GENETIC AND ENVIRONMENTAL VARIATION IN INFESTATIONS WITH TICKS AND INFECTIONS WITH GASTROINTESTINAL NEMATODES OF SHEEP IN SEMI-ARID AND SEMI-HUMID ZONES OF KENYA.

By

PETER BUSAKA OGORE

Dip. AHU, BSc. Animal Production, (Egerton University)

A

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DECLARATION:

This thesis is my original work unless otherwise stated and all sources of information has been acknowledged by means of references. This thesis has not been presented for a degree in any other University.

Signed.....Date.....

This thesis has been submitted with our approval as University supervisors:

Signed.....Date.....

1. DR. ROBERT LEYDEN BAKER

Signed.....Date.....

2. DR. WILLIAM THORPE

DEDICATION

To parents, my beloved wife Grace, my children

Beatrice, Nancy, Brian and Marvin.

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ABSTRACT

A total of 347, 213 and 169 lamb records were used to characterise the genetic resistance to gastrointestinal (GI) nematodes in Red Maasai (R), Dorper (D) and their crosses at 3, 8 and 13 months of age, respectively, at Diani in the semi-humid zone of coastal Kenya. Thereafter the remaining 160 yearlings were evaluated for tick resistance at Nguuni farm in the same region. At Ol'Magogo in the semi-arid highlands of Kenya a flock of both R and D genotypes of 101 and 108 individuals from the 1992 and 1993 lamb crops, respectively, were evaluated concurrently for GI nematode and tick resistance.

The indicators of resistance were: Faecal Egg Count (FEC) defined as the number of worm eggs in a gram of faeces; Packed Cell Volume (PCV) defined as the proportion of red cells to total blood volume; and tick count (TC) measured as total body count of engorged female ticks. Lamb survival rate was used as a measure of flock productivity.

At Diani Estate there were no significant differences in live weights among genotypes measured between 3 and 13 months of age. Survival rate from birth to weaning was 91 % with no significant difference ($P > 0.05$) among genotypes. However, for post-weaning survival the mean was 60 % with a highly significant difference ($P < 0.01$) between R and D lambs (74 % and 27 %, respectively). The R and D genotypes differed significantly for PCV ($P < 0.05$) with R having higher PCV at 3 and 13 months of age. There was no significant difference among

R and D genotypes differed significantly for PCV ($P < 0.05$) with R having higher PCV at 3 and 13 months of age. There was no significant difference among genotypes for FEC, although the R lambs consistently maintained lower FEC than D lambs at all ages. The effect of lamb breed was highly significant for TC with R lambs having lower counts than D lambs at all infestation periods both at Nguuni and Ol'Magogo farms.

Heritabilities, estimated from paternal half-sib correlations, were characterized by large standard errors because of the small data set and limited number of sires. The heritability estimate for logarithm-transformed tick count in the second infestation period at Nguuni farm was low ($0.13 \pm .24$) but would be expected to increase to 0.20 or 0.24 if measuring of TC had been done 2 or 3 times within the same infestation period, respectively. The phenotypic correlation between TC on the ears and the total body count was 0.97 indicating that ear count alone was a good indicator of resistance to ticks in sheep.

It was concluded that utilization of resistant animals is an attractive complementary approach to the use of chemotherapy as a means of increasing productivity of sheep under GI nematode infections, tick infestations and poor feed resources.

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1. INTRODUCTION

Sheep farming is a popular enterprise in Kenya with over 75 % of all farmers keeping some small ruminant livestock (Peters and Thorpe, 1988). ILCA (1993) estimated the population of sheep in Kenya to be about 7.2 million with an annual growth rate of 3.6 %. Therefore they contribute significantly to Kenya's national income and food security, and produce an estimated 19 % of the red meat on the domestic market, with an offtake of about 60,000 metric tonnes of meat per annum (Statistical Abstracts, 1990; KARI,1991). Kenya has about half a million exotic wool type sheep. These are mostly Corriedale and Romney breeds and are found in the cool highlands where the climatic conditions are favourable. The hair sheep (mainly Red Maasai (R), Somali or Black Head Persian breeds) or synthetic sheep breeds (e.g the Dorper (D)) are concentrated in the semi-arid and arid areas of Kenya, but some are also found in the semi-humid areas.

The D was first introduced to Kenya in 1952 at the then Katumani research station of the Ministry of Agriculture. The breed was developed at Grotfontein College of Agriculture in South Africa by *inter se* mating of crosses of Dorset Horn and Black Head Persian sheep breeds (Haas, 1971). The breed developed a reputation for its ability to walk long distances and forage well in dry areas. D ewes

have good mothering ability, high fertility and vigour. They have a white body with black legs and head. In the 1970's more D were imported into Kenya from South Africa for the purpose of research and multiplication (Kiriro, 1986). It has undergone short term investigations in research stations.

The R are hardy and are widely distributed in almost all ecological zones. The highest concentrations are in the south-west region of the Rift Valley province of Kenya and the northern part of Tanzania. Similar animals are found in north-eastern Uganda (especially among the Karamoja), Zambia, in southern Zimbabwe, Malawi and Botswana (Devendra and McLeroy, 1982). They are characterised by short, coarse hair coat with a light undercover of wool, red and light brown to dark brown body colour, a fat tail (although there is some variation in the tail type) and a dewlap. They are considered to be indigenous to Kenya having been identified with the Maasai community for a long time, thus the name Red Maasai. In Kenya today the D and R and their crosses dominate the sheep population. This is because they have been associated with relative resistance to both extreme environmental factors and disease incidence (Kiriro, 1986; Inyangala *et al.*, 1990). They have been characterised for growth and other production traits, and phenotypic and genetic parameters were estimated by Kiriro (1986) and Inyangala (1989) using data from the Ol'Magogo flock in Naivasha.

Ticks, tick-borne diseases and gastrointestinal (GI) helminths of economic importance are prevalent over approximately 15 million square kilometres in sub-Saharan Africa. They are the major health constraints of the small ruminant industries in this region when both the direct and indirect losses associated with these diseases are considered. For example, in 1987, Kenya spent approximately US$ 10 million in the importation of acaricides and chemotherapeutic drugs for the control and treatment of tick-borne diseases (Young *et al.*, 1988). In a study carried out on farms in the same year (1987) in Nakuru District in Rift Valley, Kenya the total cost of tick control alone was estimated at US$ 13.64 per cow per annum (Young *et al.*, 1992). The cost of controlling GI helminths in small ruminants is estimated at 20-26 million Kenya pounds per year (Preston and Allonby, 1979; Shavulimo *et al.*, 1988; Reynolds *et al.*, 1992). Ticks, tick-borne diseases and GI helminths cause depression in productivity, high mortality and a reduction in reproduction efficiency.

In pursuit of the commercialisation of livestock industries in Africa at the beginning of this century, many exotic temperate breeds were introduced and farmers were urged to upgrade their indigenous livestock. This resulted in high mortalities in naive exotic breeds as a result of tick-borne diseases. Consequently tick control was enforced by legislation. The innate potential of genetic resistance of indigenous livestock to endo- and ecto-parasites and possibly tick-borne diseases is still not

adequately exploited in the control of parasites and in disease management strategies. Thus, large numbers of these livestock in tropical countries are subjected to unnecessary acaricide and anthelmintic applications. Moreover, there is now evidence that excessive use of chemicals and drugs not only pollutes the environment through residual effects on pastures and in animal products, but parasites continuously evolve resistance to most of the biocides (Pritchard, 1994; Peregrine, 1994).

Fortunately, there is evidence of genetic variation in the resistance of farm animals to both ticks and GI helminths (Stewart *et al.*, 1937; Whitlock, 1958; Turner and Short, 1972; Preston and Allonby, 1978, 1979; Norval, 1990; Gray, 1991; Norval *et al.*, 1992; Baker *et al.*, 1992) and this can be harnessed by incorporating it in integrated parasite control programme (Sutherst *et al.*, 1988; Alexander *et al.*, 1984; Albers, *et al.*, 1987; Scholtz *et al.*, 1991; Sykes, 1994). The earliest recorded evidence for resistance of cattle to ticks was in 1912 in Australia (de Castro, 1991). Later it was confirmed that *Bos indicus* cattle had innate ability to reduce the number of ticks completing their life cycles on their body (Heweston,1968; Utech *et al.*, 1978a, 1978b; Seifert, 1971; Turner and Short, 1972; de Castro *et al.*, 1985; Bosma, 1981; Tatchell , 1986; Kaiser *et al.*,1982). There is also considerable variation in individual resistance within breeds, especially in *B. indicus*. The resistance of indigenous cattle, together with their innate ability to withstand virulent

forms of *Theileria parva* (Dolan and McHardy, 1977; Moll *et al.*, 1986) allow these cattle to survive without tick control in eastern and southern Africa.

In Australia and New Zealand breeds or strains have been identified or developed which have a relatively high genetic resistance to the "blue tick" (*Boophilus microplus*) in cattle and GI helminths in sheep (Seifert, 1971; Turner and Short, 1972; Utech and Wharton, 1982; Reason, 1983; Alexander *et al.*, 1984; Gray and Woolaston, 1991; Gray *et al.*, 1995). The indigenous livestock in sub-tropical and tropical countries are relatively resistant to parasites and when exposed to artificial and/or natural parasite infestation the number of parasites maturing on/ or in them is usually low. This provides the most viable option for reducing reliance on chemical control of parasites. While there has been considerable research on tick resistance in cattle, to date there is no published evidence of either breed differences or within-breed genetic variation for tick resistance in sheep. Thus there is the need to evaluate resistance of sheep to parasites in different mating systems and at specific levels of resource availabilities and management and in discrete geographic areas and climatic conditions. There is also the likelihood that genetic resistance to diseases may offer an economically more viable and longer lasting means of improving sheep productivity in tropical Africa.

The overall objective of this study is to contribute to the assessment of genetic resistance of small ruminants to parasitism by GI helminths and ticks.

The specific objectives are:-

1. To develop a protocol for tick counting in sheep using total body count versus specific predilection sites.

2. To evaluate the comparative genetic resistance to GI nematodes and ticks in R and D and their crosses. The performance and resistance traits measured will include:- faecal egg count (FEC), packed cell volume (PCV), live weight (WT) and survival rate (SRATE) at 3, 8 and 13 months of age during GI nematode infection and tick count (TC), WT and PCV at different periods of tick infestation.

3. To estimate concurrently the influence of systematic environmental factors on these traits.

4. To estimate genetic and phenotypic parameters for these traits.

2. LITERATURE REVIEW

With the increasing cost of parasite control and the growing evidence of drug resistance, there has been renewed interest in utilizing host resistance of domestic livestock in integrated parasite control programs in endemic areas of the world. The results from field observations and experimental trials reveal a relatively high degree of genetic resistance to ecto- and endo-parasites among and within ruminant livestock breeds when challenged with artificial or natural infestation. Tropical indigenous livestock are the most resistant to both ecto- and endo-parasites (Owen and Axford, 1991). Although the productivity of tropical indigenous livestock is often lower than that of temperate breeds, they maintain reasonable production levels under parasite burden due to long coexistence with parasites, thus making them the most adapted genotypes in the tropics. Important production traits of temperate livestock decline when animals without previous parasite exposure are artificially or naturally challenged with either ecto- and/or endo-parasites. Indigenous animals exhibit resistance, indicating "innate" or "acquired" ability to respond to parasite infestation. Cattle with low resistance, especially the exotic breeds or those with a high proportion of exotic genes, have reduced live weight ranging on average from

0.6 to 4.4 g for each tick completing its life cycle on the body (Norval, 1990; Norval *et al.*, 1992).

In most regions of sub-tropical and tropical Africa, there is concurrent parasite infection and infestation of multiple genera of gastrointestinal (GI) nematodes and ticks. The interplay of such infestations may give different results from those reported from other parts of the world, especially from Australia where there is only one tick species (*Boophilus microplus*). Heritability estimates for resistance to ecto- and endoparasites range from moderate to highly heritable. The estimates range from 0.30 to 0.50 for tick infestation in cattle and 0.20 to 0.40 for worm infestation in sheep (Woolaston *et al.*, 1991; Davis, 1993). There are no heritability estimates for resistance to tick infestation in sheep. There is the need therefore to estimate genetic parameters for resistance to ecto- and endo-parasites in sheep for use in the formulation of breeding programs incorporating host resistance.

2.1 Resistance and its measurements

Clunies-Ross (1932), cited by Baker (1995b), was among the first to recognize the distinction between "resistance to infection" and "resistance to the effect of infection." Albers *et al.* (1987) referred to the latter as resilience. Albers *et al.*(1987),

Gavora and Spencer (1978), ILCA (1991), Baker *et al.* (1992), Gray *et al.*, (1995) have proposed the following:-

Resistance, defined as the initiation and maintenance of the response provoked in the host to suppress the establishment of parasites and/or eliminate parasite load;

Resilience, defined as the ability of the host to maintain a relatively undepressed production level under parasite challenge;

Tolerance, defined as the ability of the host to survive in the face of parasite challenge.

It seems that resistance is a more practical and important mode of estimating host response to parasite challenge than resilience and tolerance because it is associated with a gradual reduction in the effects of parasitism such as reduction in faecal egg output from the host. More resistant livestock will therefore result in less pasture contamination and reduced infection of other susceptible hosts. The containment of parasites to a tolerable level possibly requires expenditure of resources that reduces an animal's productivity.

Resilience is difficult to measure and heritability estimates are usually low and close to zero (Albers *et al.*, 1987). A positive genetic correlation between resistance and resilience was reported by Albers *et al.* (1987) working with Merino lambs in Australia. A low genetic correlation between resistance and resilience for log FEC has

been reported in Romney sheep by Morris *et al.* (1995). Although there is still considerable debate in Australia and New Zealand about the relative merits of selecting sheep for resistance or resilience to endo-parasites (Bisset *et al.*, 1994), selection based on resistance has resulted in resistant and susceptible lines with considerable genetic differences between them after several generations of selection.

Two main modes of infection are used in estimating livestock resistance to parasite challenge, i.e natural and artificial infections/infestations. Both modes have been used successfully to estimate genetic resistance to both ticks and GI nematodes in New Zealand and Australia (Seifert, 1971; Woolaston *et al.*, 1991; Baker *et al.*, 1991). Although few estimates of the genetic correlation have been made between the two modes of infection, there is obviously a very close association between response to artificial and natural challenges (Gray and Woolaston, 1991; Gray *et al.*, 1995; Owen and Axford, 1991). In field conditions animals are exposed to a wide diversity of GI nematodes and ticks, thus natural infection is the ideal since it provokes, in the case of tick infestation behaviourial traits such as parasite avoidance and grooming (de Castro *et al.*, 1985).

Natural infection/infestation involves exposing animals to an unknown level of multi-species challenge of either nematodes or ticks. It is mostly used when determining the seasonal dynamism of parasites. However, it is not appropriate for

GI nematodes where environmental conditions are unfavourable for rapid development of non-infective stages of parasites (e.g. semi-arid and arid regions where rainfall is unreliable). In such situations, a natural parasite challenge sufficiently severe to allow assessment of host resistance is not always forthcoming, thus it is expedient to artificially dose the host since this guarantees a positive worm egg count.

Artificial infection is appropriate where there is one important parasite species. For example, in Australia the most important tick species is *Boophilus microplus*, while *Trichostrongylus columbriformis* and *Haemonchus Contortus* are the most important GI nematodes. In such situations artificial infection is commonly employed. This involves use of a known dosage of worm larvae (L3) or tick nymphs for a specific period of time (Wharton *et al.*, 1970). Artificial (experimental) infection/infestation has an advantage in that between and within breed variation to specific parasites can be estimated (Gruner, 1991a and Gruner, 1991b). In both artificial and natural infection/infestation it seems that resistance is well expressed if animals are "Primed" with a trickle of infection to trigger an immune response before challenge, especially in naive animals (Windon, 1991). There is evidence that "inexperienced" livestock show no genetic competence to resist parasite infection and that comparisons should be conducted in animals which have been reared in a

common environment (Woolaston *et al.*, 1991; Baker *et al.*, 1991). To assess genetic variation for resistance the protocol adopted should allow moderate infection because excessive or very low infections masks genetic differences among animals or breeds.

2.1.1 Faecal egg count

FEC is widely used as an indicator of nematode infections (Gray and Woolaston, 1991). It has been noted that FEC s not always closely related to worm burden and is affected by other factors such as age of the animal, the level of host immunity, species of worm and physiological status of the host. Despite these reservations, there is a large volume of experimental evidence which shows that FEC can be used to assess the resistance/susceptibility status of different livestock genotypes. FEC is heritable and relatively easy to measure, is repeatable within infection cycles and there are positive phenotypic and genetic correlations between infection cycles (Baker, 1995b; Gray *et al.*, 1995; Morris *et al.*, 1995). While FEC is a good indicator of GI nematode infection, it is also a valuable trait in its own right as a measure of the degree to which the animal is contaminating pasture with worm eggs. Correlation between individual egg count and worm count range from 0.74 to 0.83 (Woolaston and Eady, 1995; Gray *et al.*, 1995).

2.1.2 Packed cell volume

PCV is a measure of the host's ability to restrict the development of anaemia. It is important to have haemo-parasite screening when PCV is used as a measure of resistance to GI nematodes such as *Haemonchus contortus* and ticks to avoid confounding effects of other anaemia-producing pathogens or parasites. PCV is a good indicator of host resistance to parasites, especially when the host is infected with blood-sucking parasites such as ticks or *Haemonchus contortus*. Correlations between FEC and PCV ranging from -0.17 to -0.74 have been reported (Woolaston *et al.*, 1995) indicating that there is an inverse relationship between PCV and worm load. Similar results have been reported by Matioli *et al.* (1995) in cattle infested with several tick species.

2.1.3. Worm Counts

This is the best indicator of host resistance to helminths, but can only be determined after slaughter. It is not a suitable measurement for selection programs, but has been measured in breed comparisons.

2.1.4 Tick Counts

Tick counts (TC) have been used intensively in estimation of genetic resistance to ticks. Animals with less than 1 % of ticks surviving after artificial infestations are considered resistant while those with a 10 % survival rate of ticks or greater are considered susceptible. TC is a heritable and repeatable trait (Turner and Short, 1972; de Castro *et al.*, 1985; Norval *et al.*, 1992). Tick counting is commonly based on mature female ticks (engorged)(standard tick 4.5 - 8.5 mm). Counting is usually done on one side of the animal, then doubled to give the approximate tick load per animal (Seifert, 1984a).

2.2 Effect of parasitism on productivity.

Ecto- and endo-parasites rank high among the factors that limit the productivity of small ruminants in sub-Saharan Africa. Although the effect of parasites is often underestimated, the sub-clinical manifestation is now recognized to be associated with retarded growth, delayed and reduced productivity and increased susceptibility to other infections (Allonby and Urquhart, 1975; Sykes, 1994). The pathogenic effects of constant intake of 600 worm egg/kg herbage will, for instance, reduce live weight, growth rate and efficiency of food utilization by 50 % in clinically normal animals. In lactating ewes, consumption of 24 kg of fresh matter

per day with less than 200 nematode larvae per kg fresh herbage causes a 20 % reduction in milk production (Sykes, 1994).

In Kenya losses associated with anthelmintic cost and treatment have been estimated to be Kenya pounds 20-26 Million per annum (Preston and Allonby, 1979; Shavulimo *et al.*, 1988; Reynolds *et al.*, 1992). No work has been done on the effect of ticks on sheep, but the evidence from cattle indicates that ticks can inflict severe damage to the host. Tick infestation *per se* causes reduction in production due to :-

1. "Worry" compounded of irritation, allergic responses and blood losses from the feeding of different instars of ticks
2. Death or debilitating effects with possible damage to the skin including the udder, thus reducing milk production
3. Paralysis or toxicosis produced by the feeding of certain ticks and transmission of pathogenic organisms (Norval, 1990)

Norval *et al.* (1989) reported that in the absence of secondary infection each feeding female tick which completed engorgement caused comparable loss in productivity in *B. taurus* and *Bos indicus* cattle. He reported an average annual reduction in live weight of 25 to 30 kg in Africander steers heavily infested with *Amblyomma hebruem*. This resulted in a 5-20 % lower expected annual live weight

gain. Other studies in Australia have estimated reduction in live weight ranging on average from 0.6 to 4.4 g for each tick (*Boophilus microplus*) completing its life cycle on the body (Norval *et al.*, 1992).

In Africa, studies indicate that annual natural tick infestations in cattle are about 2,500-11,000 ticks and that *Rhipicehalus appendiculatus* is the main genera (Kaiser *et al.*, 1982; Pegram *et al.*, 1989). Extrapolation of this indicates that a reduction of 15 to 66 kg live weight per year is expected under African conditions when *Rhipicephalus* are the predominant tick species. Despite species differences, proportional losses can be expected in sheep. Seebeck *et al.* (1971) showed that under controlled nutritional conditions 65 % of weight loss is attributable to anorexic effects, while 35 % is ascribed to tick effects such as toxicosis and sucking of blood.

The total economic losses due to ticks and tick-borne diseases remain unquantified for most African countries, probably due to inadequacy of data on their impact on livestock productivity. In Kenya, Young *et al.* (1988) have estimated the cost of tick control and the treatment of tick-borne diseases to be US$ 10 million per annum.

Until recently strategies for controlling parasites have concentrated on the use of chemicals and drugs. But with the emergence of parasite resistance, some of these drugs have been rendered ineffective (Peregrine, 1994). Alternative control methods

are being sought such as vaccines and utilization of host resistance. This has resulted in the development of cattle resistant to the cattle tick (*Boophilus microplus*) in Australia (Alexander *et al.*, 1984; Reason, 1983) and sheep breeds resistant to GI nematodes in Australia and New Zealand (Baker *et al.*, 1991; Gray and Woolaston, 1991; Gray *et al.*, 1995).

2.3 Genetic variation in resistance traits

Genetic variation is estimated in breeding studies after adjusting for known environmental effects. This is done by including them as factors in the statistical models. This allows one to separate genetic and environmental effects to obtain more accurate estimates of the magnitude of differences between genotypes that arise from differences in genetic composition. Environmental effects include, year and season, dam parity, type of birth, sex, age and their interactions.

Breed differences for resistance to GI nematodes have been reported in many studies for sheep and cattle (Gray and Woolaston, 1991; Gray et al., 1995; Vercoe and Frisch, 1992), while breed differences for resistance to ticks has been demonstrated in cattle (Norval *et al.*, 1992; Vercoe and Frisch, 1992).

2.3.1 Between breed differences

The underlying principles of breed comparisons is well documented by Dickerson (1969). An important requirement is that breeds should be compared contemporaneously, otherwise variation between breeds may reflect differences in environments. But, of particular concern is the statistical power of breed comparisons and the representativeness of animals in each breed being studied. For instance, breed comparisons require a large number of sires of each breed to achieve appropriate statistical power.

2.3.1.1 Production traits

2.3.1.1.1 Live weight

Sheep reared in diverse environments have evolved as a result of climatic and or management differences. Variation in the quality and quantity of feed resources is perhaps the major environmental constraint dictating the level of growth performance of a given livestock genotype. Diversity also exists in the type of livestock being maintained in a particular environment (Vercoe and Frisch, 1992).

There are many reports of breed-variation for production traits, especially for growth and reproduction in sheep (Turner and Young, 1969). Comprehensive

breeding strategies have been developed in temperate countries to utilize genetic variation among breeds (i.e. stratified sheep industries) (Clarke, 1982; Terril, 1982; Read, 1982). Many studies have reported high live weight estimates for birth, weaning and mature weight in temperate breeds (Dzakuma *et al.*, 1978; Fitzhugh and Bradford, 1983; Stobort *et al.*, 1986). But estimates from the tropics are often relatively low (ILCA, 1979; Fitzhugh and Bradford, 1983). The relatively small mature size of these tropical breeds may be associated with innate ability to adapt to unfavourable tropical conditions (Terrill, and Sree, 1991).

Several studies have reported birth weights (BWT) of different tropical breeds in different regions and in varied levels of management. ILCA (1979) reported an average BWT of 1.8 kg in village flocks and 2.6 kg in on-farm trials in West Africa. Other studies in indigenous sheep have reported slightly higher values: 3.20 ±.02 for Bikaneri sheep (Dass and Acharya, 1970), 3.61 ± .54 for Navajo sheep (Eltawil *et al.*, 1970), 2.4 ± .04 for Morada Nora sheep (Fernades, 1985), 2.9 ± .04 for Red Maasai, Dorper and their crosses (Kiriro, 1986), 4.17 ± .07 for Dorper (Inyangala *et al.*, 1990) and 2.63 ± .01 for Sabi sheep (Matika *et al.*, 1995).

