in Rubber Plantations in Sumatra


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.
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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.

<table>
<thead>
<tr>
<th>Breed (n)</th>
<th>Faecal Egg Count (epg) ± sem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sumatra (43)</td>
<td>2470 ± 660</td>
</tr>
<tr>
<td>Java Fat-tail (34)</td>
<td>837 ± 340</td>
</tr>
<tr>
<td>Virgin Island (50)</td>
<td>382 ± 110</td>
</tr>
<tr>
<td>Virgin Island × Sumatra (65)</td>
<td>976 ± 200</td>
</tr>
</tbody>
</table>

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 (F1) and Virgin Island × Sumatra (F2) 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 (F2) had similar worm burdens to the Virgin Island × Sumatra (F1). Java Fat-tail × Sumatra (F1) 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 x 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 x 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.

Acknowledgments

This work is conducted with funds from the Small Ruminant Collaborative Research Support Program, USAID Grant DAN 1328-G-SS-4093-00, and the European Economic Community through the Prince Leopold Institute for Tropical Medicine, Antwerp and INI ANSREDEF, Bogor. We thank Mr Torop Siallagan, Mr Pungu Nababan and staff of Suka Dame for looking after the animals and collecting routine samples, Mrs Melinda Hutauruk and laboratory assistants for processing the faecal and blood samples and Dr Hakan Sakul for assistance with data analysis.

References


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 focusing 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).

<table>
<thead>
<tr>
<th>Country</th>
<th>Sheep</th>
<th>Goat</th>
<th>Human</th>
</tr>
</thead>
<tbody>
<tr>
<td>Philippines</td>
<td>30</td>
<td>2132</td>
<td>62</td>
</tr>
<tr>
<td>Indonesia</td>
<td>5900</td>
<td>11250</td>
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</tr>
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<td>206</td>
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</tr>
<tr>
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<td>121</td>
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</tr>
<tr>
<td>Cambodia</td>
<td>NA</td>
<td>NA</td>
<td></td>
</tr>
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<td>NA</td>
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<td>NA</td>
<td>413</td>
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</tr>
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<td></td>
</tr>
<tr>
<td>China</td>
<td>113508</td>
<td>98313</td>
<td>1153</td>
</tr>
<tr>
<td>Total</td>
<td>120082</td>
<td>113736</td>
<td>1589</td>
</tr>
<tr>
<td>% of world population</td>
<td>10.1%</td>
<td>19.1%</td>
<td>30%</td>
</tr>
</tbody>
</table>

NA = Not available.
Breeding for Resistance to Infectious Diseases in Small Ruminants

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 crossbreeds 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 C₃ molecules, as well as C₃ 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
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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.

Acknowledgments

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


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
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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 epg/g, 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 ($0.08 \pm 0.06$). In adult goats, the estimate of a permanent environmental effect was zero ($0.00 \pm 0.11$), 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 $0.25 \pm 0.38$. Combining data from goats of all ages utilised repeat records on 361 animals, which resulted in a heritability estimate of $0.04 \pm 0.02$, and again, a permanent environmental effect of zero ($0.00 \pm 0.05$).

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.
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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, it 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>
<thead>
<tr>
<th>Option</th>
<th>Stage</th>
<th>Stage II</th>
<th>Annual gain in:</th>
</tr>
</thead>
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<tr>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>1</td>
<td>Best 5% on HW</td>
<td>–</td>
<td>1.0%</td>
</tr>
<tr>
<td>2</td>
<td>Best 5% on HW &amp; FEC</td>
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<td>0.9%</td>
</tr>
<tr>
<td>3</td>
<td>Lowest 50% on FEC</td>
<td>Heaviest 10% on HW</td>
<td>0.9%</td>
</tr>
<tr>
<td>4</td>
<td>Heaviest 50% on HW</td>
<td>Lowest 10% on FEC (1 count)</td>
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</tr>
<tr>
<td>5</td>
<td>Heaviest 50% on HW</td>
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</tr>
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<td>6</td>
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</tr>
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<td>7</td>
<td>Heaviest 30% on HW</td>
<td>Lowest 17% on FEC (3 counts)</td>
<td>0.9%</td>
</tr>
</tbody>
</table>

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.
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.

Acknowledgments

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