Kiriro (1986) reported that Red Maasai were 0.74 kg lighter at birth than Dorper in sheep in semi-arid zone of Kenya. But studies conducted in a flock in

coastal Kenya, under severe GI nematode challenge reported a negligible breed difference for live weight in lambs from birth to weaning (Baker, 1995a).

Breed comparisons for weaning weight showed no large differences in America hair sheep (Fitzhugh and Bradford, 1983). Kiriro (1986) and Inyangala *et al.* (1990) reported an average weaning weight of 19.5 kg in a flock the in semi-arid zone with varied gene composition of Red Maasai and Dorper. This result was similar to that of 17.1 kg reported in Sabi sheep (Matika *et al.*, 1995). But in a flock under GI nematode challenge weaning weight of 10.7 kg was reported (Baker, 1995a).

The mature size of ewes varies with season depending on nutritional status, stage of pregnancy and milk production. Most of this variation occurs when the ewe has attained full growth of lean and bone tissues. In hair breeds, variation for mature size is large ranging from 40 kg Barbados Blackbelly to 27 kg for the West African Forest sheep. (Fitzhugh and Bradford, 1983). Matika *et al.*, (1995) reported 18 months live weight of 35.1 kg in Sabi sheep. This was similar to most estimates of mature weight of Africa's indigenous sheep which range from 21-40 kg (Wilson, 1982).

3.3.1.1.2 Lamb survival

The potential increase in the biological and economical efficiency of sheep production in tropics is much greater from more lambs weaned per ewe than from faster growth rate or less body fat. Survival to weaning and subsequently to yearling stage has a major effect on lambs weaned per ewe and on annual off-take. The correlation between number of lambs weaned with weight weaned per ewe is favourable (Gama *et al.*, 1988). Losses from lambs mortality is often high but information on causes of genetic variation is sparse (Cundiff *et al.*, 1982).

Breeds of large size (e.g Suffock) have favourable maternal influence on pre-weaning survival but an unfavourable direct transmitted influence. Prolific genotypes such as Barbados Blackbelly, Javanese thin tailed and D'man have a high number of lambs weaned per ewe exposed. A study conducted in coastal Kenya reported a post-weaning (3-13 months of age) mortality rate of 51.7 % in Red Maasai and 18 % in Dorper in a flock under natural GI nematodes challenge of predominantly *Haemonchus contortus* (Baker, 1995a). There was a favourable additive genetic merit for lamb survival in Red Maasai and their crosses. Matika *et al.* (1995) reported a 15 % pre-weaning mortality rate in Sabi lambs in a semi-arid environment in Zimbabwe. These results show the generally observed variability in production among tropical indigenous breeds (Devendra and McLoery, 1982; Wilson, 1982; Fitzhugh

and Bradford, 1983; Turner, 1991; Ponzoni, 1992). Thus, there is scope for effective selection in tropical breeds to improve productivity.

2.3.1.2 GI nematodes

There are many reports of breed-variation for nematode burdens, particularly *Trichostrongylid* nematodes in sheep. Stewart et al. (1937) reported the first breed differences in natural nematode challenge of predominantly *Ostertagia circumcinta* in Romney, Rambouillet, Hampshire, South down and Shropshire sheep.

Subsequent studies have confirmed between breed variation to GI nematode challenge using both natural and artificial infections. A summary of sheep breed comparisons prepared by Baker *et al.* (1992) with the addition of more recent publications are presented in **Appendix 1**. Most studies indicate that indigenous/unimproved sheep breeds are relatively more resistant to single or mixed infection of nematode species than exotic or improved breeds. In nearly all studies FEC and FEC transformations have been used as diagnostic criteria for measuring resistance. Worm counts have been reported in some studies, a few of which also report production traits such as survival rate, wool growth, ewe reproduction (ewes lambed compared to ewes joined) and growth (i.e live weight or live-weight gain). **Appendix 1** shows that there are a number of breeds which are resistant to *Haemonchus contortus*. These breeds include

the Scottish Blackface (Abbot *et al.*, 1985a, 1985b), Red Maasai (Preston and Allonby, 1978, 1979; Bain *et al.*, 1993; Leitch *et al.*, 1993; Mugambi *et al.*, 1993; Baker *et al.*, 1994), Barbados Blackbelly, Florida Native, St. Croix (Loggin *et al.*, 1965; Rhadakrishnann *et al.*, 1972; Bradley *et al.*, 1973; Yazwinski *et al.*, 1979, 1981; Courtney *et al.*, 1984, 1985a, 1985b; Gamble and Zajac, 1992; Romjali, 1995), Cigaja (Cvetkovic *et al.*, 1973), Navajo (Knight *et. al.*, 1973) and Horro (Asegede, 1990).

Resistance is demonstrated in both lambs and mature animals. Baker *et al.* (1994a, b) showed that Red Maasai lambs and ewes were consistently more resistant to natural GI nematode challenge than Dorper sheep. Bain *et al.* (1993) demonstrated that Red Maasai ewes had 10 times lower egg output than Romney ewes. Studies by Baker *et al.* (1992, 1993, 1994a, 1994b) indicated that resistance develops with lamb age and is best expressed at 10 months of age. Hence acquisition of resistance is genetically controlled and develops with time.

Unbiased estimates of between breed difference are best obtained if animals are from diverse sources. This can be achieved by using offspring from a large sample of sires, while avoiding using offspring from predominately susceptible or resistant sires. As noted both by Gray (1991) and Baker (1995b) nearly all the studies in **Appendix 1** are characterised by poor experimental design. The studies had small

numbers of each of the breeds tested and there was lack of information on the numbers of sires used to generate the animals being evaluated or/on how they were sampled.

2.3.1.3 Tick infestation

Cattle breed comparisons for resistance to tick infestations are shown in **Appendix 2**. Between breed differences in resistance to tick infestation are well-established. Most comparisons of breed difference in tick infestations are loosely divided into *B. indicus* and *B. taurus*. Several studies indicate that Zebu and Africander cattle and their crosses are much more resistant to cattle ticks than European cattle (*B. taurus*) breeds. Breed differences result from interacting factors such as anatomical, behaviourial, physiological and immunological - which reduce the number of ticks successfully attaching and engorging on the host. The morphological differences include skin thickness, type of coat and subcutaneous musculate. *B. indicus* cattle have short glossy hair, thick skin with well developed subcutaneous musculature and their skin is relatively more sensitive to tactile stimuli. They respond to ticks walking on the skin and their attachment by rapid skin flickering, scratching against objects and frequent grooming (de Castro and Newson, 1993). Resistance of *B. indicus* has also been attributed to their visual and olfactory

avoidance behaviours. This has been reported in addition to *Boophilus* spp, *Rhipicephalus appendiculatus* and *Amblyomma herbraem* (Bosma, 1981; Sutherst *et al.*, 1986; Norval *et al.*, 1988, 1989; de Castro and Newson, 1993).

The first observation suggesting that resistance to the cattle tick (*Boophilus microplus*) was hereditary, was reported in 1912 (de Castro *et al.*, 1985). Later research (Hewetson, 1968, 1971, 1972; Turner and Short, 1972; Utech, *et al.*, 1978a, Sutherst and Wharton, 1979; Utech and Wharton, 1982; Seifert, 1984b; Sutherst et al., 1986, 1988; Rechav *et al.* 1990) confirmed this and led to the development of cattle resistant to *B. microplus* in Australia (Reason, 1983; Alexander *et al.*, 1984). Seifert (1971) analyzed 3,000 counts from over 1,000 animals of several breeds and reported no difference between Africander and Brahman cattle (both *B. indicus*). This was confirmed by Utech *et al.* (1978b) and Sutherst *et al.* (1988) using crossbreeds of *B. taurus* and *B. indicus*. Garris *et al.* (1979) found that Brahman cattle carried significantly fewer adult and nymphs of *Amblyomma americanum* than Hereford cattle when the two breed were exposed to natural infestation.

In Africa, natural infestations involve multiple tick species (Kaiser *et al.*, 1982; de Castro *et al.*, 1985; Tatchell, 1986, 1988). One, two and three-host tick species are normally found simultaneously on cattle and their numbers fluctuate with the season (Kaiser *et al.*, 1982). A number of studies in Africa have shown that *B.*

indicus and Sanga breeds of cattle are more resistant than *B. taurus* breed and their crosses to a variety of tick species, including important vectors of theileriosis such as *Rhipicephalus appendiculatus, Amblyomma habraeum and Amblyomma variegatum* (Utech *et al.*, 1978a; Rechav, 1990). Tick resistance of *B. indicus* cattle, together with their "innate" ability to withstand challenge from virulent form of tick borne disease allow these cattle to survive without tick control in Eastern and Central Africa (Dolan and McHardy, 1977; Moll *et al.*, 1986). Fivaz and Norval, (1990), Norval *et al.* 1992 and Mattioli *et al.* (1993) reported that fewer tick-resistant cattle were infected with *Theileria parva* than tick-susceptible cattle when *R. appendiculatus* were used in transmission trials, indicating that resistance was across parasite genera and species. However, preliminary evidence suggests that N'dama and Boran cattle are equally susceptible to *Theileriosis* (Dolan et al., 1992).

Although small ruminants are generally grazed with cattle in the same fields in Africa, there has been limited research on resistance to ticks or tick-borne diseases, Studies conducted in sheep experimentally infested with single tick species indicate that resistance is acquired though genetically controlled and it develops over time and it is evident after several challenges (Norval, 1978; Barriga *et al.*, 1996). Thus, need to conduct resistance of sheep to natural infestation.

2.3.2 Within breed differences

Many genes are involved in traits inherited quantitatively and there is no sharp distinction between the different phenotypes. Many economically important traits in farm animals such as fertility, rate of gain, fleece weight, body weight, body measurement and milk production are examples of this kind of inheritance. The expression of these traits is affected by many pairs of genes as well as environmental factors.

Improving the level of expression of economic characteristics in sheep through breeding requires an effective use of genetic variation. Pertinent to the effective use of this genetic variability is a knowledge of its magnitude as estimated by the heritability of production-related traits. Genetic and phenotypic correlations among various traits are also important in planning selection procedures. An essential step to the successful application of genetic principles in improvement of sheep is therefore the estimation of the heritabilities of those traits which the breeder desires to improve.

Traits are often described as being "highly" heritable or "lowly" heritable depending upon how closely parents and offspring, brothers and sisters, or other close relatives resemble each other phenotypically. An accurate estimate of heritability is important because it indicates the fraction of the phenotypic superiority of selected

parents which is transmitted to the offspring. Thus, progress from selection may be relatively rapid for some traits and relatively slow for others even when equally intense selection efforts are made to improve them. For this reason, knowledge of the respective heritabilities of different traits, as well as the phenotypic and genetic correlations among them, are the important factors in determining how to practice selection for several traits simultaneously.

As pointed out by Falconer (1981), the most important function of heritability in a genetic study involving quantitative characters is its predictive role in expressing the reliability of the phenotypic value as an estimate of breeding value. The size of the standard errors of the estimate of heritability gives some indication of the precision of the estimate.

The heritability of a trait may be defined in two ways. In the broad sense it is the fraction of the phenotypic variation which is due to the effects of the genes singly and in complexes. Thus, it includes the additive effects of genes plus any variation within the population due to non-allelic gene interaction, dominance and interaction between hereditary and environment. In the narrow sense, heritability is the fraction of the phenotypic variation which is attributable to the additive effect of the genes, that is attributable to the linear regression of phenotype on genotype.

Since only the additive genetic effects contribute to permanent gain from selection in a population, an estimate of heritability in the narrow sense is more desirable for predicting the results of a selection programme. This estimate may contain some dominance deviations and little epistatic variance, depending on the method by which it is measured. Therefore, most of the estimates of heritability fall somewhere between the broad and narrow sense definitions of heritability.

Heritability estimates can be divided into genetic effects peculiar to an individual and that originating from maternal effect. In the last decade, it has become increasingly possible to estimate both sources of genetic variation by use of an animal model (Meyer, 1989). The total heritability estimate obtained is the regression of an animal's total genotype (direct and maternal) on its phenotype.

2.3.2.1 Production traits

The heritability (h^2) estimates in **Appendix 3** for live weight from both temperate and tropical regions are low to medium in magnitude for pre-weaning traits. The general pattern is that h^2 estimates increase substantially for post-weaning live weights. The pre-weaning live weights are complex because they depend not only on additive genetic effects but also on maternal genetic effects. The maternal additive genetic effects has a tendency of increasing component of variance that is

environmental to the lamb thereby lowering pre-weaning h^2 estimates (Rae, 1982). Matika *et al.* (1995) confirmed that maternal heritabilities are significant for BWT and WWT in Sabi sheep, but thereafter they decline with increasing lamb age (**Appendix 4**). Thus, the best time to select lambs for the genetic merit for live weight would be to use post-weaning estimates, since maternal influence is low. However, selection of ewes as dams must be based on lamb performance during the pre-weaning period and live weight at weaning. It is clear from **Appendices 3** and **4** that there is no significant difference in h^2 estimates between temperate and tropical breeds, despite large between-breed differences for live weights.

The h^2 estimates for lamb survival in temperate breeds are low. When expressed as a lamb trait, the estimates range between 0.02 ± .02 to 0.05 ± .03 for survival from birth to weaning, while an estimate of 0.08 has been reported when expressed as a dam trait (Cundiff *et al.*, 1982; Gama *et al.*, 1988). In contrast, Baker (1995a) reported h^2 estimates for mortality of 0.00 ± .04 for birth to weaning and 0.12 ± .06 for weaning to 12 months of age when the trait is expressed as a lamb trait and 0.10 ± .03 to 0.00 ± .05 respectively, as a dam trait in tropical breeds. These estimates suggest that the maternal influence is only important during the pre-weaning period, therefore lamb genetic merit for survival is best expressed during post-weaning period.

2.3.2.2 GI nematodes

2.3.2.2.1 Heritabilities

Evidence of within-breed differences for resistance to nematode infection in sheep was first reported in the late 1930's. Later, Whitlock (1955, 1958a, 1958b) and Albers *et al.*(1984) confirmed that progeny of resistant sires had consistently low FEC in predominantly *Haemonchus* spp infection. Since then, many reports on the genetic control of resistance in laboratory model systems (Brown, 1985, Wakelin, 1985, 1887), in cattle (Davis, 1993) and sheep (Gray, 1991; Gray and Woolaston, 1991; Gray *et al.*, (1995) have shown that variation in resistance within breeds is a universal phenomenon. The 23 heritability estimates presented in **Appendix 5** are from Australian and New Zealand estimated in Merino and Romney sheep, respectively. Studies have concentrated on both natural and experiment infection with mainly *Haemonchus contortus* and *Trichostrongylus*. The heritability of FEC in both countries (Australia and New Zealand) appears to be around 0.2 to 0.3 under typical challenge conditions. But the figure is higher under highly contolled artificial infection conditions or when several measurements are averaged. The large standard errors (0.12-0.15) observed in initial studies have reduced in later studies utilising larger data sets and more efficient statistical methods (e.g. REML animal models).

While a heritability of 0.3 for FEC and PCV is at the lower end of the range typically found for production traits (0.3-0.5) (Turner and Young, 1969), FEC is also an extremely variable trait with a coefficient of variation in excess of 100 %, compared with 7-15 % in most objectively measured production traits (Woolaston and Eady, 1995). Thus potential rates of genetic improvement are therefore quite rapid.

Very few estimates of heritability of FEC or PCV have been reported from Africa (**Appendix 6**) and except those reported by Baker (1995a) they have high standard errors. A moderate heritability of 0.22 ± .07 for logarithm-transformed FEC was reported by Baker (1995a) in yearling sheep, but the heritability estimates was higher in Dorper-sired lambs (0.32 ± .13) than Red Maasai-sired lambs (0.11 ± .07). This suggests that after many centuries of natural selection under endoparasite challenge, in R breed might have become fixed for some of the important genes for resistance, yet still retain a significant amount of within-breed genetic variation. However several studies are required to quantify this fully.

2.3.2.2.2 Selection experiments

Divergent selection lines based on resistance and susceptibility to GI nematodes of different genera (mainly *Haemonchus contortus* and *Trichostrongylus)* have been established in Australia, New Zealand and France (Baker *et al.*,1992).

Details of these selection studies are presented in **Appendix 7.** Both artificial and natural challenge with different GI nematodes have been employed in establishing these lines and encouraging responses to selection have been reported in most of these studies (Morris *et al.*, 1995; Woolaston and Eady, 1995). Phenotypic standard deviation differences of 0.86 and 1.65 have been achieved in natural selected lines in New Zealand after a period of 10 and 18 years of selection, respectively. After 14 years of experimental selection, a substantial reduction in FEC has been achieved in CSIRO *Haemonchus* selection flock and the *Trichostrongylus* lines in Australian (Woolaston and Eady, 1995). Differences between selected and unselected lines are almost invariably found whenever FECs are positive. On a percentage basis, the difference can be as higher as 95 % or as little as 50 % depending on the time of measurement and other factors yet to be determined. Many of the heritability estimates presented in **Appendix 5** were derived from these selection lines.

The heritability estimates for FEC are moderate (0.2 to 0.3), but to date only one realised heritability estimate from the CSIRO *Trichostrongylus* selection lines of 0.39 ± .27 has been reported (Woolaston *et al.*, 1991). This estimate is comparable to the paternal half sib estimate of 0.41 ± .10 reported by Windon and Dineen (1984). Thus, resistance to GI nematode is heritable and selection is feasible.

2.3.2.2.3 Repeatabilities

Repeatability estimates for measures of resistance to internal parasites depend on whether measurements are made within or between infections. Estimates for FEC within an infection cycle have been reported to range between 0.6 to 0.7 for a single artificial infection with *Haemonchus contortus* (Woolaston et al., 1991) and 0.69 for artificial infection of *T. colubriformis* after vaccination with irradiated *T. colubriformis* (Eady, 1995). Barger and Dash (1987) reported a repeatability estimate of 0.6 for fortnightly FEC measurement in a flock artificially infected with a trickle infection of *H. contortus*.

Repeatability between infections with *H. contortus* was found to be 0.3 (Barger and Dash, 1987). In New Zealand, the repeatability of FEC across two natural infection cycles has ranged from 0.4 to 0.5 (Baker *et al.*, 1991), while in Australia it ranged from 0.11 to 0.28 with a mean of 0.27 (Cummins *et al.*, 1991). In both countries the interval between measurements was about 3 months. Within infection repeatability estimates for measures of resistance to internal parasites in small ruminants in Africa are shown in **Appendix 6** and they range from 0.07 for log FEC to 0.44 for PCV. Repeatability between sampling is generally low and variable (Karlsson *et al.*, 1991). This has been attributed to varying stages in development of

resistance especially when unadjusted by anthelmintic treatment which in itself cause a loss of natural resistance (Barger, 1987; Reynolds *et al.*, 1992)

A repeated measurement of FEC after a fairly short interval within an infection cycle, can increase the heritability a little. For example assuming a repeatability of 0.6 for FEC and heritability of 0.3, two measurements within an infection cycle can increase heritability to 0.37 using the formula given by Woolaston *et al.* (1991) (i.e $2h^2/1 + r$ where r is repeatability and h^2 is the single record heritability). To gain the highest return from investment of resources in a breeding program for parasite resistance, it is of greater benefit to measure FEC over two consecutive infection cycles. In this case if we assume a heritability of 0.3 and a repeatability of 0.3, then the heritability of the average of two reported measurement is 0.46.

2.3.2.3 Ticks

There is evidence of within breed variation in tick infestations (Wharton *et al.*, 1970; Bosma, 1981; Latif, 1984; Rechav *et al.*, 1990). Estimates for heritability of resistance to *Boophilus microplus* by cattle in Australia are presented in **Appendix 8**. They range from 0.10 to 0.58 with an average of 0.32. The most accurate estimate of 0.34 ± .05 was reported by Mackinnon *et al.* (1991) using a large data set with

1329 sires. There is evidence that the use of a *Bos indicus* breed in a cross breeding programme is the most rapid method of increasing resistance to tick infestation of European breeds (Utech and Wharton, 1982). Heritability estimates suggest that although it is possible to select for tick resistance in *B. taurus* cattle, the rate of improvement will be much slower than in *B. indicus* infused breeds (Utech and Wharton, 1982; Seifert, 1984a, b). In a series of experiments lasting up to 17 years, it was shown that resistance levels in Australian Illawara cows (AlS) and Brahman-AlS herds could be increased using both selection and the introduction of resistant individuals. The increase in tick resistance observed after four generations of selection in purebred AIS was approximately the same as that observed in the F_1 progeny of highly resistant Brahman bulls and AlS cows. The average proportion of *Boophilus microplus* larvae maturing on AlS cattle was reduced by about 10 fold (Utech *et al.*, 1978a; Utech and Wharton 1982). The repeatabilities of tick counts in cattle from both natural and artificial infestation vary between 0.5 to 0.9 (Wharton *et al.*, 1970; Seifert, 1971; Mackinnon *et al.*, 1991).

2.4 Genetic and phenotypic correlations

The genetic correlations between two characters may be defined as a ratio of the genetic covariance to the product of their genetic standard deviations (Falconer,

1981). A genetic correlation is thus a measure of the relationship between the genetically additive deviations of the two traits. When the genetic correlation between two traits is positive, simultaneous improvement of the two traits is feasible. A negative correlation, however, implies that selection for one trait will automatically cause some deterioration in the other. Net progress for each trait in a selection index can be achieved if the traits are independent or favourably correlated. Index selection can still be applied to traits that are unfavourably correlated but the rate of genetic improvement for each trait will be slower.

Phenotypic correlations estimate the extent to which characteristics in the current flock are associated, either positively or negatively. Hence, the extent to which selection will raise production in the current flock depends on the heritability of the trait and, when more than one trait has to be considered, on the phenotypic and genetic correlations traits. The objective in determining the phenotypic correlations between traits is their use in constructing selection indexes to attain the maximum rate of genetic improvement.

2.4.1 Phenotypic correlations among traits

The phenotypic correlations between production traits and resistance traits (FEC and FEC functions) are summarised in **Appendix 9**. The phenotypic

correlation between live weight gain (LWG) and FEC are consistently slightly negative, (-0.4 to -0.12), as would be expected in lambs that are left undrenched. Comparing different lamb genotypes, Baker *et al.* (1993) reported a strong and negative association between mortality and PCV (i.e lower mortality associated with lower FEC) and a negative correlations between logarithm transformed FEC and live weight (-0.46), which is a desirable association for growth and resistance.

Phenotypic correlations of tick count with post-weaning LWG in cattle are generally negative and significant, but not strong. Significant increases in live weight have been found in different genotypes by removing ticks by chemical treatment (Seifert, 1971; Turner and Short, 1972; Frisch, 1984; Vercoe and Frisch, 1992). However, these studies failed to show a significant relationship between TC and post-weaning live weight within groups of untreated animals. Mackinnon *et al.* (1991) reported phenotypic correlations of -0.02 and 0.05 between logarithm-transformed TC and live weight at 12 and 18 months of age, respectively. The relationships between average tick numbers and growth of individual animals are weak and only account for a small proportion of the total variation in growth rate.

2.4.2 Genetic correlations among traits

Genetic correlations between FEC and production traits from several studies are presented in **Appendix 9**. These estimates are close to zero and characterised by large standard errors. Baker *et al.* (1991) and Woolaston *et al.* (1991) have indicated that genetic correlations which include disease traits are bound to biased unless the production trait is measured in absence of the disease. They have proposed use of analytical methods which allow estimation of genetic correlations from a design where the two traits are measured on different but closely related group of individuals (e.g. half sibs). Under such circumstances, the group on which the production traits are measured could be maintained in a disease-free state so that genetic correlation estimates will not be affected by the presence of GI nematodes. It is not known to what extent such bias may exist in the data presented in **Appendix 9**, but it is unlikely to be high since the flocks were managed according to a recommended worm control program except for a relatively short period when they were exposed to infection. The effect of GI nematodes is expected to have been low due to short interval of exposure. Despite this potential bias, there is no evidence of significant favourable or unfavourable genetic correlations between resistance and production traits.

Genetic correlations between TC and growth traits are negative and small. Mackinnon *et al.* (1991) reported estimates of -0.10 and -0.08 between transformed tick count and live weight at 12 and 18 months of age in cattle with varied genotypes. These results suggest that selection for growth would not change resistance to tick infestation.

2.5 Conclusion

With the widespread development of resistance to biocides and the high cost of developing new drugs, interest in exploiting and developing animals that are genetically resistant to nematode infections and tick infestations has been stimulated in the last few decades. This seems the most realistic option, especially for the sub-Saharan region, where resources are scant and livestock industries are fragile. It appears from the literature that some indigenous small ruminant breeds are resistant to GI nematode infections. Resistance is shown by the ability of these breeds to maintain low FEC, resist anaemia (i.e. maintain high PCV) and markedly lower lamb mortality. It is of interest to see if there is resistance to tick infestation in sheep. This review indicates that host resistance to ticks and gastrointestinal nematodes is heritable and that selection for this trait is feasible, yet this approach is not being used in Africa to date.

3. MATERIALS AND METHODS

3.1 Data source and experimental design

Genetic resistance to gastrointestinal (GI) nematode infections and tick infestations in sheep was evaluated in semi-arid and semi-humid agro-ecological zones of Kenya. Three farms were used for this study; Diani Estate and Nguuni farm in the semi-humid coastal zone and Ol'Magogo farm in the semi-arid zone. The study in the semi-humid zone was divided into two distinct parts, namely :- GI nematodes resistance at Diani Estate in the 1993 born lambs. They were evaluated from birth to one year of age in 1993/94. Thereafter a 3-month study using yearlings from Diani was carried out to evaluate resistance to tick infestation at Nguuni. In the semi-arid zone the study included evaluation of resistance to both nematodes and ticks. The Diani data set (a sub-set of a larger ILRI research programme) was made available for analysis as part of this thesis.

3.1.1 Diani Estate and Nguuni farm (Baobab Farm Ltd), Mombasa

Both farms belong to Boabab Farm. Diani Estate is located 20 km south of Mombasa while Nguuni farm is about 20 km north of Mombasa on the Malindi-Mombasa road. They lie between latitude 0^0 - 4'S and longitude 38^0 - 41'E and are

approximately 20-30 metres above sea level. The area is in the coastal lowland semi-humid zone (coconut-cassava agro-ecological zone, CL3) (Jaetzold and Schmidt, 1983).

When the semi-humid zone mean annual rainfall is within the range 800-1350 mm, generally distributed bimodally. Long rains fall in the April-June season, while the short rains, which are less reliable, come in the October - November season. The mean monthly maximum temperatures range between 28^{0}C to 33 ^{0} C (Jaetzold and Schmidt, 1983), with relative humidity of 60-90 %.

The soils at Diani Estate are sandy and well to excessively drained, while at Nguuni the soils are acrisol-luvisol and orthic soil types and mediumly drained. The soils are characterized by low macronutrients, especially phosphorus and nitrogen compounds and the organic matter and cation exchange is low.

The vegetation is natural pasture, tree shrubs and bushes. The predominant tree species are *Acacia senegal, Acacia tortolis* and *Acacia seyal,* while the common grass species are *Heteropogon contortus, Aristida adoensis, Andropogon chinensis, Digitaria abyssinica, Setaria spp, Eragrotis spp, Hyperrhenia hirta* and *Hyperrhenia rufa.*

The main enterprises at Diani are sheep, goats, dairy cattle and forestry. The sheep breeds are Dorper (D), Red Maasai (R) and their crosses, while the goat breeds

are Galla and Small East African. At Nguuni farm the main enterprise is game farming which started in 1976 with a herd of 34 Oryx *(Oryx biesa callotis)* and 14 Eland *(Tragelaphus oryx)*. Four Eland were purchased from Rift Valley Province in late 1970's, while seven Oryx were acquired from Galana ranch in Tsavo (Rene Haller, personal communication). Bee keeping and fish farming are also carried out on this farm, but on a smaller scale. Previously other enterprises had been tried on the farm but their economic output was poor (e.g sheep farming).

Research on small ruminants at Nguuni and Diani Estate was initiated in 1987 (Bullerdiek, 1989; Bullerdiek *et al.*, 1990) and the main thrust was to evaluate the effects of genotype (D and R x D crosses), nutrition and anthelminthic treatment regime on helminthiasis and production in a joint ILCA/GTZ study. During this study high mortalities were recorded at Nguuni and all animals were transferred to Diani Estate when GTZ ended their involvement in 1990. Currently ILRI is conducting research on genetic resistance to endoparasites in sheep and goats at Diani Estate (ILCA,1992; Baker *et al.*, 1993, 1994a).

3.1.1.1 Experimental protocol and design for the nematode resistance study (Diani Estate)

In 1990, D and F_1 (R x D) ewes were mated to R and D rams in a diallel crossbreeding design at Diani Estate. The results from this lamb crop were reported by Reynolds *et al.* (1992). The lambs born since 1992 have been generated in a diallel mating design involving 3 ewe genotypes (D, R and their F_1) and two sire breeds (D and R). Both the R and D rams and ewes were purchased from as wide a range of sources and districts as possible, to ensure a broad and representative genetic sample of the breeds.

Ewes were herded separately from rams on natural pastures at Diani Estate. The grazing took place by day. At night all sheep were confined in bomas where mineral blocks and water were provided *adlibitum*. During the mating season of approximately six weeks, the ewes were penned in single-sire groups overnight. Immediately after birth (within 24 hours) lambs were identified, weighed, male lambs were castrated and the umbilical cord was disinfected with a tincture of iodine. Thereafter up to weaning at three months of age, lambs were weighed every two weeks. At one and two months of age, PCV and FEC were recorded. Before weaning lambs were allowed to graze with their dams but thereafter lambs were herded

separately from the mature flocks (rams and ewes). All sheep and goats at Diani were sprayed fortnightly with acaricide for tick control.

The ewes were weighed at least six times during their reproductive cycle; that is at mating, three months after mating, two weeks before lambing and at one,two and three months post partum. Blood and faecal samples were collected at each weighing for determination of PCV (a measure of anaemia) and FEC (a measure of GI nematode infection level). Blood was also examined for the presence of trypanosomes.

All animals were exposed to natural GI nematode infections. Grazing ewes and rams found to have a FEC greater than 4,000 egg per gramme (epg) of faecal material and/or a PCV below 20 % at any sampling time were treated individually with an anthelminthic drug. All ewes were strategically drenched at weaning. Individual lambs were treated with anthelminthic during the preweaning monthly sampling times (1 and 2 months of age) if FEC was greater than 2,000 and/or if PCV was less than 20 %. All the lambs were drenched with anthelmintic at weaning (3 months of age). They were then grazed on pasture until a monitor group of 50 lambs, which was sampled every week, reached a mean FEC of 1,500-2,000 epg. Once this threshold level was reached all lambs were weighed and FEC and PCV recorded on two consecutive days. They were then drenched and the protocol was repeated. This

procedure was repeated five times between weaning and one year of age for the 1993 lamb crop (**Figure 4.1**).

3.1.1.2 Experimental design for tick infestations (Nguuni farm)

A total of 161 yearling sheep representing six genetic groups (i.e D; R; 50 % D 50 % R; 50% R 50 % D; 75 % R 25 % D; and, 75 % D 25 % R) (in the crosses the first breed represents the breed of the sire) were moved from Diani to Nguuni in June 1994 after undergoing a GI nematode resistance study for approximately one year (August 1993 to May 1994). They were given two weeks to acclimatize before exposure to ticks. During these 2 weeks, animals were drenched and sprayed to control endo- and ectoparasites, respectively.

The yearling sheep were deliberately mixed with the wild game, for tick interspecies cross infestation. The status of the tick population and genera were assessed before exposing the experimental animals to flock natural infestation in the bomas. This was done by sampling wild game (Eland and Oryx) (**Plate 1 and 2)** and D sheep which were already on the farm. In the first infestation period, the experimental sheep trailed the wild game during the day while at night they were confined in the same boma. However, after an outbreak of "heartwater" (*Cowdriosis*)

the flock was withdrawn from the wild game boma in the second and third infestation periods but the same grazing pattern was maintained (i.e trailing the wild game).

Six D and 14 R (randomly sampled from 19 available R) were used as a monitor group for tick infestation build up. Tick counts (TC) were done at an interval of three days in each period (of approximately 21 days) on the monitor group. Total body count was done with emphasis on predilection sites (i.e ears, face, belly, hooves and tail regions). WT, PCV and FEC were recorded before the start of the study.

At the end of each infestation period, all animals were weighed, ticks counted, and faeces and blood samples taken. Ticks of standard mature size (4.5-8.0 mm) were counted on the entire body but nymphs and larvae instars were ignored. Each sheep was restrained by two people and then ticks counted systematically starting from the head, ears, neck, feet, legs, undersurface and finally the sides and back. Visible ticks were counted first, then a hand was run slowly over the whole surface, feeling through the hair coat for slight irregularities that were detectable to the fingers

Figure 4.1

DIANI LAMBS BORN 1993 - MONITOR GROUP (PERIOD 1-5)

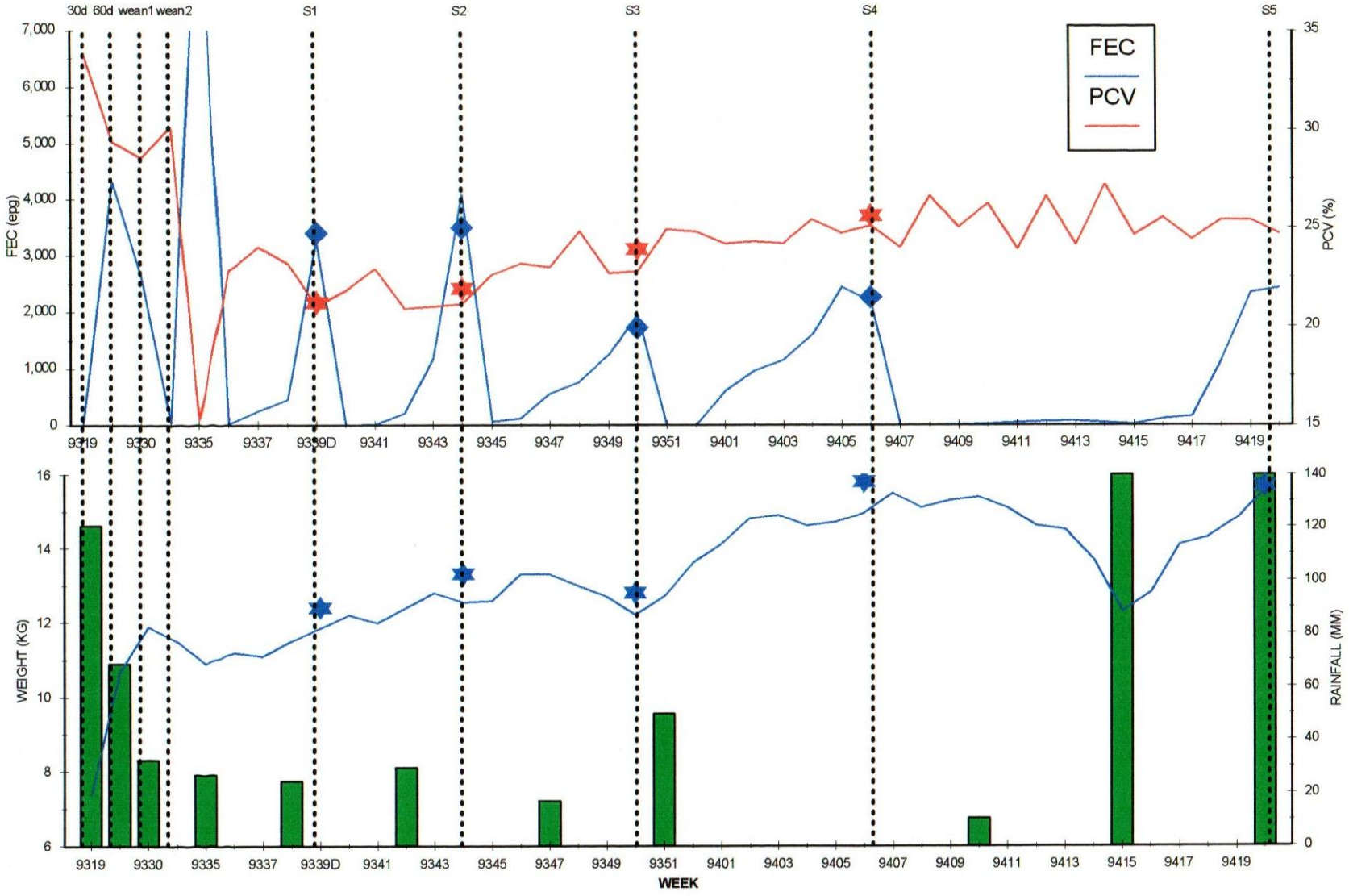


Plate 1: A flock of Elands (*Tragelaphus oryx*) at Nguuni farm.

Plate 2: A flock of Oryx (*Oryx biesa callotis*) at Nguuni farm

and palm, which indicated attached ticks. Two people counted the ticks in turn on each sheep and then an average was calculated for each individual animal. At the end of each infestation period all animals were drenched with anthelmintic drugs (levamisole and albendazole) to control GI nematodes and flukes and sprayed with Triatix (Amitraz) to control ticks. Long acting tetracyclines were administered to animals showing clinical signs of "heartwater" such as nervous signs and high temperature (over 41^0 C). Other diseases monitored were foot rot and trypanosomiasis. All cases of trypanosomiasis were treated with Diminazene aceturate (Berenil) at a rate of 35 mg/kg body weight. Foot trimming was done regularly. All the sheep were passed through a footbath with copper sulphate solution daily. Tick wounds and any other lesions were treated promptly and sprayed with terramycin aerosol spray.

3.1.2 Ol'Magogo farm (Naivasha).

Ol'Magogo is a sub-station of the Sheep and Goat Development Project (Naivasha) of the Ministry of Agriculture, Livestock Development and Marketing. The main research activities embraces all the researchable small ruminant production areas, i.e nutrition, breeding and diseases. The farm is 50 km north west of Naivasha. It lies on latitude 37^0 East, at an altitude of 2,000 meters above sea level. The average annual rainfall is about 600-750 mm and an inter-year variation of 300

-1,000 mm. Long rains begin in late March and decrease in frequency towards the end of May and early June. Short rains occur from Mid-October through to December, although these are generally not as reliable as the long rains. Temperature fluctuates from a minimum of 18^0C to a maximum of 26^0 C.

3.1.2.1 Flock history

A group of 69 D breeding ewes and 6 rams were transferred to Naivasha from the Mariakani Research Station in 1970 and comprised the foundation stock. In 1973 some D sheep, previously imported to the Kiboko Range Station from South Africa, were transferred to Ol'Magogo. More D rams were transferred from Katumani Research Station, Machakos for use at Ol'Magogo in 1972 and 1979. The R sheep that formed the foundation stock at Ol'Magogo were purchased from producers around Nanyuki, Gilgil and Baringo areas of the country. By 1971, a total of 170 R sheep had been purchased. To propagate the foundation flock the D and R were straightbred to establish and expand the flocks. In the case of the D breed the need to increase flock size was paramount to increase the availability of D rams for breeding. As purebreeding and multiplication of the D and R sheep continued, some short-term breed characterization studies were conducted. Some joint studies of the Kenya Government and FAO in the seventies were carried out specifically on the

effects of frequent mating (joining every 8 months) on the productivity of the D as compared to once a year joining; resistance or tolerance to GI nematodes; economics of production of the two breeds in this medium potential ecological zone; reproductive performance; body size at various stages of maturity; and other production aspects (Odenya, 1982; Kiriro 1986).

3.1.2.2 Breeding policy

Strict measures were instituted to prevent inbreeding. The rams were used in the same flock for no longer than three breeding seasons. The sires used or purchased were selected for conformation, breed character and performance. Except for a small number of ewes used for frequent mating studies, all ewes were bred once a year. The replacement hoggets were generated from within the flock and about 20 % of the top quality ewe lambs were retained as replacements. About 5 % of the rams were selected from the flock for breeding on the basis of the parent's performance records and individual performance.

3.1.2.3 Breeding and feeding management

The breeding flock was screened before each mating and all the undesirable ewes and rams were culled. The resulting breeding flock was moved into a new

paddock where they were foot trimmed, weighed and grouped into mating groups at random, with a sire to dam ratio not exceeding 1:50. The rams were fitted with a sire-sine harness with a crayon for identification of mated ewes and the marked ewes were recorded daily. The D and R hoggets were first mated at varying ages and weights. The D crosses were bred at about 1 year of age and at about 32 kg live weight. The D and R hoggets were first joined at 1 year and 15 months of age and were about 28 kg live weight. The sheep were grazed extensively on open paddocks. They were taken to the pasture early in the morning and returned late in the afternoon. They were penned in open bomas at night. Rotational grazing was practiced to reduce worm infestation and facilitate grass re-establishment. The stocking rate was 2.5 livestock units (an African livestock unit is equivalent to a mature zebu cattle weighing 250 kilogramme) per hectare on permanent pasture commonly of Naivasha star grass and Kikuyu grass (*Cynodon dactylon, Cynodon plectostachyum,and Pennisetum clandestinum*). Salt was provided *ad libitum* (red oxide with maclick) in troughs on the pastures and in the night sheds. Sheep were watered twice a day. Apart from mineral salt no form of supplementation was provided, except for the breeding rams, which were fed with lucerne hay one month before joining to condition them.

The pregnant ewes were vaccinated against clostridial diseases before lambing and drenched against worms a month before lambing. All the ewes were transferred into lambing paddocks just before lambing. Immediately after birth lambs were weighed and the naval cord was disinfected after the ewe had completely cleaned the young lamb. They were then identified and sex and type of birth recorded. Docking was then done using a rubber ring one week after birth. Drenching against internal parasites was done monthly. Lambs were drenched for the first time when they were one month of age. Orphan lambs were fostered and all the lambs were weighed monthly until they were one year of age. They were weighed at weaning at about 3-4 months of age.

The entire flock was dipped once a month to control ticks and other ectoparasites. Hoof trimming was done regularly and more critically during the rainy seasons. Foot bathing was done before the rains. Other sickness was handled as condition the dictated. Sick animals were isolated during any treatment period.

3.1.2.4 Experimental design: Helminth and tick infections/infestations (Ol'Magogo)

Data were collected from two groups of weaners. The first group of (101 weaners) was monitored from May 1993 to November 1993 and the second group

from December 1993 to June 1994. Recording of TC, FEC and PCV was done at monthly intervals. TC was done on the entire body with emphasis on predilection sites (i.e ears, face, belly, hooves and tail regions). All animals were also weighed and sampled for PCV and FEC before the start of the study. Only standard size (4.5-8.0 mm) ticks were counted at the end of each month. All animals were drenched alternatively (to avoid drug resistance) with levamisole and albendazole and dipped with triatix (Amitraz) to control ticks after the end of each sample collection period. Fifteen monthly samplings were carried out on the Ol'Magogo flock. Procedures for TC, PCV and FEC sampling were similar to that adopted for tick infestations at Nguuni farm and GI helminth studies at Diani Estate.

3.2 Diagnostic facilities

Identification of common/prevalent ecto- and endoparasites in the Diani, Nguuni and Ol'Magogo flocks was accomplished using KARI's Regional Research Centre at Mtwapa, ILRI's field laboratory at Diani-Mombasa, ILRI's Tick Unit in Nairobi and the Department of Animal Health Egerton University.

3.2.1 Tick identification

Samples of standard ticks were collected randomly from the predilection sites of representative genotype and sex groups and then stored in well labelled sample bottles (3"x 1") containing 70 % alcohol or 5 % formalin solution. These ticks were later identified by using the dichotomous key as described by Hoogstraal (1956) and Mattheysee *et al.* (1978). Briefly, ticks were mounted under a dissection microscope with magnification of X 40. The presence and shape of the following features were observed :- eyes, ornate and inornate, festoons, punctations, anal groove, anal plates, palps and capitula. The host specificity, predilection sites and natural vegetation in the farm were used in final classification of ticks.

3.2.2 Estimation of anaemia by packed red cell volume

Blood was collected in two heparinized capillary tubes (75 x 1.5 mm) for each animal following prick puncture of the peripheral ear vein using sterile needles. Each capillary was filled 3/4 of its length after which one end of the tube was sealed with cristaseal. The filled tubes were then placed in the cardboard holders ensuring easy identification of samples from each animal. The whole blood in heparinized capillary tubes were centrifuged at 12,000 rpm for 5 minutes using a micro-haematocrit centrifuge. After centrifugation, PVC was determined using a Hawksley

micro-haematocrit reader and was recorded as percentage of packed red blood cells to total volume of the whole blood.

3.2.3 Detection of trypanosomes and cowdriosis

The dark background/phase contrast buffy coat technique (Murray *et al.*, 1977) was used to detect and identify trypanosomes, at the Nguuni and Diani farms since they were tsetse infested areas. After centrifugation of the haematocrit capillary tube, it was cut 1 mm below the buffy coat/plasma interface (to include the top layer of red cells) and 1 mm above (to include plasma). These were then expressed onto a clean slide, mixed and covered with 22 x 22 mm glass coverslip. The preparation was examined microscopically for trypanosomes by phase contrast or dark illumination using a X 40 magnification. Trypanosome species were identified by their size and motility characteristics. Further identification was done by use of Giesma stain for morphological conformation of the species under oil immersion X 100 magnification.

Trypanosoma congolese and *Trypanosoma vivax* were detected in fifteen animals at Nguuni using the dark buffy coat contrast technique, but there was no observable clinical symptoms of trypanosomiasis. The autopsy examinations of 9 out of 11 dead yearlings at Nguuni at the end of second tick exposure period and within the third exposure phase had typical and confirmatory symptoms of "heartwater"

(cowdriosis). Further staining confirmed presence of *Cowdria ruminantium* on impression smears of aorta vessel and brain tissue.

3.2.4 Faecal egg count

A two consecutive day faecal sampling protocol was used at Diani, while single day sampling was done at both Nguuni and Ol'Magogo. Faecal samples were collected from the rectum of animals using polythene bags. The samples were then stored in a cool box at 4^0C and analyzed within two days after sampling in all study areas.

Samples were analyzed by the modified McMaster technique as described by Hansen and Perry (1994). Briefly, 3 gms of faeces were crushed through a sieve into a beaker along with 42 ml of tap water then homogenized and poured through a tea sieve strainer collecting the filtrate. 15 mls were then transferred to a flat bottomed centrifuge tube and spun at 3,000 rpm for 5 minutes. The supernatant was discarded and the sediment resuspended in saline. Sufficient suspension was then transferred onto McMaster slide chambers and examined using a x25 objective of a stereo microscope. The total eggs counted in both chambers were multiplied by 50 to estimate the number of eggs per gram. The common worm eggs were strongyles in both agro-ecological zones

3.2.5 Faecal egg culture

To identify the specific species of nematodes, faecal material bulked by genotype was cultured. The faecal material was broken up into small pieces by use of a depressor, then mixed with sand and transferred into jars and stored under room temperature for 14-21 days. Water was added regularly at intervals of 1-2 days. The harvesting/isolation of infective larvae (L_3) was done by simple Baechmann technique (Hansen and Perry, 1994). The material was wrapped in cheese cloth and then placed overnight in a wine jar containing warm water. The larvae moved out of the faeces and ultimately collected by gravitational force into the bottom of the jar. These were collected using a pasteur pipette. Identification of larvae was by morphology of larval stage three (L_3), i.e. body length, prolongation of sheath beyond the tail and retractile bodies.

3.3 Data editing

Initial analyses were carried out using SAS (SAS, 1987) to edit the data for subsequent analyses. The 1993 lamb crop from Diani Estate was used to study resistance of sheep to GI nematodes infections at Diani and tick infestations at Nguuni farm in Mombasa. A total of 380, 272, 213 and 169 records were analyzed at birth, 3, 8 and 13 months of age, respectively, during GI nematode challenge. At

Nguuni, a total of 160, 151 and 150 records were analyzed during the three periods of tick infestations, respectively. At Ol'Magogo 101 and 108 records from 1992 and 1993 lamb crops respectively, were analyzed for GI nematode infections and tick infestations.

Due to skewed dispersion of FEC and TC, for purpose of analyses they were transformed using logarithm to base 10 to normalize distributions, i.e.

$$LFEC = \log_{10} (FEC + 25)$$

and

$$LTC = \log_{10} (TC + 10),$$

3.4 Classification of effects

The sire breeds were D and R. The dam genotypes were D, R and 50 % R 50 % D (F_1). The lamb genotypes generated from the diallel crossing of the two sire breeds with the three dam genotypes were:- D; R; 75 % D 25 % R; 50 % D 50 % R; 50 % R 50 % D and 75 % R 25 % D (in the crosses, the first breed represents the breed of sire). The age of the dam consisted of the second through sixth years which were coded 1 to 5. The sixth and greater ages were combined and coded as dam age 6. Sex of lamb was coded as female = 1 and male = 2. Type of birth was

coded 1 = single birth and 2 = multiple birth. The reasons for exit for those lambs that never reached weaning (3 months), 8 months and 13 months of age were coded as (i.e after post mortem) 01 = died due to helminthiasis; 02 = died from pneumonia; 03 = died from other diseases. A total of 211 lambs (46 % of those born) died before attaining the age of 13 months of age due to various reasons. At Diani, lambs that survived to weaning of 3 months of age (SRATE3) were coded "1," while those not present were coded "0". Post weaning survival rate (i.e between 3-8 months) (SRATE8) were classified as "1" if the lamb was sampled for FEC and PCV at 8 months and "0" if the lamb was not sampled at 8 months. The annual survival rate (0-13 months) (SRATE13) was also calculated. If the lamb was sampled at 13 months of age, it was coded "1" if not it was coded "0". At Ol'Magago-Naivasha, the age of the dam, the sex of lamb and type of birth were classified as above. Because of the purebred nature of the flock, the genotypes of lamb were D and R.

3.5 Data analyses

Fixed effect least squares analyses of variance were used to establish appropriate statistical models by first fitting all main effects and their first-order interactions. All non-significant ($P>0.05$) interactions were removed from the model used in the final analyses.

Table 3.1: Number of records analyzed by trait[a] and data source.

Data source	performance traits				resistance traits			
	n	Live weight	n	Survival rate	n	FEC	PCV	TC
Diani								
	380	BWT						
	374	WWT3	380	SRATE3	347	WFEC3	WPCV3	
	213	WT8	347	SRATE8	213	FEC8	PCV8	
	169	WT13	380	SRATE13	169	FEC13	PCV13	
Nguuni								
	160	WT1				160	PCV1	TC1
	151	WT2				151	PCV2	TC2
	150	WT3				150	PCV3	TC3
Ol'Magogo								
	101	WT12			101	FEC12	PCV12	TC12
	108	AVWT12			108	FEC12	PCV12	TC12

[a] BWT, birth weight; WWT3, 3 months weaning weight; WT8 and WT13, average weights at 8 and 13 months; WT1, WT2 and WT3, weights at periods 1, 2 and 3; AVWT12 (92) and AVWT12 (93), average weights in 1992 and 1993 ; SRATE3, SRATE8 and SRATE13, survival rate at 3, 8 and 13 months; WFEC3, FEC8 and FEC13, faecal egg count at 3, 8 and 13 months; WPCV3, PCV8, PCV13, packed cell volume at 3, 8 and 13 months; PCV1, PCV2 and PCV3, packed cell volume at periods 1, 2 and 3; TC1, TC2 and TC3 , tick counts at pperiods 1, 2 and 3; FEC12 (92) and FEC12 (93), 12 months faecal egg count in 1992 and 1993; PCV12 (92) and PCV12(93), 12 months packed cell volume in 1992 and 1993; TC12 (92) and TC12 (93), 12 months tick counts in 1992 and 1993.

3.5.1 Analyses of performance traits

Analyses were done using Model 3 of Harvey's (1990) least squares and maximum likelihood computer program. These traits included (**Table 3.1**):- BWT, WWT3, WT8, WT13, SRATE3, SRATE8 and SRATE13 (Diani study); WT1, WT2 and WT3 (Nguuni study); and AVWT12 (92) and AVWT12(93) (Ol'Magogo study).

The following mixed model was used for Diani study, in subsquent analyses the model was modified for Nguuni and Ol'Magogo studies:

$$Y_{ijklmno} = u + B_i + R_j + S_k + Y_l + W_m + (BR)_{ij} + N_{in} + b\,(X_1-X_2) + e_{ijklmno}.$$

Where,

Y_{ijklmn} is the observation on the o^{th} lamb born to i^{th} sire breed and i^{th} dam genotype of k^{th} age of l^{th} sex and of m^{th} type of birth.

u is the underlying population constant common to all records.

B_i is the effect of the i^{th} sire breed.

R_j is the effect of the j^{th} dam genotype.

S_k is the effect of the k^{th} dam age

Y_l is the effect of the l^{th} sex of the lamb

W_m is the effect of the m^{th} type of birth (only fitted for BWT)

N_{in} is the effect of the n^{th} sire nested within i^{th} sire breed.

$(BR)_{ij}$ is the effect of the interaction between i^{th} sire breed and j^{th} dam genotype.

b is the partial regression of day of birth on average lambing days

X_1 is the actual day of birth/ birth date

X_2 is the overall average flock lambing days

$e_{ijklmno}$ is the random residual, assumed to be normally distributed with mean 0, and variance δ^2_e

In the analysis of BWT at Diani, because of a spread lambing period of 6 weeks, birth date was fitted as a linear covariate. In subsequent analyses, day of birth/ birth date was subsituted for by lamb age as a linear covariate. Non of the environmental factors considered in this study significantly ($P>0.05$) influenced survival rate, thus they were removed in the final model. The main effects fitted for Nguuni data were:- Sire breed, dam breed, sire breed x dam breed interactions, sex of the lamb and dam age. To analyse for AVWT (both groups) at Ol'Magogo the effects of the sire breed and dam genotype and their interaction were substituted by the effect of the lamb breed (genotype). Other main effects fitted were:- birth-type, age of the dam and the sex of the lamb. Sires were nested within sire breed as a random effect for Diani and Nguuni studies.

3.5.2 Analyses of resistance traits

The earlier model described for live weight analyses was fitted for these traits (WFEC3, FEC8, FEC13 (and their transformations), WPCV3, PCV8 and PCV13) at 3, 8 and 13 months of age (Diani study); PCV1, PCV2, PCV3, TC1, TC2 and TC3 (Nguuni study); and FEC12 (92), FEC12 (93), PCV12 (92), PCV12 (93) TC12 (92) and TC12 (93) (Ol'Magogo study).

To determine the significance of specific class differences, linear contrasts of least squares means were computed using a fixed effect model. This was done by removing the random effect in the above mixed model (i.e sire nested within sire breed, N_{in}).

3.5.3 Estimation of genetic and phenotypic parameters

3.5.3.1 Heritabilities and correlations

Paternal half sib procedure (Harvey, 1990) was used to estimate heritabilities and phenotypic correlations for performance and resistance traits from Diani and Nguuni data, the above mixed model was fitted. Heritability estimates for these traits from Ol'Magogo data could not be derived because of a negative genetic variance. This was due to limited number of sires and progeny per sire.

A fixed model 1 of Harvey (1990) was fitted to estimate correlations between infestation periods for Nguuni data. The same model was used to derive correlations estimates between predelation sites and total body counts and linear contrasts. The specific number of ticks per predilection site per period were considered as a specific trait. There were a total of six predilection sites (traits) per period. These included:- Ears, Head, Body, Scrotum/udder, Anal and Total count.

3.5.3.2 Repeatabilities

Repeatabilities were estimated as within period correlations in monitor group data only (Nguuni flock) using Model 2 of Harvey (1990) fitting within period sampling intervals (**section 3.1.1.2.**) as a linear covariable. The following model was fitted:

$$Y_{ij} = u + A_i + b\ (N_1-N_2) + e_{ij}$$

Where

Y_{ij} is the observation of the j^{th} measurement on i^{th} animal.

u is the underlying population constant common to all records.

A_i is the effect of i^{th} animal

b is the partial regression of count on sampling interval

N_1 is the actual sampling interval

N_2 is the overall duration of a period of sampling

e_{ij} is the random residual, assumed to be normally distributed with mean 0, and variance δ^2_e

4. RESULTS

4.1 Mean and variances

4.1.1. Diani Estate

Tables 4.1, 4.2, 4.3, 4.4 and **4.5** represents the descriptive statistics and levels of significance of the main effects fitted for resistance and performance traits during GI nematode infections at Diani Estate between birth and 13 months of age. While **Figure 4.1** shows the general patterns and trends in GI nematode infections in the monitor group of about 50 lambs that were weekly sampled. The mean(± RSD) BWT was 2.25 ± 0.50 kg. Lambs attained mean weights of 12.0 ± 2.2 kg, 12.8 ± 1.7 kg and 15.5 ± 2.0 kg at 3 (96 ± 6.1 days), 8 (237 ± 8.7 days) and 13 (396 ± 8.7 days) months of age, respectively. Mean PCV ranged from 29.0 ± 5.5 % at 3 months to 24.9 ± 2.4 % at 13 months. Logarithm transformations of FEC was effective in reducing the rather high CV for FEC at different ages. The CV for WFEC3, FEC8 and FEC13 were reduced to 16.2, 6.3 and 13.6 %, respectively, after transformation.

Time lapse for FEC to reach the threshold levels of 1,500-2,000 epg (**Figure 4.1**) was influenced mainly by seasonal fluctuations in rainfall. High FEC was

recorded during and immediately after the rainy season (the threshold was attained in about 5-6 week interval).

The time lapse was prolonged during the dry spells (threshold was attained in 13-14 weeks interval). The cultured faeces from individual sampling times revealed that 66 % of all infective larvae were of *Haemonchus contortus*, 30 % *Trichostongylus spp* and 4 % *Oesophagostomum spp.* with negligible variations between sampling. During GI nematode infections in young lambs (1-5 months of age) there was the expected inverse relationship between PCV and FEC.

At Diani survival rate from birth to weaning (SRATE3) was high (91 %) but post-weaning survival from weaning to 8 months (SRATE8) was much lower (60 %) leading to an overall survival rate from birth to 13 months (SRATE13) of 44 %.

Table 4.1: Least squares means for birth weight (kg) for the Diani lamb crop of 1993

Effect	No.	LSM	SE
SIRE_BRD			
Dorper	188	2.35	0.11
Red Maasai	192	2.16	0.12
DAM_BRD			
Dorper	116	2.25	0.12
F1 (RD)	190	2.26	0.12
Red Maasai	74	2.24	0.14
SIRE_BRDxDAM_BRD			
D	57	2.38	0.12
D x RD	93	2.35	0.12
D X R	38	2.31	0.15
R X D	59	2.14	0.12
R X RD	97	2.18	0.11
R	36	2.17	0.15
SEX			
Female	186	2.18	0.12
Male	194	2.32	0.12
DAM_AGE			
2	38	1.92	0.14
3	105	2.18	0.12
4	81	2.47	0.13
5+	156	2.46	0.12
TYPE_ BIRTH			
Single	372	2.60	0.08
Twins	8	1.91	0.20
REG.BIRTHDT		0.01	0.003
OVERALL MEAN	380	2.25	
RSD		0.50	
CV (%)		21.7	
ANOVA[a]			
SIRE_BRD		**	
SIRE/SIRE_BRD		ns	
DAM_BRD		ns	
SIRE_BRDxDAM_BRD		ns	
SEX		**	
DAM_AGE		***	
TYPE_BIRTH		***	
BIRTHDATE		***	

*ANOVA[a], analysis of variance; Reg. Birthdat, Regression on birthdate; CV, coefficient of variation; RSD, Residual standard deviation; ns, non significant; SE, standard error; *=(P<0.05); **=(P<0.01); ***=(P<0.001)*

Table 4.2: Least squares means for weaning weight(WT,kg), weaning packed cell volume (PCV,%), weaning faecal egg count (FEC, epg), logarithm transformed FEC(LFEC) for the 1993 lamb crop at Diani Estate (Average age 94±6.6d)

		WT		PCV		FEC		LFEC	
Effect	No.	LSM	SE	LSM	SE	LSM	SE	LSM	SE
SIRE_BRD									
Dorper	168	11.9	0.3	28.1	0.6	2885	320	2.34	10
R.Maasai	179	11.7	0.3	30.1	0.6	2493	316	2.56	10
DAM_BRD									
Dorper	104	11.5	0.3	27.2	0.6	3041	369	2.34	0.12
F_1 (RD)	178	11.9	0.3	28.7	0.5	2472	290	2.59	0.09
R.Maasai	65	12.0	0.4	31.3	1.0	2553	632	2.42	0.21
SIRE_BRD x DAM_BRD									
D	50	11.5	0.4	25.5	0.8	3364	516	2.29	0.17
DxRD	84	11.9	0.3	28.4	0.7	2652	404	2.61	0.13
DxR	34	12.3	0.6	30.3	1.3	2639	760	2.13	0.25
RxD	54	11.5	0.4	29.0	0.8	2718	496	2.38	0.16
RxRD	94	11.9	0.3	29.0	0.6	2293	381	2.58	0.12
R	31	11.8	0.6	32.3	1.3	2468	780	2.72	0.26
SEX									
Female	169	11.7	0.3	29.6	0.5	2462	308	2.52	0.10
Male	178	11.9	0.3	28.6	0.5	2917	310	2.39	0.10
DAM_AGE									
2	35	10.6	0.4	28.7	1.0	2790	635	2.32	0.21
3	93	10.7	0.3	27.2	0.7	2411	450	2.44	0.15
4	76	13.1	0.3	30.6	0.8	2690	468	2.58	0.15
5+	82	12.6	0.3	29.4	0.8	2925	470	2.46	0.15
6+	61	12.1	0.4	29.6	0.8	2629	515	2.45	0.17
REG. AGE		0.11	0.02	0.02	0.05	269	30.7	0.14	0.01
MEAN	347	11.8		29.1		2689		2.45	
RSD		2.2		5.4		3465		1.14	
CV (%)		18.9		18.6		128.9		46.5	
ANOVA[a]									
SIRE_BRD		ns		*		ns		ns	
SIRE/SIRE_BRD		**		ns		ns		ns	
DAM_BRD		ns		**		ns		ns	
SIRE_BRDxDAM_BRD		ns		ns		ns		ns	
SEX		ns		ns		ns		ns	
DAM_AGE		***		*		ns		ns	
LAMB AGE		***		ns		***		***	

ANOVA, analysis of variance; Reg. age, Regression on lamb age; CV, coefficient of variation; RSD, Residual standard deviation; *ns, non significant; SE, standard error; *=(P<0.05); **=(P<0.01); ***=(P<0.001)*

Table 4.3: Least squares means for average live weight (WT, kg), average packed cell volume (PCV, %), average faecal egg count (FEC, epg), average logarithm transformed FEC (LFEC) for the 1993 lamb crop at Diani Estate, at 8 months of age (237±9d)

		WT		PCV		FEC		LFEC	
Effect	No.	LSM	SE	LSM	SE	LSM	SE	LSM	SE
SIRE-BRD									
Dorper	74	13.0	0.3	22.7	0.5	1933	127	3.26	0.03
R.Maasai	139	12.6	0.3	24.9	0.4	1642	102	3.17	0.03
DAM-BRD									
Dorper	57	12.5	0.4	23.4	0.6	2028	152	3.27	0.04
F_1 (RD)	111	12.9	0.3	23.8	0.4	1760	106	3.20	0.03
R.Maasai	45	13.0	0.5	24.2	0.8	1573	204	3.17	0.05
SIRE_BRD x DAM_BRD									
D	13	12.6	0.6	22.2	0.9	2293	250	3.35	0.06
DxRD	40	13.0	0.4	22.2	0.6	1942	154	3.26	0.04
DxR	21	13.4	0.6	23.9	0.9	1562	242	3.17	0.06
RxD	44	12.5	0.3	24.7	0.5	1762	145	3.19	0.04
RxRD	71	12.7	0.3	25.3	0.4	1578	112	3.15	0.03
R	24	12.5	0.6	24.6	0.9	1585	248	3.16	0.06
SEX									
Female	112	12.4	0.3	24.1	0.4	1773	105	3.21	0.03
Male	101	13.1	0.3	23.5	0.4	1802	109	3.22	0.03
DAM_AGE									
2	18	12.5	0.5	25.2	0.8	1812	222	3.21	0.06
3	61	11.6	0.4	22.8	0.6	1895	154	3.25	0.04
4	53	13.7	0.3	24.1	0.6	1816	146	3.24	0.04
5+	81	13.3	0.3	23.2	0.5	1625	132	3.16	0.03
REG.AGE	213	0.06	0.02	0.08	0.03	-2.88	7.2	-0.002	0.002
MEAN	213	12.8		23.8		1787		3.21	
RSD		1.7		3.1		812		0.2	
CV (%)		13.4		13.1		45.4		6.3	
ANOVA[a]									
SIRE_BRD		ns		**		ns		*	
SIRE/SIRE_BRD		*		ns		ns		ns	
DAM_BRD		ns		ns		ns		ns	
S_BRDxD_BRD		ns		ns		ns		ns	
SEX		**		ns		ns		ns	
DAM_AGE		***		ns		ns		ns	
LAMB_AGE		***		**		ns		ns	

*ANOVA, analysis of variance; Reg. age, Regression on age; CV, coefficient of variation; RSD, Residual standard deviation; ns, non significant; SE, standard error; *=(P<0.05); **=(P<0.01); ***=(P<0.001)*

Table 4.4: Least squares means for average live weight(WT, kg), average packed cell volume (PCV, %), average faecal egg count(FEC epg), average logarithm transformed LFEC (LFEC) for the 1993 lamb crop at Diani Estate, at 13 months of age (396±9d).

		WT		PCV		FEC		LFEC	
Effect	No.	LSM	SE	LSM	SE	LSM	SE	LSM	SE
SIRE_BRD									
Dorper	52	15.6	0.5	24.2	0.5	2704	220	3.41	0.08
R.Maasai	117	15.3	0.4	25.5	0.3	2211	156	3.26	0.06
DAM_BRD									
Dorper	40	15.0	0.5	24.0	0.6	2614	272	3.36	0.10
F_1(RD)	92	15.5	0.4	24.1	0.4	2229	171	3.27	0.06
R.	37	15.9	0.6	26.4	0.7	2531	348	3.37	0.13
SIRE_BRD X DAM_BRD									
D	7	14.9	0.9	23.0	1.0	2861	477	3.47	0.18
DxRD	28	15.5	0.5	23.6	0.5	2387	262	3.35	0.10
DxR	17	16.4	0.8	26.1	0.9	2865	411	3.39	0.15
RxD	33	15.0	0.5	25.0	0.5	2366	242	3.25	0.09
RxRD	64	15.6	0.3	24.6	0.4	2071	168	3.19	0.06
R	20	15.3	0.8	26.8	0.8	2197	404	3.35	0.15
DAM -AGE									
2	15	15.3	0.7	25.8	0.8	2622	371	3.47	0.14
3	50	14.3	0.5	23.4	0.6	2656	265	3.36	0.10
4	40	15.8	0.5	25.2	0.5	2174	241	3.25	0.09
5+	64	16.5	0.4	25.0	0.5	2380	222	3.25	0.08
REG.AGE	169	0.05	0.02	0.04	0.03	-1.70	11.8	0.01	0.01
MEAN	169	15.5		24.9		2458		3.3	
RSD		2.0		2.4		1176		0.5	
CV(%)		12.8		9.8		48		13.6	
ANOVA[a]									
SIRE_BRD		ns		*		ns		ns	
SIRE/SIRE_BRD		*		ns		ns		ns	
DAM_BRD		ns		*		ns		ns	
S_BRDxD_BRD		ns		ns		ns		ns	
DAM_AGE		**		ns		ns		ns	
YEARLING AGE		*		ns		ns		ns	

*ANOVA, analysis of variance; Reg. Birthdat, Regression on birthdate; CV, coefficient of variation; RSD, Residual standard deviation; ns, non significant; SE, standard error; *=(P<0.05); **=(P<0.01); ***=(P<0.001)*

Table 4.5: Least squares means for survival rate (SRATE) under gastrointestinal helminth challenge in the 1993 lamb crop at Diani Estate.

	SRATE 3 (0-3 MONTHS)			SRATE 8 (3-8 MONTHS)			SRATE 13 (0-13 MONTHS)		
Effect	No.	LSM	SE	No.	LSM	SE	No.	LSM	SE
SIRE_BRD									
Dorper	188	0.90	0.02	169	0.45	0.05	188	0.29	0.04
R.Maasai	192	0.92	0.02	178	0.76	0.05	192	0.59	0.04
DAM_BRD									
Dorper	116	0.92	0.03	107	0.52	0.05	116	0.34	0.04
F_1(RD)	190	0.92	0.02	175	0.62	0.04	190	0.48	0.04
R.Maasai	74	0.88	0.03	65	0.67	0.06	74	0.49	0.06
S_BRDxD_BRD									
D	57	0.90	0.04	51	0.27	0.07	57	0.12	0.06
DX DR	93	0.91	0.03	84	0.47	0.06	93	0.31	0.05
DxR	38	0.89	0.05	34	0.61	0.09	38	0.43	0.08
RxD	59	0.95	0.04	56	0.78	0.07	59	0.56	0.06
RxDR	97	0.94	0.03	91	0.77	0.05	97	0.65	0.05
R	36	0.86	0.05	31	0.74	0.09	36	0.55	0.08
MEAN	380	0.91		347	0.60		380	0.44	
RSD		0.41			0.30			0.46	
CV (%)		45.1			0.50			105	
ANOVA[a]									
S_BRD		ns			***			***	
S/S_BRD		ns			*			ns	
D_BRD		ns			ns			*	
S_BRDxD_BRD		ns			ns			ns	

*ANOVA[a], analysis of variance; CV, coefficient of variation; RSD, Residual standard deviation; ns, non significant; ±SE, standard error; *=(P<0.05); **=(P<0.01); ***=(P<0.001)*

4.1.2 Nguuni farm

Tables 4.6, 4.7 and **4.8**. presents the descriptive statistics and levels of significance for main effects fitted for performance and resistance traits measured on sheep at the end of each tick infestation period. The pattern of tick infestation (tick counts) and associated trends in live weight and PCV over the same period in monitor group (Dorper and Red Maasai) are shown in (**Figure 4.2**). There was no definitive seasonal influence on tick infestations but high TC was recorded in both monitor group and the whole flock in period 2 and 3. Time lapse to obtain maximum TC was approximately 16 day after every exposure across all periods (**Figure 4.2**) At the end of GI nematode challenge at Diani Estate the WT13 was 15.5 ± 2.0 kg (**Table 4.4**). At Nguuni farm, lambs were acclimatized for a period of 2 weeks before exposure to ticks (**section 3.1.1.2**) during which they were drenched and sprayed to control both G.I nematodes and ticks. The animals had gained 3.1 kg by the end of period 1 of tick challenge. Most of this gain was during the 2 weeks of acclimatization. Thereafter there was no marked increase in live weight (i.e 18.6 kg in period 1 vs 19.5 kg in periods 2 and 3). The PCV levels reduced from period 1 to period 3 (23.0 ± 3.2 to 19.0 ± 3.3), while TC increased from approximately 56 in period 1 to 286 in period 3. This indicated that the number of ticks on the animal had a direct effect on the PCV levels, as also was seen in the monitor sheep (**Figure 4.2, Plate 3 and 4**). This was expected since ticks are blood sucking parasites. The common ticks were

Rhipicephalus appendiculatus (45 %), *Rhipicephalus evertsi* (45 %) and *Ambylomma variegatum* (10 %).

Table 4.6: Least squares means (LSM) and standard errors (SE) at the end of the first infection for traits of sire breed, dam breed, sire breed x dam breed, dam age and sex for the flock at Nguuni.

		PCV1 (%)		TC1		LTC1		FEC1 (epg)		LFEC1		WT1 (kg)	
Effect	No.	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
SIRE_BRD													
D	48	23.5	0.6	59	5.5	1.8	0.04	174	41.6	2.0	0.11	18.6	0.5
R	112	22.5	0.4	52	3.9	1.8	0.03	187	26.5	2.0	0.07	18.1	0.3
DAM_BRD													
D	38	24.3	0.8	68	6.3	1.9	0.04	149	51.9	1.9	0.13	18.5	0.6
F_1 (RD)	86	22.7	0.5	50	4.1	1.8	0.03	209	29.8	2.1	0.08	19.1	0.4
R	36	22.7	0.8	49	8.1	1.7	0.05	183	69.6	2.1	0.18	17.4	0.5
SIRE_BRDxDAM_BRD													
D	6	25.3	1.4	75	11.0	1.9	0.07	159	92.3	2.0	0.24	18.5	1.1
DxRD	25	22.6	0.7	53	5.8	1.8	0.04	237	48.7	2.1	0.13	19.4	0.6
DR	17	22.7	1.2	48	9.5	1.7	0.07	125	79.8	1.9	0.21	17.9	0.7
RD	32	23.6	0.7	60	5.5	1.8	0.04	140	43.8	1.9	0.11	18.6	0.5
RxRD	61	22.8	0.5	47	3.8	1.7	0.03	112	30.3	2.0	0.08	18.8	0.4
R	19	21.6	1.2	50	9.7	1.8	0.07	241	77.4	2.3	0.20	16.9	0.7
DAM_AGE													
2	15	23.3	1.0	61	8.0	1.9	0.05	249	67.7	2.2	0.18	17.1	0.8
3	47	23.2	0.7	54	6.3	1.8	0.04	161	51.8	1.9	0.13	17.5	0.6
4	37	23.0	0.7	54	5.7	1.8	0.04	146	46.6	2.0	0.12	19.1	0.6
5	31	23.1	0.8	62	6.3	1.8	0.04	194	51.7	2.2	0.13	19.4	0.6
6+	30	22.7	0.8	46	6.3	1.7	0.04	153	51.8	2.0	0.13		
Mean	160	23.0		56		1.8		181		2.0		18.6	
RSD		3.2		25		0.2		217		0.6		2.5	
CV(%)		13.9		44		11.1		120		30.0		13.4	
ANOVA[b]													
SIRE_BRD		ns		ns		ns		ns		ns		ns	
SIRE/SIRE_BRD		ns		ns		*		ns		ns		ns	
DAM_BRD		ns		*		ns		ns		ns		ns	
S_BRDXD_BRD		ns		ns		ns		ns		ns		ns	
DAM-AGE		ns		ns		*		ns		ns		*	

RSD, Residual standard deviation; ANOVA, Analyses of variance; ns, non significant (p>0.1); p<0.05 p<0.01** p<0.001*** TC, Tick count, LTC, Transformed*

Table 4.7: Least squares meams(LSM) and standard errors (SE) at the end of the second infection period for sire breed, dam breed, sire breed*dam breed and sex for the flock at Nguuni.

Effect		PCV2 (%)		TC2		LTC2		FEC2 (epg)		LFEC2		WT2 (kg)	
	No.	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
SIRE_BRD													
D	46	20.3	0.7	295	17.8	2.5	0.04	360	117.0	2.1	0.12	19.6	0.7
R.Maasai	105	21.1	0.5	201	11.9	2.3	0.02	281	74.1	2.0	0.07	19.3	0.5
DAM_BRD													
Dorper	36	21.3	0.8	285	22.3	2.4	0.04	200	153.6	1.9	0.15	20.0	0.7
F_1 (RD)	83	20.8	0.5	256	13.2	2.4	0.03	352	86.4	2.1	0.09	20.3	0.5
R.Maasai	32	20.1	0.7	203	18.3	2.3	0.04	409	124.3	2.2	0.12	18.1	0.6
S_BRDxD_BRD													
D	6	20.6	1.5	335	40.7	2.5	0.09	130	279.9	1.7	0.28	20.2	1.3
DxRD	25	19.6	0.8	299	21.5	2.4	0.04	382	147.9	2.2	0.15	20.5	0.7
DR	15	20.8	1.0	252	26.9	2.4	0.05	566	184.6	2.5	0.18	18.3	0.8
RD	30	22.0	0.7	235	18.7	2.4	0.04	270	126.1	2.1	0.13	19.8	0.6
RxRD	58	22.1	0.5	213	13.3	2.3	0.03	321	89.6	2.0	0.09	20.1	0.4
R	17	19.4	0.9	155	24.6	2.2	0.05	252	165.6	1.9	0.16	18.0	0.8
SEX													
Female	79	20.6	0.5	253	13.6	2.4	0.03	248	89.2	2.1	0.09	19.0	0.5
Male	72	20.9	0.5	244	14.1	2.4	0.03	393	93.6	2.1	0.09	19.9	0.5
Mean	151	21.0		248		2.4		320		2.1		19.5	
RSD		3.4		95		0.2		671		0.7		2.6	
CV(%)		16.4		38		8.3		210		33.3		13.3	
ANOVA[b]													
SIRE_BRD		***		***		**		ns		ns		ns	
S/S_BRD		ns		ns		ns		ns		ns		ns	
DAMBRD		ns		**		**		ns		ns		***	
S_BRDxD_BRD		*		ns		ns		ns		*		***	
SEX		ns		ns		ns		ns		ns		ns	

RSD, Residual standard Deviation; ANOVA, Analyses of variance; ns, non significant ($p<0.1$;+$p<.1$) $p<0.005^{*}$ $p<0.01^{**}$ $p<0.001^{***}$ TC, Tick count, LTC, logarithm (TC+10) FEC, Faecal egg count; LFEC, logarithm (FEC+25); WT live body weight.

Table 4.8: Least squares means(LSM) and standard errors(SE) at the end of th third infection period for sire breed, dam breed, sire breedxdam breed, dam age and sex for the flock at Nguuni.

		PCV3		TC3		LTC3		FEC3		LFEC3		WT3 kg	
Effect	No.	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
SIRE_BRD													
D	44	18.6	0.7	298	17.8	2.5	0.03	292	070.6	2.2	0.12	19.8	0.7
R	106	19.1	0.4	272	12.0	2.4	0.02	181	050.8	2.0	0.08	19.3	0.6
DAM_BRD													
D	37	18.9	0.8	252	21.2	2.4	0.03	229	078.5	2.1	0.14	20.0	0.8
F_1 (RD)	81	17.6	0.5	261	12.9	2.4	0.02	243	052.7	2.0	0.09	19.7	0.6
R	32	20.1	1.1	341	29.4	2.5	0.05	238	105.7	2.2	0.20	19.0	1.0
SIRE_BRDxDAM_BRD													
D	6	19.6	1.4	270	37.4	2.4	0.06	298	136.5	2.2	0.25	20.7	1.3
DxRD	24	16.5	0.8	289	20.2	2.4	0.03	264	073.9	2.1	0.14	19.8	0.7
DR	15	19.7	1.3	335	34.2	2.5	0.06	315	125.0	2.4	0.23	18.0	1.2
RD	31	18.2	0.7	234	18.4	2.4	0.03	161	069.5	2.0	0.12	19.3	0.7
RxRD	58	18.7	0.5	234	12.8	2.4	0.02	223	048.3	1.9	0.09	19.6	0.5
R	17	20.4	1.3	348	33.6	2.5	0.05	161	127.1	1.9	0.23	19.0	1.3
SEX													
F	79	18.9	0.5	275	13.8	2.4	0.02	206	055.1	1.9	0.09	19.0	0.6
M	71	18.8	0.5	295	14.8	2.5	0.02	268	058.1	2.2	0.10	20.1	0.6
DAM_AGE													
2	15	18.4	1.1	317	27.7	2.5	0.05	271	099.8	2.2	0.18	18.5	0.9
3	42	17.3	0.8	225	22.2	2.4	0.04	180	081.7	1.9	0.15	18.1	0.8
4	34	19.7	0.8	297	20.1	2.5	0.03	238	075.1	2.2	0.14	20.1	0.7
5	29	18.8	0.8	302	22.1	2.5	0.04	401	081.4	2.4	0.15	20.5	0.8
6+	30	20.0	0.8	283	21.5	2.4	0.03	094	079.4	1.8	0.14	20.5	0.8
MEANS	150	19.0		286		2.5		237		2.1		19.5	
RSD		3.3		86		0.14		300		0.57		2.5	
CV (%)		17.4		30		5.6		127		27.1		12.8	
ANOVA[b]													
SIREBRD		ns		ns		ns		ns		*		ns	
SIRE/SIREBRD		ns		ns		ns		ns		ns		***	
DAMBRD		ns		*		ns		ns		ns		ns	
SEX		ns		ns		ns		ns		*		**	
DAM_AGE		ns		ns		ns		**		**		*	
S_BRDXD_RD		ns		ns		ns		ns		ns		ns	

R.S.D, Residual standard deviation; ANOVA, Analyses of variance; ns, non significant ($p<0.1$; $+p<.1$) $p<0.005^{*}$ $p<0.01^{**}$ $p<0.001^{***}$ TC, Tick count, LTC, logarithm (TC+10) FEC, Faecal egg count; LFEC , logarithm (FEC+25); WT live body weight

Plate 3 : Crossbred sheep in poor condition at the end of tick infestation.

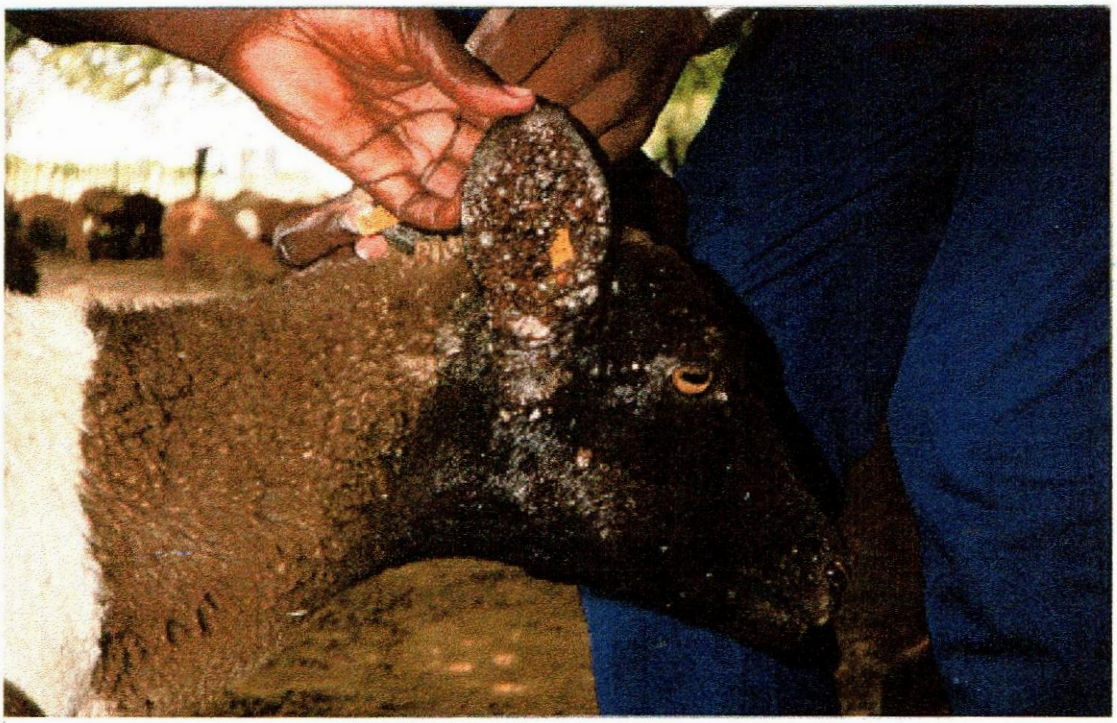
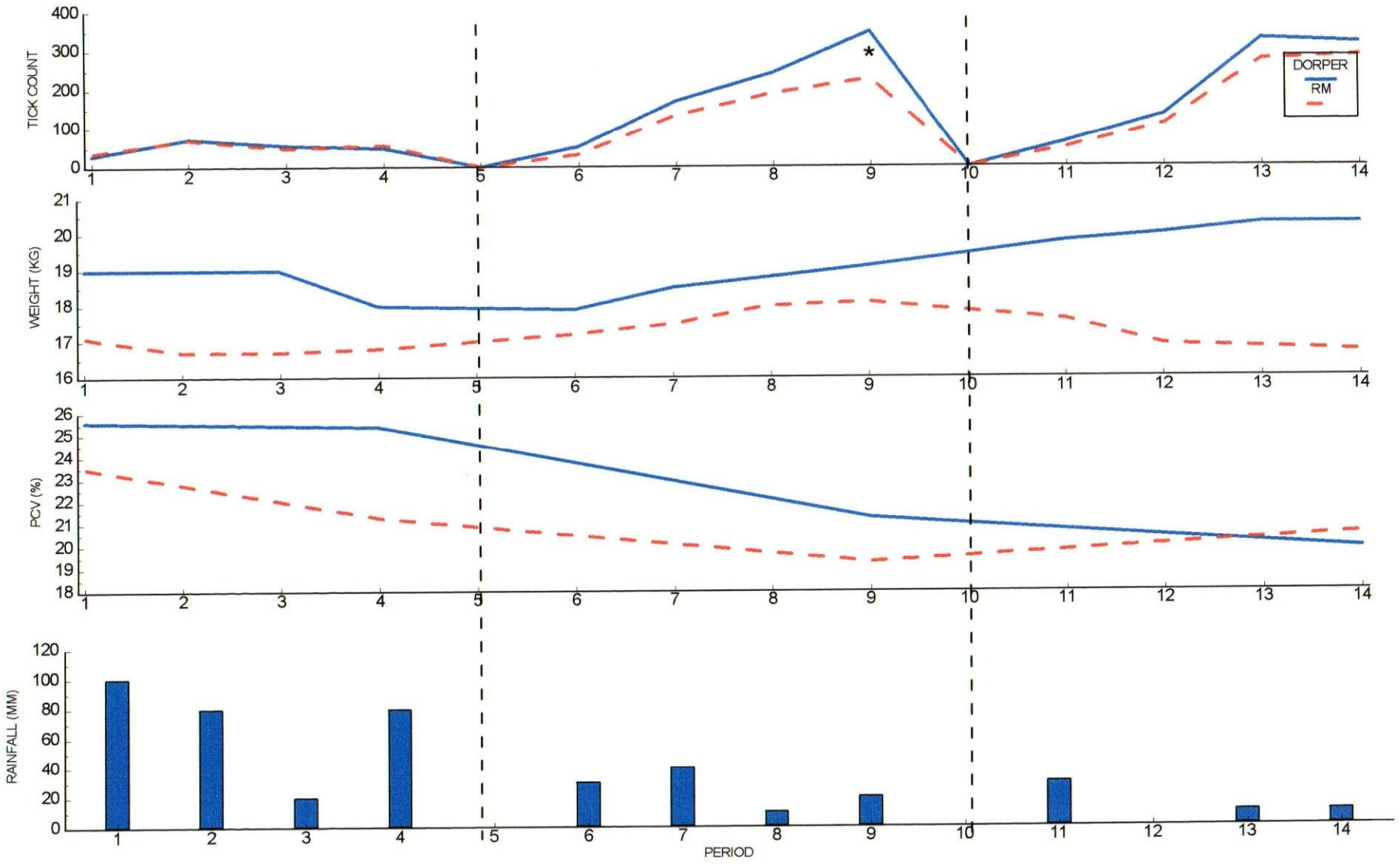


Plate 4 : Dorper sheep with heavy tick infestation in period 3

Figure 4.2

Monitor Group: Relationship between Tick count, weight and PCV



4.1.3 Ol'Magogo

Tables 4.11 and **4.12** presents descriptive statistics and levels of signifince for main effects during mixed model analyses for performance and resistance traits for 1992 and 1993 lamb crops, respectively. **Figures 4.3** (1992 lambs) and **4.4** (1993 lambs) shows graphical representation of the trends in the monthly measurements of live weight, PCV, FEC and TC by breed. Both FEC and TC were influenced by monthly rainfall fluctuations, high TC and FEC were recorded immediately after months with high rainfall. AVWT for the 1992 lamb crop was approximately 8 % greater than the AVWT for the 1993 lamb crop. PCV was higher in 1992 (28.7 %) than in 1993 (25.2 %) despite similar AFEC in the two years. The ATC was low in both years (3.7 and 5.7 in 1992 and 1993, respectively). The predominant ticks were *Rhipicephalus appendiculatus* (60 %), *Rhipicephalus evertsi* (30 %) and *Hyolomma truncutum* (10 %), while the cultured material from of monthly sampling revealed that 70 % of all infective larvae were of *Haemonchus contortus*, 20 % *Trichostongylus spp* and 10 % *Oesophagostomum spp.*

Table 4.11: Least squares means (LSM) and standard errors (SE) of average live weight (AWT), average packed cell volume (APCV), average faecal egg count (AFEC), average tick count (ATC), average logarithm transformed tick count (ALT) and average logarithm transformed faecal egg count (ALFEC) for breed, sex, and type of birth for the Naivasha'92 flock.

Effect		AWT (kg)		APCV (%)		ATC		ALTC		AFEC (epg)		ALFEC	
	No	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
BREED													
Dorper	37	27.2	0.9	28.0	0.3	4.2	0.4	1.15	0.01	1641	243	2.96	0.09
R.Maasai	64	22.8	1.1	29.3	0.3	3.2	0.3	1.12	0.01	753	217	2.74	0.08
SEX													
Female	47	22.1	1.0	28.1	0.3	4.7	0.4	1.16	0.01	1468	208	2.91	0.06
Male	54	28.0	0.9	29.3	0.3	2.7	0.3	1.10	0.01	925	193	2.79	0.08
TYB													
Single	65	26.6	0.9	28.3	0.3	3.8	0.3	1.14	0.01	1281	191	2.88	0.07
Twins	36	23.4	1.0	29.1	0.3	3.6	0.4	1.13	0.01	1112	221	2.82	0.08
Overall mean	101	25.0		28.7		3.7		1.13		1197		2.85	
RSD		5.8		1.8		2.4		0.07		1131		0.5	
CV%		16.4		5.6		60.0		6.4		84.5		8.0	
ANOVA[b]													
BREED		**		**		**		*		**		*	
SIRE:SIREBRD		**		***		ns		ns		ns		ns	
SEX		***		***		***		***		**		ns	
TYPEBRT		***		*		ns		ns		ns		ns	

RSD, Residual standard deviation; ANOVA, Analyses of variance; ns, non significant ($p>0.1$ $p<0.05^{*}$ $p<0.01^{**}$ $p<0.001^{***}$

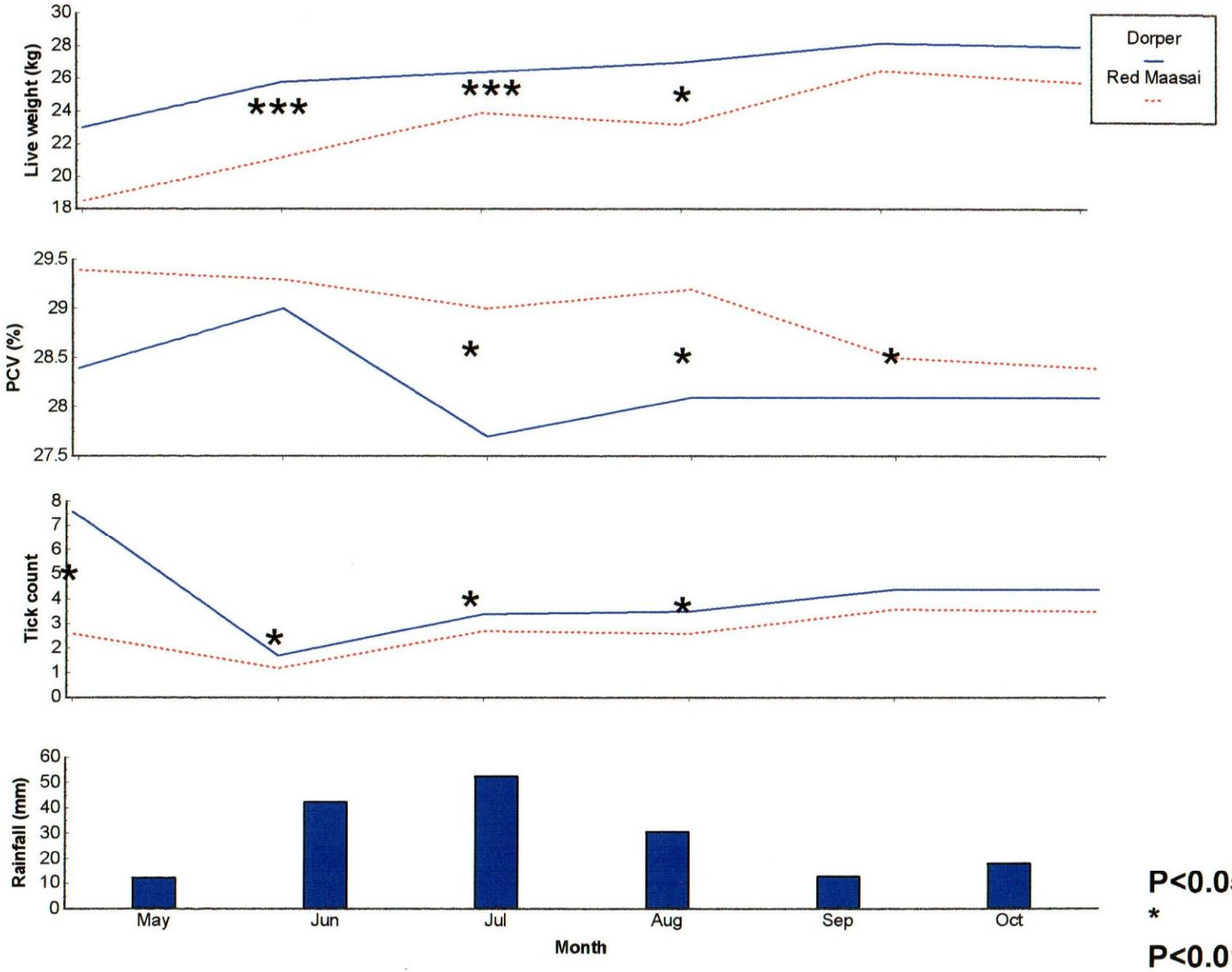
Table 4.12: Least squares means and standard errors (SE) of average live weight (AWT), average packed cell volume (APCV), average faecal egg count (AFEC), average tick count (ATC), average logarithm transformed tick count (ALTC) and average logarithm transformed faecal egg count (ALFEC) for breed and sex, for the Naivasha '93 flock.

Effect		AWT (kg)		APCV (%)		ATC		ALTC		AFEC (epg)		ALFEC	
	No.	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
BREED													
Dorper	51	24.1	0.6	24.7	0.3	6.6	0.4	1.21	0.01	1390	104	3.1	0.03
R.Maasai	57	22.3	0.6	25.7	0.3	4.7	0.4	1.16	0.01	818	103	2.9	0.03
SEX													
Female	57	20.2	0.6	25.0	0.2	6.7	0.3	1.21	0.01	1070	87	3.0	0.03
Male	51	26.1	0.6	25.3	0.3	4.7	0.4	1.16	0.01	1138	91	3.0	0.03
Mean	108	23.2		25.2		5.7		1.2		1104		3.0	
RSD		4.0		1.6		2.6		0.07		539		0.2	
CV%		17.2		6.4		45.6		5.8		48.8			
ANOVA[b]													
BREED		ns		*		**		**		**		***	
SIRE:BRD		ns		ns		ns		ns		ns		ns	
SEX		***		ns		***		ns		ns		ns	

RS.D, Residual standard deviation; ANOVA, Analyses of variance; ns, non significant ($p<0.1$; +$p<.1$) $p<0.005^{*}$ $p<0.01^{**}$ $p<0.001^{***}$

Figure 4.3

Naivasha weaners 1992



P<0.05 - *

P<0.01 - **

P<0.001 -

4.2 Environmental factors

The levels of significance of environmental effects for performance and resistance traits in the three study areas are shown in **Tables 4.1, 4.2, 4.3, 4.4, 4.7, 4.8, 4.9, 4.11** and **4.12**.

4.2.1. Effects of type of birth, sex, dam age and lamb age.

4.2.1.1. Performance traits

As expected, there was a significant ($P<0.001$) effect of type of birth on BWT in Diani lamb crop (**Table 4.1**). Single lambs were born 0.7 kg heavier (36 %) than twin lambs, although there were only four pairs of twins. At Ol'Magogo (**Tables 4.11** and **4.12**) type of birth was significant ($P<0.001$) for AVWT (92) but not for AVWT (93). In 1992, AVWT was 26.6 kg for single lambs and 23.4 kg for twin lambs. This represents a difference of 13 % of the overall mean.

Sex of the lamb significantly ($P<0.01$) influenced BWT and WT8 at Diani. Male lambs were 6 % heavier than female lambs at birth and at 8 months of age. Sex of lamb was not a significant ($P>0.05$) source of variation for WT3, WT13 and survival rate (SRATE3, SRATE8 and SRATE13). However, male lambs were consistently heavier than female lambs and had higher survival rates at all ages.

At Nguuni (**Tables 4.6, 4.7** and **4.8**), sex of the lambs was significant ($P<0.01$) for WT2 and WT3 but not for WT1. Male lambs were 5 % and 6 % heavier than female lambs at period 2 and 3, respectively, of tick challenge. At Ol'Magogo

(**Tables 4.11 and 4.12**), sex of the lamb significantly ($P<0.001$) influenced AVWT in both years (1992 and 1993) in favour of male lambs.

At Diani, dam age influenced lamb live weights at all ages but did not significantly influence survival rate, although lambs from mature ewes had higher survival rates at all ages. The weights increased gradually up to the fourth dam age group. This followed the expected pattern whereby lambs from young dams had the lowest weights. At Nguuni, age of the dam significantly influenced WT1 and WT3 but not WT2 in favour of older ewes. At Ol'Magogo (**Tables 4.11 and 4.12**), dam age was not a significant source of variation for AVWT in either year.

The birth date covariate fitted for BWT in the Diani study was significant ($P<0.01$). Lambs born one day later in the lambing season were 0.01 ± .003 kg heavier than those born earlier in the season. The effect of birth-date of lamb was significant ($P<0.01$) for WWT3 and WT8 but not for WT13. This indicated that the effect of lamb birth-date had diminished by the time the lambs had attained 13 months of age.

4.2.1.2 Resistance traits

Type of birth was only fitted for the Ol'Magogo study (**Tables 4.11 and 4.12**). It was significant for PCV in 1992 but not for other traits in either year. In

1992, twin lambs had higher ($P<0.05$) PCV than single lambs (29.1 vs 28.3 %, respectively).

At Diani, sex was not significant ($P>0.05$) for PCV and FEC at 3, 8 and 13 months. At Nguuni, sex of lamb was not significant for either TC or PCV at the three periods of tick challenge (**Tables 4.6, 4.7 and 4.8**). However, at Ol'Magogo sex of lamb was a significant source of variation for PCV, TC and FEC in 1992 and for TC in 1993 (**Tables 4.11 and 4.12**). The sex differences were small perhaps because of the limited data size and low GI nematode infections and tick infestations. Dam age was significant ($P<0.05$) at Diani (**Table 4.2**) for WPCV3 but not for the other resistance traits. Lambs from older dams had higher PCV at 3 months than those from young dams. At Diani, the lamb age covariate was significant ($P<0.01$) for WFEC3 and PCV8 but not for other traits. Lambs born one day earlier in the lambing season and hence older at sampling had a higher (269 ± 30.7 epg) FEC at 3 months and higher (0.08 ± .03 %) PCV at 8 months.

4.3 Genetic Factors

The levels of significance of genetic effects for performance and resistance traits in the three study sites are shown in **Tables 4.2, 4.3, 4.4, 4.6, 4.7, 4.8, 4.11 and 4.12**.

4.3.1. Effect of Sire breed

4.3.1.1 Performance Traits

Sire breed significantly ($P<0.05$) influenced BWT in favour of the D (**Table 4.1**). The lambs from D sires were 9 % heavier at birth than those from R sires. The breed of sire did not significantly influence the other live weight traits. However, the D-sired lambs were heavier at all ages in Diani (**Tables 4.2, 4.3, and 4.4**). Sire breed significantly ($P<0.001$) influenced SRATE8 and SRATE13 but not SRATE3. The R-sired lambs had superior (approximately 30 %) survival rates at both ages.

At Nguuni, sire breed was not a significant source of variation for weights at any period of tick challenge (**Tables 4.6, 4.7 and 4.8**). This is consistent with the sire effect on WT3, WT8 and WT13 at Diani indicating that the R- and D-sired lambs have similar live weights under both GI nematode and tick challenges so that survival rates become more important than live weights.

4.3.1.2 Resistance Traits

Sire breed significantly ($P<0.05$) influenced PCV at all ages in Diani but did not significantly influence FEC at any age. The R-sired lambs had higher PCV at all ages possibly because they had lower FEC. The superiority of the R-sired lambs ranged from 5 % to 10 % in PCV at all ages. This confirmed the fact that there exists

an inverse relationship between PCV and FEC and that R-sired lambs were more resistant to GI nematodes than the D-sired lambs.

At Nguuni (**Tables 4.6, 4.7** and **4.8**), the breed of sire only significantly influenced ($P<0.001$) PCV and TC at period 2 of tick challenge but not in the other periods. R-sired lambs had higher PCV than D-sired lambs (21.1 % vs 20.3 %). This could be because of higher TC in the D-sired lambs. In periods 1 and 3 of tick challenge, the R-sired lambs maintained superiority although the differences in both PCV and TC were less than 11 % of their respective means.

4.3.2 Effect of dam genotype

4.3.2.1 Performance Traits

Dam genotype did not significantly influence BWT at Diani (**Table 4.1**). However, lambs from F_1 dams were heavier at birth indicating a possible advantage due to maternal heterosis. Genotype of dam was not a significant ($P>0.1$) source of variation for the other weights at different ages at Diani. However, the advantage of lambs born from F_1 dams diminished in favour of those born from R dams. Dam genotype did not significantly influence SRATE3 and SRATE8 (**Table 4.5**). However, at 3 months, lambs from R dams had the lowest survival rate but at 8 months, the trend reversed indicating that resistance developed after 3 months of age.

At 13 months of age, dam genotype significantly ($P<0.05$) influenced survival rate. Lambs from R dams had higher survival rates than lambs from D dams (49 vs 34 %). This represented 34 % of the overall mean confirming large differences in SRATE13 between lambs from R and D dams.

At Nguuni, dam genotype only influenced ($P<0.001$) WT2. Lambs from R dams had lower weights than those from D and F_1 dams. The difference between lambs from R and D dams was only 10 % of the overall mean. At period 3, although not significant, lambs from R dams had gained approximately 1 kg while those from D dams had gained nothing. It is presumed that if tick challenge had been prolonged, then the lambs from R dams could possibly have had higher subsequent weights than those from D dams.

4.3.2.2 Resistance traits

There was a significant ($P<0.05$) effect of dam genotype on WPCV3 and PCV13 in favour of lambs from R dams but not on the other traits at all ages at Diani (**Tables 4.2, 4.3 and 4.4**). At 3 and 13 months of age, lambs from R dams had 16 % and 10 % higher PCV than those from D dams, respectively. Lambs from F_1 dams always had intermediate PCV and FEC values.

At Nguuni (**Tables 4.6, 4.7 and 4.8**), dam genotype significantly ($P<0.05$) influenced TC but not PCV at all periods of tick challenge. TC were consistently in

favour of the R in periods 1 and 2 but not in period 3. However, the PCV3 was higher in lambs from R dams. The TC in all periods for lambs from F_1 dams were always intermediate.

4.3.3 Effect of lamb genotype.

From the analyses of data from Diani and Nguuni, the sire breed x dam genotype sub class were estimates of lamb genotype performance. In the Ol'Magogo data the genotype of lamb was fitted as a main effect (**section 3.5**).

4.3.3.1 Performance traits

The sire breed by dam breed interaction was not significant ($P>0.05$) in the analyses of variance for BWT, WWT3, WT8 and WT13 and for survival rate at all ages (**Tables 4.1, 4.2, 4.3, 4.4 and 4.5**) (Diani study). However, several linear contrasts of specific class means were significant ($P<0.01$) for live weight traits and survival rates at all ages (**Table 4.9**). The comparisons of D + (D x RD) vs R + (R x RD) i.e contrast B in **Table 4.9** which estimated the difference between the mean of lambs with over 75 % genes of a particular breed resulted in small changes in live weights and only the effect on BWT was significant ($P<0.01$) (0.19 ± 0.1). It however resulted in large changes in SRATE8 (41 ± 6 %) and SRATE13 (40 ± 6 %) indicating an advantage for those lambs having over 75 % R genes.

An alternative comparison to the above is that between the lambs with 100 % genes (i.e a purebreed) of a particular breed. The contrast examining this (i.e contrast A in **Table 4.9**) showed no significant differences in live weights. For survival rate at 8 and 13 months, this contrast was highly significant ($P<0.001$) in favour of purebred R lambs. When the F_1 lambs were compared to pure breeds (contrast C in **Table 4.9**) only the effects on survival rate from 3-8 months and from birth to 13 months were significant, indicating a possible effect of individual heterosis.

Causes of mortality at Diani were diagnosed and confirmed by post mortem findings. The 177 mortalities of lambs recorded from weaning to 13 months of age in different breeds was clearly related to endo-parasites (36 %). During pre-weaning period 100 mortalities were recorded and 63 % of this was mainly due to the mis-mothering complex (i.e. stillbirth, born weak and starvation).

At Nguuni, the sire breed by dam breed interaction was only significant for WT2 but not for WT1 and WT3 (**Tables 4.6, 4.7** and **4.8**). No specific linear contrast for these traits were significant indicating that there were no marked differences in weights that can be attributed to differences in genetic composition (**Table 4.10**). At Ol'Magogo, AVWT12 for 1992 was significantly influenced by lamb genotype. D lambs were 4.4 kg (19%) heavier than R lambs. Lamb breed was not significant in the 1993 lamb crop, although D lambs were still heavier than the R lambs (24.1 vs 22.3 kg)

Table 4.9: Linear contrasts for live weight (kg) packed cell volume (PCV, %), faecal egg count (FEC, epg) and logarithm transformed FEC (LFEC) for the 1993, lamb crop at Diani Estate.

Linear contrast	Birth		3mo		8 mo		13 mo	
			LIVE WEIGHT					
	Diff.	SE	Diff.	SE	Diff.	SE	Diff.	SE
A	0.23	0.1	-0.14	0.6	0.57	0.8	0.03	1.1
B	0.19	0.1**	-0.09	0.4	0.36	0.4	-0.03	0.6
C	-0.06	0.1	0.18	0.4	0.09	0.4	0.68	0.6
			PCV					
A	N/M		-6.6	1.5***	-1.9	1.1	-3.1	1.3 *
B	N/M		-3.6	0.9***	-2.6	0.8 ***	-2.1	0.7***
C	N/M		1.0	0.9	0.6	0.7	0.5	0.7
			FEC					
A	N/M		1473	1191	654	356	673	604
B	N/M		889	681	518	196**	410	337
C	N/M		-441	684	-261	180	158	320
			LFEC					
A	N/M		-0.16	0.21	0.17	0.10	0.22	0.23
B	N/M		-0.10	0.12	0.15	0.05**	0.17	0.13
C	N/M		-0.14	0.12	0.08	0.05	-0.04	0.12
			SURVIVAL					
			0-3 mo		3-8 mo		0-13 mo	
A			-0.01	0.07	-0.49	0.10***	-0.44	0.10***
B			0.01	0.04	-0.41	0.06***	-0.40	0.06***
C			-0.01	0.04	0.20	0.07**	0.17	0.07*

A= D vs R
B= (D+DR) vs (R+ RD)
C=F1(DR+ RD) vs (R+D) = Heterosis
Diff.= difference in mean squares, SE= standard error;
N/M = not measured
(P<.05) *
(P<0.01) **
(P<0.001) ***

Table 4.10: Linear contrast for tick count(TC), logarithm transformed tick count LTC (log10 TC+10) packed cell volume (PCV), faecal egg count(FEC), logarithm transformed LFEC (FEC+25) and live weight(WT) in the three infection periods at Nguuni.

Trait	Period 1						Period 2						Period 3					
	A		B		C		A		B		C		A		B		C	
	Dif.	SE	Dif.	SE	Dif.	SE	Dif.	SE	Dif.	SE	Dif.	SE	Dif.	SE	Dif.	SE	Dif.	SE
WT	0.05	1.4	0.4	0.8	0.9	0.7	0.6	1.6	0.6	0.9	0.10	0.80	1.7	1.5	1.1	0.87	-0.26	0.8
PCV	4.6	1.7***	2.0	1.0	-.77	0.9	0.7	2.0	-0.72	1.1	2.0	1.0*	-.86	1.9	-1.4	1.0	-0.48	1.0
TC	24.5	13.9	14.4	7.7	-6.7	7.2	204	54.5***	141.9	30.0***	12.0	28.2	-55.5	48.8	0.81	2.0	23.7	25.2
Log_{10}TC	0.16	0.09	0.1	0.1	-0.06	0.05	0.4	0.1***	0.3	0.06***	0.05	0.05	-0.08	0.08	-0.00	0.04	0.04	0.04
FEC	-51.0	118.4	-11.5	65.5	-78.5	61.1	274.7	366.7	122.1	202.2	192.6	190.0	180.9	174.3	117.1	96.4	-44.2	90.2
Lg_{10}FEC	-0.12	0.31	-0.05	0.17	-0.27	0.16	0.12	0.35	0.13	0.20	0.45	0.18	0.32	0.33	0.23	0.18	0.00	0.17

A=D Minus R;
B=(D+RD) minus (R+RD);
C=F_1 (RD+DR) minus (R+D);
Dif.=difference in mean square;
SE=Standard error;
(P<0.05);*
*(P<0.01)**;*
*P<0.001)***;*

4.3.3.2 Resistance traits

At Diani, the sire breed by dam breed interaction was not significant ($P>0.05$) for any trait. Lambs with over 75 % R (i.e up to 100 % R included) had the highest PCV at all ages (**Table 4.6**) confirming superiority of the R breed over the D breed. This superiority was also reflected in the F_1 lambs. F_1 lambs had PCV values at weaning that were 4.1 ± 1.0 % higher ($P<0.01$) than the mean of purebred R and D.

At Nguuni, lamb genotype was only significant for PCV2, and there was no clear trend associated with percentage of R genes in the genotype (**Table 4.8**). TC2 was higher ($P<0.001$) in purebreed D and in lambs with greater than 75 % D (204 ± 54.3 and 141.9 ± 30.0 (**Table 4.10)** and as shown in **Figure 4.2**.

At Ol'Magogo, the genotype of lamb significantly ($P<0.05$) influenced all resistance traits in both years (i.e 1992 and 1993) with the R lambs having higher PCV and lower TC and FEC than D lambs.

4.4 Genetic and phenotypic parameters

4.4.1 Heritabilities

Paternal half sib heritability estimates for performance and resistance traits in Diani and Nguuni are shown in **Tables 4.13** and **4.14**, respectively. Estimates of heritability using animal and sire models for pooled data for 1991-1995 lamb crops are also included in **Table 4.13** for the purpose of comparison with more reliable estimates (because of their lower

standard errors). Heritability estimates of live weight increased with increasing age from 0.10 ± .10 for BWT to 0.42 ± .27 for WT13. The paternal half sib heritability estimates for pre-weaning SRATE was not estimable but increased to 0.21 ± .14 for SRATE from weaning to 8 months. The animal model analyses permitted the partitioning of the genetic variance into direct additive (h^2a) and maternal genetic (h^2m) components. For live weights h^2m ranged from 0.36 ± .04 at birth to 0.27 ± .04 at 8 months of age. The h^2a estimates was not significant at weaning (0.04 ± .04) but increased to 0.13 ± .06 at 8 months of age. Animal model heritability estimates for SRATE showed that pre-weaning h^2a was not significant (0.00 ±.04) but h^2m was significant (0.10 ± .03). However for SRATE post-weaning (3-8 months) this trend was reversed with h^2m being non significant (0.00 ± .05) and h^2a increasing to 0.12 ± .05.

Table: 4.13 Heritability estimates for lamb survival (SRATE) live weight (WT), packed cell volume (PCV), faecal egg count (FEC, epg) and logarithm transformed (LFEC) derived using paternal half-sib model for 1993 lamb crop and pooled data for 1991-1995 lamb crops at Diani Estate derived using restricted maximum likelihood and an animal model (Baker, 1995).

			REML Animal Model (1991-1995[a])					
	PHS(1993)		Animal only		Animal + dam		Sire model	
Trait	n	h^2±se	n	h^2±se	h^2_a±se	h^2_m±se	ns	h^2±se
				LWT				
Birth	380	0.10±.10	1564	0.86±.06	0.13±.05	0.36±.04	76	0.13±.05
3mo	272	0.33±.19	1258	0.56±.09	0.04±.04	0.29±.04	75	0.04±.04
8mo	213	0.34±.22	803	0.60±.09	0.13±.06	0.27±.04	61	0.12±.06
13mo	169	0.42±.27		-				
				PCV				
3mo	272	0.14±.15	1258	0.03±.04	0.01±.04	0.06±.04	75	0.01±.04
8mo	213	0.05±.16	830	0.11±.05	0.09±.05	0.04±.04	61	0.10±.06
13mo	169	0.06±.20						
				FEC				
3mo	272	ne	1004	0.00±.05	0.00±.05	0.12±.05	62	0.00±.05
8mo	213	0.10±.17	803	0.12±.05	0.11±.05	0.00±.05	61	0.23±.07
13mo	169	0.07±.21						
				LFEC				
3mo	272	ne	1004	0.05±.05	0.08±.06	0.00±.04	75	0.04±.05
8mo	213	0.04±.16	803	0.16±.05	0.16±.05	0.00±.05	61	0.22±.07
13mo	169	ne						
				SRATE				
0-3mo	380	ne	1564	0.00±.03	0.00±04	0.10±.03	76	0.00±.04
3-8mo	347	0.21±.14	1078	0.12±.04	0.12±.05	0.00±.05	59	0.12±.04
0-13mo	380	0.04±.08	1287	0.03±.03	0.04±.03	0.08±.03	59	0.03±.03

h^2a = *direct additive heritability* h^2m = *maternal genetic heritability*
n = *records analyzed*
ns = *number of sires*
ne = *the sire variance component was not estimatable*
a. 1991-95 lamb crops analyzed for all traits up to weaning (3 mo) and 1991-94 lamb crops for the post-weaning traits.

Table 4.14 Paternal half sib heritability estimates for yearling live weight (WT), Packed Cell volume (PCV), faecal egg count (FEC), tick count (TC), and logarithm transformed tick count(LTC=TC+10) and logarithm transformed faecal egg count (LFEC=FEC+25) at Nguuni in the three infection periods

Traits	Period 1 h^2±se	Period 2 h^2±se	Period 3 h^2±se
Number	160	151	150
WT	0.27±.26	0.73±.33	0.76±.34
PCV	0.10±.22	0.24±.26	ne
TC	0.25±.25	0.12±.24	0.08±.23
LTC	0.43±.28	0.13±.24	0.02±.22
FEC	ne	ne	0.31±.28
LFEC	ne	ne	0.12±.22

ne = not estimable

None of the paternal half sib heritability estimates for PCV or LFEC were significant. Similarly, neither the h^2a or h^2m estimates for the larger data set were significant at weaning for PCV or LFEC. Post-weaning (i.e at 8 months) h^2m was non-significant for both PCV and LFEC, but both h^2a and h^2s were significant. The sire model (h^2s) heritability estimates were higher for LFEC ($0.22 \pm .07$) than for PCV ($0.10 \pm .06$).

At Nguuni (**Table 4.14**), heritability estimates for live weights increased with age from $0.27 \pm .26$ in period 1 to $0.76 \pm .34$ in period 2. Heritability estimates were highest for PCV in period 2 ($0.24 \pm .26$) while for TC, they were highest in period 1 of tick challenge (0.25 ± 0.25). However the small data set and associated large standard errors of the estimates precludes any definitive interpretation of these estimates.

4.4.2 Repeatabilities

Table 4.15 presents the repeatability estimates within and between the three infection periods at Nguuni. Repeatability estimates for live weights were high and averaged 0.84 between infection periods and 0.92 within infection periods. Repeatabilities for TC and LTC were higher within infection (0.32 and 0.27, respectively) than between infections (0.18 and 0.17, respectively). Repeatabilities between infection periods for PCV, FEC and LFEC were all low (ranging from 0.02 to 0.18), but no estimates of within infection period were

available for these traits as they were not recorded on the monitor group of 20 sheep.

Repeatabilities among recorders for transformed TC at Nguuni is shown in **Table 4.16**. The repeatability estimates among recorders across all predilection sites was high. The estimate for ears count ranged between 0.93 to 0.98 with an average of 0.95. This was similar to the average of 0.93 for total TC. The high repeatability among recorders for ears TC was probably associated with high preference of ears as predilection as shown in **Table 4.17**.

Table 4.15: Phenotypic correlations between infection periods for live weight (WT), packed cell volume (PCV),faecal egg count (FEC) Logarithm transformed faecal egg count (LFEC= FEC+25) tick count (TC) and Logorithm transformed tick count (LTC= TC+10) and within phase repeatability estimates for TC, WT, and LTC in the three sampling periods at Nguuni

	BETWEEN				WITHIN			
Traits	1-2	2-3	1-3	Average	1	2	3	Average
WT	0.84	0.81	0.86	0.84	0.84±.05	0.96±.02	0.95±.02	0.92±.03
TC	0.22	0.16	0.17	0.18	0.29±.13	0.44±.13	0.24±.12	0.32±.13
LTC	0.21	0.15	0.16	0.18	0.30±.13	0.31±13	0.20±.12	0.27±.13
PCV	0.02	0.18	0.06	0.09	-	-	-	-
FEC	0.14	0.01	0.08	0.08	-	-	-	-
LFEC	0.07	0.03	0.02	0.04	-	-	-	-

Table 4.16. Repeatability of recorders for transformed tick count at different measurement sites on the animal

Site on the animal	Sampling 1	Sampling 2	Sampling 3
Ears	0.98	0.93	0.93
Head	0.81	0.73	0.99
Body	0.85	0.75	0.99
Scrotum/Udder	0.39	0.81	a
Anal area	0.54	0.80	1.00
Total count	0.96	0.89	0.93

a = No ticks recorded at this site

Table 4.17 Mean tick number and residual standard deviation (RSD) for ticks at diferent sites on the animal and at different sampling times for the two recorders (A and B)

	Sampling 1		Sampling 2		Sampling 3	
Site	A	B	A	B	A	B
Ears	43.4	43.8	197.3	195.0	235.1	236.3
RSD	18.6	19.0	84.6	81.0	90.4	90.1
Head	5.5	5.3	32.9	33.7	16.1	16.0
RSD	5.5	5.4	20.2	21.3	11.2	11.3
Body	0.8	0.8	3.0	3.6	4.6	4.6
RSD	1.8	1.7	4.3	7.6	6.3	6.6
Scrotum/udder	0.1	0.3	0.6	0.7	-	-
RSD	0.4	1.1	2.3	2.4	-	-
Anal area	0.9	1.1	1.1	1.1	2.0	2.0
RSD	2.0	4.2	1.7	1.7	3.5	3.5
Total	51.00	51.4	234.8	234.0	257.7	259.2

4.4.3 Phenotypic Correlations

4.4.3.1 Phenotypic correlations among measurement sites

The phenotypic correlations among sites during tick challenge at Nguuni is shown in **Table 4.18**. The phenotypic correlations between ears TC and total TC was high and ranged between 0.94 in period 1 to 0.99 in period 3 with an average of 0.97. The phenotypic correlations among other predilection sites and total TC was on average low and it was on average 0.44, 0.15, 0.17 and 0.09 for head, body, scrotum/udder and anal regions, respectively.

Table 4.19 shows phenotypic correlations among WT, PCV and TC at Nguuni during the three cycles of tick challenge. The correlations between PCV and live weight were positive. The correlation increased from 0.16 in period 1 to 0.22 in period 2 and 3 respectively. Phenotypic correlations between live weight, PCV and LTC was negative in periods 2 and 3, respectively.

The phenotypic correlations between logarithm-transformed tick count and FEC for tick infestations and GI nematode infections at Ol'Magogo are shown in **Table 4.20**. The phenotypic correlation between APCV and AWT was positive and high in 1992 lamb crop (0.26) but it was negligible in 1993 lamb crop. The phenotypic correlations between live weight and or PCV with either LFEC or LTC was mainly low and negative in the 1992 and 1993 lamb crops.

4.18 Phenotypic correlations for logarithm transformed tick count among measurement sites

Trait 1	Trait 2	Sampling 1	Sampling 2	Sampling 3
Ears	Head	0.06	0.55	0.19
	Body	0.08	0.07	0.04
	Scrotum/Udder	0.15	0.11	-
	Anal	-0.07	0.05	0.11
	Total	0.94	0.98	0.99
Head	Body	0.03	0.07	0.18
	Scrotum/Udder	-0.02	0.09	-
	Anal	-0.02	0.05	-0.02
	Total	0.31	0.68	0.32
Body	Scrotum/Udder	0.37	0.19	-
	Anal	0.29	0.06	0.07
	Total	0.17	0.13	0.14
Scrotum/Udder	Anal	0.20	0.00	-
	Total	0.20	0.14	-
Anal	Total	0.06	0.07	0.14

Table 4.19 Phenotypic (rp) correlation estimates between logarithm transformed faecal egg count(LFEC=FEC+25),logarithm transformed tick Count(LTC=TC+10),packed cell volume(PCV) and live weight (WT) for Nguuni flock during the three periods of tick infection.

		PERIOD 1	PERIOD 2	PERIOD 3
Trait 1	Trait 2	rp	rp	rp
WT				
	PCV	0.16	0.22	0.22
	LFEC	0.00	0.05	-0.08
	LTC	0.13	-0.05	-0.05
PCV	LFEC	0.11	-0.15	-0.26
	LTC	0.10	-0.05	-0.01
LFEC	LTC	0.11	-0.03	-0.11

1. Based on 7 and 5 degrees of freedom for sires and 9.3 and 14.7 progeny per sire in group 1 and 2 respectively.

2. ne^2 = Not estimable-negative sire component of variance

Table 4.20 Phenotypic (rp) correlation estimates between logarithm transformed faecal egg count(LFEC=FEC+25),logarithm transformed tick Count(LTC=TC+10),packed cell volume(PCV) and live weight (WT) for the Ol'Magogo flock during the two period tick and helminths infection

		Born 1992	Born 1993
Trait 1	Trait 2	rp	rp
AWT	APCV	0.26	0.01
	ALFEC	-0.04	-0.01
	ALTC	-0.15	0.21
APCV	ALFEC	-0.05	-0.26
	ALTC	-0.24	-0.10
ALFEC	ALTC	0.31	0.10

1. Based on 7 and 5 degrees of freedom for sires and 9.3 and 14.7 progeny per sire in group 1 and 2 respectively.

2. ne^2 = Not estimable-negative sire component of variance

4.4.3.2 Genetic correlations

The genetic correlations among traits measured at Diani, Nguuni and Ol'Magogo were not estimable in these data sets.

5. DISCUSSION

5.1 Diani Estate

Live weights at different ages in this study were lower than those generally reported in other studies in the tropics and sub tropics. Inyangala *et al.* (1990) reported a mean BWT of 4.12 ± 0.10 for D lambs at Naivasha. This estimate was 1.87 kg higher than that reported in this study (2.25 ± 0.05). The difference can be attributed in part to the contrasting environments.

The WWT3 in this study was similar to that reported in the same study area as the present study but for different lamb crops by Baker *et al.* (1993) (i.e 1991 and 1992 lamb crops). The WWT3 (12.0 kg) reported in this study fell in the range of 10.6-12.3 kg reported for the 1991 and 1992 lamb crops. The WT3 reported in this study and those reported by Baker *et al.* (1993) were lower than those estimated by Inyangala *et al.* (1990) of 19.5 kg.

The WT8 (12.8 ± 1.7 kg) and WT13 (15.5 ± 2.0) reported in this study were 1.1 and 3.2 kg lower, respectively, than those reported by Reynolds *et al.* (1992) at approximately the same age for the 1990 lamb crop. For the 1992 lamb crop, Baker *et al.* (1993) reported an average weight at 6 months of age of 14 kg. These differences

were probably due to the lower GI nematode challenge in 1991 and 1992 as indicated by longer intervals between sampling periods. The pre-weaning SRATE in this study (91 %) was higher than that reported by Baker (1995a) of (82 %), but the post-weaning survival was similar (61 % vs 68 %). The low SRATE of 44 % reported in this study was similar to many other estimates in the humid tropics which range from 30 % to 60 % (Eysker and Ongunsasi, 1980; Adoeye, 1984; Upton, 1984; Tuah, 1988; Okon, 1988, Baker, 1995a).

Figure 4.1 indicates the time lapse for FEC to reach the threshold levels of 1,500-2,000 epg. The time lapse was influenced mainly by seasonal fluctuations in rainfall. Non-parasitic developmental stages of GI nematodes require a temperature of 22-26°C and a minimum humidity of 85 % (Hansen and Perry, 1994). These conditions prevail in the coastal lowlands throughout the year. The levels of FEC in this study at 3 (2689 ± 3465) and 13 (2458 ± 1176) months of age were higher than those reported in the 1991 lamb crop at 3 and 15 months of age by Baker *et al.* (1993). The PCV levels declined with age in line with other studies (Karlsson *et al.*, 1991). There was a 14 % decline in PCV between weaning (3 months) and 13 months of age in this study (i.e. 29.1% to 24.9 %). Baker *et al.* (1993) reported similar PCV at all ages for the 1991 lamb crop. However, for the 1992 lamb crop the decline in PCV between weaning (3 months) and 7 months of age was 8 % .

5.1.1 Environmental effects

The Significant effect of sex, dam age and birth type for live weights was consistent with many other reports in the literature (Dass and Acharya, 1970; Magid *et al.*, 1981; Kiriro, 1986; Stobart *et al.*, 1986; Wilson, 1987; Inyangala *et al.*, 1990; Baker *et al.*, 1993). The heavier BWT in male lambs has been attributed to hormonal differences between sexes which result in differential abilities to grow prenatally. Dam age was a significant source of variation for live weight at all ages. Young ewes are still growing and thus must provide for their own growth in addition to the foetal demand thus resulting in lower BWT. It is known that mothering ability, especially milk production, increases with dam age. Older ewes are larger in body and are better milkers hence, the influence of the superior maternal environment of such ewes is expected to be translated into better lamb performance. In the present study, FEC did not differ significantly between sexes contrary to Courtney *et al.* (1985a) who found that natural resistance of female lambs to *Haemonchus contortus* is higher than that of males only after puberty. The non-significant effect of dam age on survival rates at all ages indicate that good mothering (i.e. high milk production) has no direct influence on subsequent lamb survival rates under GI nematode challenge, i.e. GI nematode challenge masks the effect of superior mothering ability.

5.1.2. Genetic effects

5.1.2.1 Breed differences

5.1.2.1.1 Production traits

Although not statistically significant, the ranking of lamb genotypes for BWT and subsequent live weights was such that lamb genotypes with high percentages of D genes were heavier than those with low percentage of D genes. This is consistent with the study of Baker (1995a).

The significant effect of sire breed reflected differences in additive direct effects between R and D sires. D-sired lambs were 9 % heavier at birth than R-sired lambs. This is consistent with the 8 % difference reported by Baker *et al.* (1993) in the same study flock but for the 1991 lamb crop. Sire breed was not a significant source of variation for the other live weight traits, contrary to other studies. Kiriro (1986) reported that D-sired lambs were heavier at weaning than R-sired lambs. Reynolds *et al.* (1992) (for the 1990 Diani lamb crop) reported that D-sired lambs were 7 % and 8 % heavier than R-sired lambs at 3 and 8 months of age, respectively. These differences can be attributed to the lower GI nematode challenge in the 1990 lamb crop than in the present study. D-sired lambs were born heavier than R-sired lambs but this

superiority was not maintained up to yearling age because they were stressed by exposed to GI nematodes. The low BWT in R-sired lambs are compensated for by their ability to grow under high GI nematode challenge.

Although not statistically significant, the effect of dam genotype was not consistent across live weights at different ages, in that there was a shift in the genotype rankings. The dam genotype which produced the lightest lambs at birth (i.e R) tended to have lambs with the heaviest live weights at weaning and thereafter. Although not significant, lambs from F_1 dams were heavier at birth indicating possible advantage due to maternal heterosis. Kiriro (1994) reported that maternal heterosis contributed significantly to BWT (5 %) in R, D and their crosses at Ol'Magogo in Naivasha. The non-significant effect of dam genotype on live weights under GI nematode challenge was contrary to the study by Banda *et al.* (1990) on milk yields, composition and growth rates of offspring of local sheep (Malawian), D and their crosses. They attributed the significant effect on superior milk yield to the D dams. Local, D x Local and D produced 37 ± 1.8, 48.9 ± 1.6 and 62.7 ± 2.1 kg milk for 12 weeks of lactation, respectively. The amount of milk produced by various breeds at different stages of lactation has a strong influence on lamb growth during the pre-weaning period, with 20 to over 60 % of the variation in weaning weight being accounted for by the volume of milk produced (Peart, 1982). It is expected that in the present study,

although D has a superior additive maternal effect for milk than R, this superiority was not expressed under GI nematode challenge. Further studies, however, are required on the relationship between GI nematode challenge and milk production in sheep to assess the overall implication of selection for GI nematode resistance. Mackinnon *et al.* (1991) reported that milk production and worm resistance were positively genetically related in a tropical beef herd.

The large differences in lamb SRATE reported in the present study clearly favour keeping of R or R crosses in coastal Kenya. Sire breed did not significantly influence SRATE from birth to weaning, but thereafter there was a significant sire breed effect in favour of the R-sired lambs. Up to 8 months of age, D-sired lambs had a mortality rate of 55 %, compared with 24 % for R-sired lambs, while, up to 13 months of age, D-sired lambs had a mortality rate of 71 % compared with 41 % for R-sired lambs. Baker *et al.* (1993) reported that D-sired lambs had a post-weaning (3-9 months) mortality rate of 49 % while those sired by R had a mortality rate of 10 %. The higher mortality rate in the D-sired lambs reported in the present study compared to that reported by Baker *et al.* (1993) can be attributed to higher endoparasite challenge in the present study. The higher SRATE in the R-sired lambs than in the D-sired lambs after 3 months of age indicates that resistance to GI nematode developed

after 3 months of age in the R. This is consistent with the finding of Windon and Dineen (1984).

Although there was no evidence from present study for any heterosis for growth, the comparison of F_1 with pure breeds indicated heterosis for SRATE at 3 and 13 months of age. Comparing the SRATE of different lamb genotypes the linear contrast indicated an advantage in lambs having over 75 % R genes (i.e. purebred R included). This confirms the reports of Preston and Allonby (1978, 1979) and Bain *et al.* (1993) that R sheep are more resistant to GI nematodes than D sheep. However, further research is needed to clearly define how much of the higher survival in R and its crosses is actually due to resistance to *Haemonchosis* and how much to other disease conditions. Indigenous or unimproved sheep breeds such as Florida native, St. Croix and R were reputed to have low productivity but high levels of resistance to helminths (Baker *et al.*, 1994a). This productivity has only been measured in terms of live weights at different ages. However, the present study shows that total productivity must include measures of lambs' SRATE at different ages.

5.1.2.1.2 Resistance traits

The non-significant effect of lamb genotype on FEC at 3 months is consistent with the study by Baker *et al.* (1993) for FEC at 30 and 60 days of age. Under the

natural challenge conditions of the present study, resistance in the R and its crosses, while under genetic control, is an acquired rather than an innate characteristic. It has also been reported that postweaning FEC measurements are a good indicator of resistance levels for most of the adult life of the animal (Gray and Woolaston, 1991; Gruner, 1991a). Animals which are resistant to one species of GI nematodes are also resistant to a range of other nematodes (Gray and Woolaston, 1991).

Lambs with over 75 % R genes had significantly ($P < 0.01$) lower FEC at 8 months than those with over 75 % D genes. However, this significance disappeared at 13 months of age indicating that the surviving genotypes with more than 75 % genes of D were comparatively as resistant as those with similar percentage of R. This result has important consequences for studies aimed at identifying differential resistance to infections. Since resistance becomes apparent with age, studies aimed at identifying resistant genotypes should include monitoring of animals from birth to approximately 12 months of age. Sheep are most susceptible to worm infections as young lambs, with their natural immunity gradually increasing to about 12 months of age (Woolaston and Eady, 1995). When there are high levels of post-weaning mortality as in this study the differential mortality levels among the genotypes is expected to bias the measurements of resistance such as FEC and PCV (i.e. most of the D and 3/4 D lambs that died are likely to be those that are more susceptible to GI nematodes).

Since R sires conferred a certain degree of resistance to both ecto- and endoparasites to their progeny and there were no significant differences in live weights between R- and D-sired lambs, there are immediate possibilities for increased production (lamb off-takes) and reduction in costs by using R as a sire breed. Therefore the recommendation in earlier studies (Odenya, 1982, 1994; Kiriro, 1986; Inyangala, 1989) that D sires be used in crossbreeding programmes for mutton production should not be generalised to environments where there are high loads of GI nematode and /or ecto-parasite challenge.

5.1.3 Within breed genetic effects

Heritabilities were estimated for live weights, PCV and FEC at different ages. The paternal half sib heritability for BWT was 0.10 ± 0.10. This estimate is similar to the estimates of 0.14 ± 0.08 (Kiriro, 1986) and 0.15 ± 0.07 (Inyangala *et al.*, 1990). The estimate of WWT3 h^2 was 0.33 ± 0.19. This was similar to the estimate of 0.28 ± 0.11 (Stobart *et al.*, 1986) but higher than that reported by Matika *et al.* (1995) of 0.14 ± 0.02 in Sabi sheep. The heritability estimate for WT13 (0.42 ± 0.27) was slightly lower than that reported by Inyangala *et al.* (1990) (0.53 ± 0.13) for adjusted 12 - month weight.

It is clear from these and related results that paternal heritability estimates for live weight increases with increasing age. This would indicate that environmental factors, in relation to additive genetic factors, had more influence on BWT than on weights after weaning. This may be attributed to the high maternal influence associated with lamb growth performance early in life. High maternal influence has a tendency to increase the environmental component of variance and therefore lowering heritability estimates. This was confirmed by the higher maternal heritability estimates reported for pooled data for 1991-1995 lamb crops. During this period h^2m estimates ranged from 0.36 ± 0.04 at birth to 0.27 ± 0.04 at 8 months of age consistent with the study of Matika *et al.* (1995). The maternal heritability estimates reduced with age . Matika *et al.* (1995) reported that maternal heritabilities were significant at birth (0.12 ± 0.03), decreased to weaning (0.06 ± 0.03) and were negligible and non-significant at 12 months and thereafter.

The non-significant h^2a (0.00 ± 0.04) and the significant h^2m (0.10 ± 0.03) for pre-weaning SRATE strengthens the earlier suggeston for live weights that improvement of this trait can be achieved by selecting resistance ewes. After weaning the maternal influence on lambs diminishes because the lambs depend more on pasture. This was confirmed by the non-significant h^2m (0.00 ± 0.05) and significant h^2a (0.12 ± 0.02) for SRATE post-weaning (3-8 months).

The individual heritability (h^2a) for the larger data set for PCV and LFEC increased with age. At 8 months, the significant h^2a and h^2s estimates are further evidence for development of resistance in lambs with age. Woolaston and Eady (1995) reported that heritability estimates of FEC varied from 0.37 ± 0.05 at three weeks post-infection to 0.47 ± 0.05 eleven weeks after experimental infection with *Haemonchus contortus*. They also reported that sheep acquire natural immunity progressively over their first year of life. The higher h^2s estimate (0.22 ± 0.07) in the present study for LFEC is a possible pointer to the existence of resistant sires. Baker (1995a) reported higher heritability estimates in D-sired lambs (0.32 ± 0.13) than R-sired lambs (0.11 ± 0.07).

Breeding for resistance to GI nematodes can be achieved by use of resistant sires (Albers *et al.*, 1987). As a measure of anaemia, PCV could be considered more an indicator of resilience than resistance and thus the finding of lower heritability for PCV than for LFEC is consistent with the conclusion of Albers *et al.* (1987). Thus resistance can be measured quite simply and cheaply using FEC. FEC is also a valuable trait in its own right as a measure of the degree to which an animal is contaminating pasture with worm eggs (Woolaston and Eady, 1995).

5.2 Nguuni and Ol'Magogo

The 3.1 kg gain in weight after termination of GI nematode challenge at Diani Estate and subsequent minimal growth rate during tick challenge in periods 2 and 3 at Nguuni revealed the severity of tick infestations. This is in line with the finding of O'Kelly and Kennedy (1981) that tick infestations depress growth through direct and indirect anorexic ways. Irritative effects of ticks on sheep diverts the latter's attention from grazing and browsing. These results have important consequences, especially in coastal Kenya, in that animals should be sprayed or dipped to control ticks at an interval of less than 21 days (preferably a 7-14 day interval). This is because application of acaricide at an interval of 21 days resulted in reduction in the growth rate of lambs. Frequent dipping or spraying did not prevent drastic losses in productivity when exotic breeds, with a high susceptibility to tick infestation, are utilized in farming areas with high tick incidence.

The 8 % difference in AVWT12 in 1992 between the 1993 lamb crops at Ol'Magogo could be attributed mainly to dry conditions which prevailed in 1993. The 1993 lamb crop was reared when pasture quality was poor. The relatively low threshold levels of 1,500-2,000 epg for FEC at Ol'Magogo was expected. This is due to unfavourable climatic conditions which did not favour faster development of non-infective stages of GI nematodes and the close interval of drenching. However, an

increase of GI nematode infection was observed after and during the rainy seasons (**Figure 4.2**).

5.2.1 Breed differences

5.2.1.1 Nguuni Farm

The breed of sire significantly influenced PCV and TC in period 2 but not in periods 1 and 3. These results confirm the reports of Norval (1978), Barriga *et al.* (1991a,b) and Dossa *et al.* (1996). That an animal requires a certain period of challenge before developing resistance. Thus, resistance is not innate but acquired and it is genetically controlled (Gray and Woolaston 1991). Lack of significant sire breed effect in period 3 could possibly be attributed to overwhemingly high exposure and exhaustion of immune system and/or lack of complete protection across different tick species. This merits further studies to quantify the mechanism of breakdown. However, there was evidence of between breed differences in tick infestations. TC were higher in purebred D lambs and in lambs with greater than 75 % D genes. This is an indication of genetic resistance to ticks in small ruminants.

A number of studies (Heweston, 1968; Wharton *et al.*, 1970; Turner and Short, 1972; Wagland, 1975, 1978; Utech *et al.*, 1978a, 1978b; Bonsma, 1981; Utech

and Wharton, 1982; Norval *et al.*, 1988; Spickett *et al.*, 1989; Mackinnon *et al.*, 1990; de Castro, 1991; Scholtz *et al.*, 1991; Norval *et al.*, 1992; Davis, 1993, Tawah, 1993; Matioli *et al.*, 1993, 1995) have shown that Zebu and Sanga breeds of cattle are more resistant than taurine breeds and their crosses to a variety of tick species, and that there is considerable variation in individual resistance within breeds.

The significantly lower tick burden observed in this study in purebred R and in lambs with greater than 75 % R genes in comparison with purebred D strengthens the suggestion for the presence of a genetic basis of resistance in R genotype. However, further research and a concerted extension effort are required in order for tick or tick-borne diseases (e.g *Cowdriosis*) resistance of sheep to be actively exploited in tick control (i.e as on alternative to acaricides). There are some indications of genetic resistance to *Cowdriosis* in indigenous goats in Guadeloupe (Matheron *et al.*, 1987) and in South Africa (Stewart , 1987; Donkin *et al.*, 1995).

5.2.1.2 Ol'Magogo Farm

The R lambs were superior to D lambs in resistance to both GI nematode infections and tick infestations. Since R sires conferred a certain degree of resistance to both ecto- and endoparasites to their progeny and there were no significant

differences in live weights between R- and D lambs, there are immediate possibilities for increased production (lamb off-takes) and reduction in costs by using R.

The significantly higher PCV and lower TC and FEC in the R lambs than D lambs conforms with what has been reported in the Diani and Nguuni studies. Under simultaneous GI nematode and tick challenges, the R breed maintained higher PCV, lower TC and low FEC, indicating possibilities of multi-parasite resistance. However, the experimental design used for this comparison was poor. 1. In particular, the number of animals evaluated for each breed was small. 2. Variation among sires within breeds and confounding of both parasite species was not taken into account. The possibility of multi-parasite resistance encourages utilisation of both between and within breed variation for resistance to ecto- and endoparasites to develop more resistant genotypes. Further research is required to interpret these findings.

5.2.2 Within breed genetic effects.

5.2.2.1 Nguuni

Heritabilities were estimated for live weights, PCV and TC at different periods of tick challenge. They were associated with high standard errors and this precludes any definite conclusions. The within period repeatability estimates were

highest in period 2 for TC (0.13). This indicated that much could have been gained from repeated measurements. If several counts could have been done within period 2 we would have expected a higher heritability estimate. The heritability of the average of several (n) measures of the same trait is $nh^2 / (1+(n-1)r$, where h^2 is the single record heritability and r is the repeatability (Woolaston *et al.*, 1991). Thus by averaging two TC, heritability would have increased by about 54 % (i.e from 0.13 to 0.20) and by 85 % for the mean of three counts (0.24). However, slightly more can be gained by the repeated measurement of TC in different infection periods. Assuming a heritability of 0.13 for a single TC measurement within an infection and a repeatability of 0.18 between infections then the heritability increases to 0.22 for the average of two TC and to 0.29 for the average of three TC. Therefore the additional effort required to obtain the extra information is justified, particularly if the experimental period (duration) is long. The possibility of selecting sheep that are resistant to several tick species should therefore be considered as a complementary approach to the use of acaricide.

The high positive correlation between the tick count on the ears and total count (0.97) indicated that counting ticks (especially in a situation where predominant tick species is *R. appendiculatus*) on ears alone would give a good indication of the total

number of ticks on the animal. Further work on this time-saving approach should be encouraged. The validity

of this approach is also supported by the similar and high correlation (>0.93) estimates between periods for the number of ticks found in the ears. Donald *et al.* (1989) and Schotz *et al.* (1989) in South Africa found similar results in cattle, i.e. counting certain defined predilection sites was highly correlated with total body count. Since tick burdens vary with the predominant species, quantity and predilection sites on the animal, different methods for other eco-climatic zones may need to be developed. The two independent samplers in this study were both experienced (especially after the first period), but differences between heavily infested and "clean" animals were inevitably clear and the repeatability of sampling was high averaging 0.93.

5.2.2.2 Ol'Magogo

The heritability estimates were associated with large standard errors due to the small data set. However, from the magnitude of the repeatability estimates, given a larger data set and repeated measurements, heritability estimates might increase.

5.3 Resistance to endoparasites

5.3.1 Breed effects

The results of both investigations (Diani and Ol'Magogo-Naivasha) demonstrate clear differences in susceptibility of the two breeds of sheep to naturally acquired nematode infection. In Diani, the genotypes in order of increasing susceptibility, as judged by the mean FEC during the whole period of exposure (up to 13 month of age) to nematodes infection were:- 100 % R, 75 % R 25 % D, 50 % R 50 % D, 75 % D 25 % R and 100 % D.

Throughout both experiments, the R sheep consistently maintained higher PCV levels, lower FEC and higher SRATE. These results confirm the previous reports of Preston and Allonby (1978 , 1979), Bain *et al.* (1993), Leitich *et al.* (1993), Mugambi *et al.* (1993), Baker *et al.* (1993, 1994a) and Baker (1995a, b) that R sheep are more resistant to GI nematode than D sheep. The R breed is indigenous to the tropics, whereas the D originated from South Africa from crossing of the Dorset Horn (temperate breed) sires with Blackhead Persian dams. Since the importation of D, it has been kept under strictly controlled management systems, with regular anthelmintic treatment (Kiriro, 1986), while R have been under poorer management and lack of helminth control thus permitting opportunity for natural selection. Previous breed

comparisons have often indicated a high level of resistance to endoparasites in indigenous or "unimproved" sheep breeds such as the R. Florida Native and St. Croix (Baker *et al.*, 1992).

The question arises as to whether the difference between the breeds were of innate or an acquired nature. In the present study, there were no significant differences among genotypes in FEC and SRATE at a young age (i.e measurement at 90 days of age). Resistance became apparent in lambs postweaning depending on exposure with high challenge triggering an early development of resistance (Karlsson *et al.*, 1991; Gruner, 1991a; Baker *et al.*, 1993) suggesting the development of acquired resistance.

The low annual SRATE (44 %) in the present study shows that the humid conditions in coastal Kenya are not favourable for sheep production despite the fact that sheep and goats were owned by 60 % of rural house holds in Kenya's coastal region (Thorpe *et al.*, 1990). The most practical option to most Kenyan small holders and livestock producers whose sheep suffers from GI nematode infections is to replace their animals with sheep of the R breed or its crosses. While breed substitution may appear simplistic, it is one of the few examples of a feasible scientific solution to a major constraint to livestock production, especially in Africa. D remains a popular sheep breed in favourable farming conditions as reviewed by Kiwuwa (1985) and

supported by Kiriro (1986), Inyangala *et al.* (1990) and Angwenyi (1990) at Ol'Magogo (Naivasha). Hence high growth rates favour D in Kenya highlands where parasite control is intensive. But the low FEC in R in the present study at Ol'Magogo favours R as productive sheep breed in most agro-ecological zones. While this study showed small differences between genotypes in live weights, the large differences in SRATE clearly favour keeping R or R crossers (> 50 % R) in Kenya.

5.3.2 Within breed effects

In sheep most of the heritability estimates of resistance to endoparasites (assessed in terms of either FEC or PCV) are from Merino and Romney sheep in Australia and New Zealand. The increase of heritability with age for both FEC and PCV is further evidence for development of acquired resistance in lambs. Morris *et al.* (1995) suggested that the change in FEC heritability between sampling may be a measure of development of immunity. In New Zealand, the heritabilities were 0.11 ± 0.07 for the difference in FEC between sampling 1 and 2 (3 months apart) and 0.29 ± 0.11 for the difference between sampling 2 and 3 (approximately 3 months apart) (Baker *et al.*, 1991). The significant heritability for LFEC (0.22 ± 0.07) estimated using the sire model was encouraging confirming that resistance to GI nematode infections is a heritable trait. The estimate for LFEC was similar to those calculated by

Woolaston and Piper (1995) using an animal model and using data from a Merino flock selected for resistance to *Haemonchus contortus* (0.29 ± .03). Woolaston *et al.* (1991) estimated the heritability of cubed transformed FEC to be 0.41, but these data were the averages of five FEC measurements and recorded on housed animals and might therefore be expected to reflect less environmental variance. Although FEC may not always accurately reflect worm burden, the trait has value in its own right as a breeding objective because it determines the extent to which animals are contaminating pastures. PCV, as a measure of anaemia, could be considered more of an indicator of resilience than resistance. Thus the lower h^2s for PCV (0.10 ± 0.06) when compared to that of LFEC (0.22 ± 0.07) is consistent with the conclusions of Albers *et al.* (1987) and Morris *et al.* (1995) that resilience is less heritable than resistance. Because genetic correlations between resistance and resilience are positive (between 0.31 to 0.37) (Albers *et al.*, 1987) selection for resistance would result in progress for resilience as well and vice versa.

5.4 Resistance to ticks

5.4.1 Breed effects

The results from experiments in Nguuni and Ol'Magogo, although with different experimental designs and protocols, demonstrate lower tick burden on purebred R and in lambs with greater than 75 % R genes in comparison with purebred D. This strengthens the suggestion for the presence of a genetic basis of resistance in R genotype. The lack of significant differences between lamb genotypes in tick burden in the three periods of infestation at Nguuni, could be due to the short period of study. This reasoning is supported by the significant effect of lamb genotype on TC in the Ol'Magogo study which lasted approximately 12 months. At Nguuni, there was a significant difference in period 2 of tick infestation between R and D lambs in the whole flock (**Table 4.15**) and the monitor group (**Table 4.18**) and relatively small differences in period 1 and 3. This is evidence that under the natural tick challenge conditions of this study, the resistance in the R, while under genetic control, is an acquired rather than an innate characteristic. Resistance to ticks is only expressed after initial exposure to tick salivary gland antigens as a result of successful tick feeding (Norval *et al.*, 1992, Dossa *et al.*, 1996). This type of resistance seldom affords complete protection against the feeding of any particular tick species and alone, rarely

affords sufficient protection against heavy tick challenge. Hence the lack of a significant difference between R and D in period 3 of tick infestation. Further studies are warranted in sheep to estimate an optimal tick burden which can sustain immuno-competence.

5.4.2 Within breed effects

Heritability estimates for logarithm-transformed TC were imprecisely estimated and difficut to interpret. The average heritability over the three infection cycles was about 0.20 but its standard error was larger than this estmate (0.25). However, since repeatability estimates sets the upper limits of its possible heritability, given a larger data set, the heritability estimate in period 2 could be approximately 0.31. However, this is rarely achieved in practice due to the occurrence of undefined permanent environment effects. The average heritability for tick resistance in cattle is 0.34 (Davis, 1993). Repeatability estimates in Ol'Magogo are encouraging and lie between 0.17 and 0.24 for log transformed TC measured at monthly intervals. The results thus provide strong encouragement to select for tick resistance in sheep. Heritability may be high enough to make possible rapid progress in improving resistance if this was deemed desirable.

6. CONCLUSIONS AND RECOMMENDATIONS

Protocol for tick counting in sheep.

1. There was a high positive correlation (0.97) between the tick count on the ears and total body count. The repeatability estimate between recorders for total tick count was 0.93 and for ear tick count 0.95. Thus, future characterization studies for tick resistance in sheep can be achieved by replacing the costly and laborious total body count by concentrating on ears alone and using one well trained recorder. Since tick burdens vary with the predominant species, quantity and predilection sites on the animal, different methods for other eco-climatic zones may need to be developed.

Resistance to tick infestations.

1. The R breed and crossbreds with high proportion of R genes had consistently low TC in all infestation periods indicating between breed difference among genotypes. None of the environmental factors considered for in this study significantly ($P > 0.05$) influenced resistance to tick infestations.
2. The moderate heritability estimates (0.20 - 0.24) indicate that selection for tick resistance is feasible. However, there is need for further studies to

quantify genetic correlations among measurements at different ages and to estimate genetic correlations between resistance and production traits.

Gastrointestinal nematode resistance.

1. This study demonstrated that there was evidence of between breed variation in resistance to GI nematode infections. The R breed was relatively more resistant to natural infection with GI nematodes than D. There was an additive breed effect in crossbred lambs for resistance to endoparasite (i.e increased resistance with increasing proportion of R genes in the crossbred). None of the environmental factors considered in this study significantly ($P>0.05$) influenced resistance traits. Thus, adjustments for those factors need not be considered when selecting for resistance.
2. Although the heritability estimates had large standard errors they were similar to estimates from larger data sets generated in the experiment at this site. This indicates that it could be possible to breed for resistance in either Dorper or Red Maasai sheep.
3. The annual survival rate of 55% for Red Maasai vs 12% for Dorper lambs and lack of a significant difference in yearling weight between the two

genotypes in the present study, shows that the Red Maasai can perform much better than the Dorper in the humid conditions in coastal Kenya. Hence breed substitution of D with R or/and keeping of the R crosses rather than Dorper should be recommended to farmers in this zone.

Therefore utilization of resistant animals is an attractive option as a means of increasing productivity of sheep under GI nematode infections, tick infestations and poor feed resources. Host resistance should be considered as an alternative and/or a complementary approach to the use of chemotherapy in parasite control programs.

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8. APPENDICES

Appendix 1: Sheep breed comparisons for resistance to internal parasites

Resistant breed(s) (n)[1]	Comparison breed(s) (n)[1]	Trait[2]	Type of infection[3]	Parasite species[4]	Age months	Reference
Romney	Rambouillet Southdown Shropshire Crosses	E	N	Oc	6-20	Stewart *et al.* (1937)
Rambouillet	Romney, Cheviot	S	N	Hc	Rams	Warwick *et al.* (1949)
Targhee(32) Panama(21)	Rambouillet(27) Hampshire(35) Suffolk (95)	E,W	N	Osp,Nsp	4-7	Scrivner (1964)
Florida Native	Rambouillet Hampshire	E,W,S	N	Hc	Lambs & Ewes	Loggins *et al.* (1965)
Targhee(8)	Suffolk(8)	E	A	Osp+Hc	3-11	Scrivner (1967)
Merino	Targhee	E,P,W	N	Hc,Str	2-7	Colglazier *et al.* (1968)
Florida Native(120)	Rambouillet(60)	E,P	N	Hc	Ewes	Jilek & Bradley (1969)
Scottish BlackFace	Dorset	W,Bw	A	Ta	Lambs	Ross (1970)
Florida Native(19)	Rambouillet(8)	E,W	A	Hc	5	Rhadakrishnan *et al.* (1972)
Florida Native(33)	Rambouillet(8)	E,W	A	Hc	5	Bradley *et al.* (1973)
Cigaja(10)	Merino(10)		N	Str	12	Cvetkovic *et al.* (1973)
Navajo(24)	Suffolk(11) Rambouillet(23) Targhee(15) Corriedale (15)	E,W	A	Hc	4-5	Knight *et al.* (1973)
Scottish Blackface (24)	Dorset(22)	E,W,P	A	Hc	7-10	Altif & Dargie (1978)
Red Maasai(16)	Merino(16) Corriedale(16) Hampshire(16)	E,W	A	Hc	24-36	Preston & Allonby (1978)
Merino(5)	Awassi(5)	E,W,P	A	Hc	5-6	Al-Khshali & Altif (1979)
Columbia Crosses(50)	Suffolk Crosses (50)	E	N		Ewes	Norman & Hohenboken (1979)

Appendix 1 (Cont) **Sheep breed comparisons for resistance to internal parasites**

Resistant breed(s) (n)[1]	Comparison breed(s) (n)[1]	Trait[2]	Type of infection[3]	Parasite species[4]	Age months	Reference
Red Maasai(10)	Black-head Persian(10) Merino(10) Dorper(10) Corriedale(10) Hampshire(10)	E,W,S	N	Hc	Ewes & Wethers	Preston & Allonby (1979)
Barbados x dorset(69)	Dorset(50) Crossbred(15)	E,W	N/A	Cooperia Tsp,Osp	Ewes &lambs	Yazwinski *et al.* (1979)
Barbados(8) BxDorset(14)	British crossbred(15)	E,W	A	Hc	3-5	Yazwinski *et al.* (1981)
African Dwarf W.A Long-legged	Nungua Black-head	E	N	Mixed (Oc,Tsp,Hc)	Ewes & lambs	Assoku (1981)
Border Leicester xMerino(66)	Merino(66)	E,W	N	Osp	Ewes	Donald *et al.* (1982)
Florida Native(13) St. Croix(10) Barbados(14)	Domestic(14) St. Croix-cross(8)	E,P_p	A	Hc,Tsp Osp	Ewes	Courtney *et al.* (1984)
Florida Native(30) St.Croix(29)	Barbados(27) Domestic(41)	E,P,W	A	Hc	5-6	Courtney *et al.* (1985a)
Florida Native(5)	Barbados(9) St.Croix(4) Domestic(5) Domestic-cross(12)	E,P,W	N	Hc,Tsp	Ewes	Courtney *et al.* (1985b)
3/4 East Friesian	Corriedale	E,W,Bw	N	Mixed		Suarez (1985)
Laucane(50	Romonov(50) RxL(50)	E,W	N	Osp,Nsp	Ewes	Gruner *et al.* (1986)
Laucane(5)	Romonov(5)	W	A	Mixed Osp,Tc	5-6	
Merino d'Arles	Romonov MerinoxRomonov	E	N	Mixed	Ewes	Gruner *et al.* (1987)
Florida Native (21)	Dorset x Rambouillet(45)	E,P_p,W	N	Hc,Tsp Osp	Ewes	Zajac *et al.* (1988)
Horro(32) Arsi (32)	B.H.Somali(32) Adal(32)	E,P,W S,Bw	N	Hc	6-12	Asegede (1990)
Merino d'Arles(30)	Romonov(30)	E,W	A	Oc	Ewes & Lambs	Gruner (1991a)

Appendix 1 (Cont) **Sheep breed comparisons for resistance to internal parasites**

Resistant breed(s) (n)[1]	Comparison breed(s) (n)[1]	Trait[2]	Type of infection[3]	Parasite species[4]	Age months	Reference
Perendale(216) RxP(342)	Romney(221)	E,B,W (Osp)	N	Mixed	4-8	Watson *et al.* (1992a)
Red Maasai(15)	Dorper(15) Romney(15) B.H.Somali(15)	E,P,W,S	N/A	Hc	Ewes	Bain *et al.* (1993) Leitch *et al.* (1993)
Red Maasai(27)	Dorper(15)	E,P,W,S	N/A	Hc	Ewes	Mugambi *et al.* (1993)
Red Maasai(154) 3/4RM¼D(404)	Dorper(288) 3/4D¼RM(392) F_1(326)	E,P,S Bw, P_p	N	Hc+Tsp	Lambs & Ewes	Baker (1995a)

1. Number of sheep of each breed
2. E= Eggs per gram; P=Packed cell volume; W= Worm count; S= Survival; Bw= Body weight; P_p=Periparturient; rise in epg
3. N= Natural; A= Artificial
4. Hc: *Haemonchus contortus*; Tsp: *Trichostrongylus species*; Tc: *T. colubriformis*
   Ta: *Trichostrongylus axei*; Oc: *Ostertagia (Teladorsagia) circumcincta*; Osp: *Ostertagia (Teleadorsagia)* species
   N.sp: *Nematodirus* species; Str: *Strongyloides*

Appendix 2: Cattle breed comparisons for resistance to tick infestations

Resistant breed(s) (n)[1]	Comparison breed(s) (n)[1]	Trait[2]	Type of infection[3]	Parasite species[4]	Age months	Reference
AMZ	Friesian	TC	A	B.micr.	M	Heweston (1968)
Zebu crosses	Hford x Short horn	TC	N	B.micr.	M	Wharton (1970)
Zebu (10)	Friesian (10)	TC	N	R.app	M	Latif et al (1991)
Zebu (4)	Friesian (4)	TC	A	R.app	M	Nakoe *et al.* (1993)
Horro (5)	Horro x Friesian (5)	TC	N	A. chaerens	M	Mohammed and de Castro (1993)
Gaudali	Wakwa	TC	N	Mixed	M	Tawal, (1993)
N'Dama (20)	Zebu (10) N'Dama x Zebu (20)	TC,PCV	N	A. var.	M	Mattioli et al. (1993)
Sanga (33) Nkoni (33)	Friesian x Hereford (16)	TC, LWG	A	R.app	M	Norval et al (1988)

1. Number of cattle () each breed
2. TC= Tick count; PCV=Packed cell volume; LWG= live weight gain;
   N= Natural ; A= Artificial
3. R.app: *Rhipicephalus appendiculatus*
   A.var: *Amblyomma variegatum*
   B.micro: *Boophilus microplus*

Appendix 3 Heritability estimates for live weights in temperate and tropical sheep breeds.

Trait[1]	Region[2]	Breed(s)	Estimate ± se	Source
BWT	1	Various	0.10-0.30	Review Rae, 1982
	1	Chois	0.13±.07	Mavrogenis *et al.* (1980)
	2	Bikaneri	0.45±.20	Dass and Acharya (1970)
	2	Dorper	0.18±.07	Inyangala *et al.* (1990)
WWT	1	Columbia Rambouillet Targhee	0.28±.11	Stobart *et al.* (1986)
	1	Chois	0.36±.12	Mavrogenis *et al.* (1980)
	2	Dorper	0.15±.07	Inyangala *et al.* (1990)
6 month WT				
	1	Various	0.20-0.40	Review Rae, 1982
	1	Columbia Rambouillet Targhee	0.28±.11	Stobart *et al.* (1986)
	2	Dorper	0.31±.09	Inyangala *et al.* (1990)
12 months WT				
	1	Various	0.40-0.60	Review Rae, 1982
	1	Columbia Rombouillet Targhee	0.26±.10	Stobart *et al.* (1986)
	2	Dorper	0.31±.09	Inyangala *et al.* (1990)
Mature	1	Various	0.30-0.70	Review Carles, 1983
	1	Columbia Ramboiullet Targhee	0.53±.12	Stobart *et al.* (1986)
	2	Dorper	0.47±.11	Inyangala *et al.* (1992)

1. BWT, birth weight; WWT, weaning weight

2. 1, Temperate; 2, Tropics

Appendix 4: Heritability estimates for live weight in Sabi sheep

Trait	Model 2		Model 5	
	h^2a	h^2m	h^2a	h^2m
BWT	0.23 ±.04	0.21 ±.03	0.25 ±.04	0.12 ±.03
WWT	0.10 ±.03	0.12 ±.01	0.11 ±.03	0.06 ±.03
12mo. WT	0.26 ±.06	0.06 ±.03	0.28 ±.004	0.00 ±.004
18mo. WT	0.38 ±.06	0.014 ±.03	0.33 ±.07	0.003 ±.03
Mature ewes	0.35-0.48		0.004-0.03	

Source Matika *et al.* (1995)

Appendix 5: Heritabilty estimates for measures of resistance to internal parasites in sheep

Trait[1]	Heritability[2]	Type of infection[3]	Age (months)	Parasite species[4]	Reference (breed)
FEC	0.29±.12(phs)	N	3-4	Mixed(*Osp)*	Piper *et al.*(1978)
FEC	0.11±.12(phs)	N		*N.sp*	(Merino)
FEC(Max)	0.29±.12(phs)	A	3-6	*Hc*	Albers *et al.*(1984) (Merino)
FEC(Av)[5]	0.39±.27(R)	A	4-8	*Tc*	Windon &Dineen(1984)
	0.41±.10(phs)				(Merino)
Log FEC	0.34±.19(Resm)	N	4-8	*(Tsp & Osp)*	Watson *et al.*(1986)
	0.57±.24(Resm)	N		*Nematodirus*	(Romney)
FEC(Max)	0.27±.13(phs)	A	18-20	*Hc*	Piper(1987)
LogFEC(Max)	0.23±.13(phs)				(Merino)
PCV(decline)	0.25±.13(phs)				
SQRFEC(4wk)[6]	0.34±.10(phs)	A	3-6	*Hc*	Albers *et al.*(1987)
SQRFEC(5wk)[6]	0.26±.09(phs)				(Merino)
PCV(4wk)[6]	0.45±.12(phs)				
PCV(5wk)[6]	0.35±.11(phs)				
LogFEC	0.35±.12(Resm)	N	5	Mixed	Baker *et al.*(1991)
	0.39±.13(Resm)		7	*(Tsp & Osp)*	(Romney)
	0.66±.18(Resm)		11		
LogFEC(Av)	0.53±.15(Resm)		5&7		
SQRFEC(4wk)[6]	0.22±.04(Ream)	A	3-6	*Hc*	Woolaston *et al.*(1991)
SQRFEC(5wk)[6]	0.21±.04(Ream)				(Merino)
SQRFEC(Max)	0.20±.04(Ream)				
SQRFEC(Av)	0.24±.04(Ream)				
LogFEC(Max)	0.33±.03(Ream)	A	5-7	*Hc*	Woolaston *et al.*(1991)
SQRFEC(Max)	0.31±03(Ream)				(Merino)
SQRFEC(Av)[5]	0.44±.04(Ream)	A	4-8	*Tc*	Woolaston *et al.*(1991)
CBRFEC(Av)[5]	0.41±.04(Ream)				(Merino)
LogFEC(Av)	0.42±.14(phs)	N	3-8	*Osp*	Cummins *et al.*(1991)
LogFEC(Av)	0.38±08(So)				(Merino)
LogWBL(Av)	0.29±13(phs)				
SQRFEC	0.30±.22(phs)	N	10	*Tsp*	Karlsson *et al.*(1991)
SQRFEC	0.41±.04(phs)		13		(Merino)
LogFEC	0.13±.07(phs)	N	4-5	Mixed	McEwan *et al.*(1992)
LogFEC	0.25±.09(phs)			*Nsp*	(Romney)
FEC	0.34±.08(Resm)	N	7-8	Mixed	Bisset *et al.*(1992)

Appendix 5 (Cont..) Heritabilty estimates for measures of resistance to internal parasites in sheep

Trait[1]	Heritability[2]	Type of infection[3]	Age (months)	Parasite species[4]	Reference (breed)
LogFEC	0.27±.07(Resm)			(Mainly *Tsp*)	(Romney)
LogFEC	0.21±.05(Resm)	N	3-6	Mixed *(Tsp & Osp)*	Bisset *et al.*(1994) (Romney)
LogFEC	0.24±.07(Resm)	N	5	Mixed	Douch *et al.*(1995)
	0.29±.07(Resm)		7	(Mainly *Tsp*)	(Romney)
	0.29±.08(Resm)		11		
LogELTC	0.27±.08(Resm)				
LogFEC	0.15±.03(Resm)	N	5	*Tsp&Osp*	McEwan *et al.*(1994)
LogFEC	0.22±.05(Resm)		7	*Tsp&Osp*	(Coopworth)
LogFEC	0.19±.06(Resm)		5	*Nsp*	
LogFEC	0.17±.06(Resm)		7	*Nsp*	
LogELTC	0.40±.06(Resm)		7		
LogFEC	0.49±.07(OMP)	A	6-8	*Hc&Tc*	Sreter *et al.*(1994) (Merino)
LogFEC	0.21±.06(Resm)	N	5	*Tsp&Osp*	McEwan *et al.*(1995)
LogFEC	0.42±.10(Resm)		7	*Tsp&Osp*	(Romney)
LogFEC	0.19±.06(Resm)		5	*Nsp*	
LogFEC	0.17±.06(Resm)		7	*Nsp*	
LogELTC	0.26±.07(Resm)		7		
CBRFEC(Av)[7]	0.37±.04(Ream)	A	3-6	*Tc*	Woolaston & Eady(1995)
CBRFEC(Av)[7]	0.39±.11(Ream)	N		Mixed	
CBRFEC(3wk)[8]	0.36±.04(Ream)	A	3-6	*Tc*	Woolaston & Eady(1995)
CBRFEC(5wk)[8]	0.35±.04(Ream)				(Merino)
CBRFEC(7wk)[8]	0.37±.04(Ream)				
CBRFEC(9wk)[8]	0.38±.04(Ream)				
CBRFEC(11wk)[8]	0.45±.05(Ream)				
CBRTFEC(AV)[8]	0.40±.04(Ream)				
FEC	0.23±.03(Ream)	A	3-6	*Hc*	Woolaston & Eady(1995)
CBRFEC	0.29±.03(Ream)				(Merino)
PCV(decline)	0.21±.03(Ream)				

1.FEC=Faecal Egg count (eggs per gram of faeces),PCV= Packed Cell volume, WBLC= Whole Blood Culture Assay to Measure in vitro lymphocytes stimulation to trichostrongyloid worm antigens; ELTC = Elisa(EL) assay for the level of antibodies to a mixture of *T. colubriformis* (Tc) antigens); SQR = Square root; CBR = Cube root.

2.phs= Paternal half sib estimates; R = Realised heritability; Ream= restricted maximum likelihood estimates (animal model); Resm= restricted maximum likelihood estimates (sire model);So= Sire offspring regression; OMP = regression of offspring on mid-parent

3. N = Natural; A = Artificial

4. Hc: *Haemonchus contortus*; Tsp: *Trichostrongylus species;* Tc: *T. colubriformis*
Osp: *Ostertagia (Teleadorsagia)* species; N.sp: *Nematodirus* species

5. Mean of 5 egg counts at 2 week intervals from 3 weeks post infection

6. FEC or PCV taken 4 or 5 weeks post infection

7. Average of 5 counts when artificially infected; natural pasture infection average of 3 counts

8. FEC taken 3,5,7,9 and 11 weeks post infection. FEC(Av) is the mean of all 5 counts

Appendix 6: Heritability(h^2) and within infection repeatability(R) estimates for measures of resistance to internal parasites in small ruminants in Africa.

Trait[1]	Parameter	Estimate	Species[2]	Age (months)	Parasite[3]	Infection[4]	Reference
LogFEC	h^2	0.40	Goats	10-12	Mixed	N	Rohrer *et al.*(1991)
PCV	h^2	0.22	(DPG)		(Mainly *Hc)*		
LogFEC	R	0.07±03	Goats	Does	Mixed	N	Baker *et al.*(Unpub.)
PCV	R	0.42±.04	(Galla)	Does	*(Hc&Tsp)*		
PCV	R	0.32±.09		2-8			
LogFEC	R	0.09±.01	Sheep	Ewes	Mixed	N	Bekele *et al.*(1992)
PCV	R	0.44±.01	(Ethiopia)		(mainly *Tsp*)		
FEC	R	0.15±.05	Sheep	Ewes	*Hc*	A	KARI/ODA(1992)
LogFEC	R	0.32±.06	CD/RM)				(unpublished)
FEC	R	0.27±.04	Sheep	Ewes	Mixed	N	KARI/ODA (1992)
LogFEC	R	0.19±.03	(D/RM/R/BHS)		(Mainly *Hc*)		(unpublished)
LogFEC	h^2	0.04±.05	(D,RM	3	Hc + Tsp		Baker (1995a)
PCV	h^2	0.01±.03	& crosses)	3			
LogFEC	h^2	0.22±.07		8			
PCV	h^2	0.10±.06		8			
PCV	h^2	0.10±.05	Sheep	3	*Osp,Tsp*	N	Baker (1995a)
LogFEC	h^2	0.20±.08	(Menz	3			
			& Horro)				

1. FEC= Faecal Egg Count (egg per gramme); PCV= Packed Cell Volume
2. DPG= Kenya Dual Purpose Goat; D=Dorper; RM= Red Maasai; R=Romney; BHS= Blackhead Somali
3. Hc= *Haemonchus contortus*; Tsp= *Trichostrongylus* species; Osp=*Ostertagia* species
4. N=Natural; A=Artificial

Appendix 7 Selection experiments for resistance to internal parasites in sheep

Location[1]	Date started	Selection lines[2]	Selection criteria[3]	Type of infection[4]	Parasite species[5]	Breed	Reference
Armidale(CSIRO) Australia	1975	R.S.C	FEC + vaccination	A	*Tc*	Merino	Windon(1991) Woolaston & Eady(1995)
Armidale(CSIRO) Australia	1978	R.S.C	FEC	A	*Hc*	Merino	Woolaston (1990) Woolaston & Eady(1995)
Wallaceville New Zealand	1979	R.S	FEC	N	*Tsp,Osp*	Romney	Baker *et al.*(1991) Morris *et al.* (1995)
Armidale(UNE) Australia	1980	R.C	FEC	A	*Hc*	Merino	Albers *et al.*(1987) Woolaston & Eady (1995)
Ruakura New Zealand	1985	R.S.C	FEC	N	*Tsp,Osp*	Romney	Baker *et al.*(1991) Morris *et al.*(1995)
Ruakura New Zealand	1986	R.S	FEC	A	*Hc+Tc*	Perendale	Watson *et al.* (1992b) Morris *et al.* (1995)
Rylington Park West Australia	1987	R.C	FEC + Prod	N	*Tc+Oc*	Merino	Karlsson *et al.*(1991)
Hamilton,Victoria Australia	1988	R.S	FEC + LSA	N	*Oc*	Merino	Cummins *et al.*(1991)
France	1990	R.S	FEC + NIL	N+A	*Oc*	Romanov	Gruner(1991) Gruner & Lantier(1995)

1. CSIRO:- Commonwealth Scientific and Industrial Research Organisation,UNE:- University of New England.
2. R= Resistant; S= Susceptible; C= Control (random-bred unselected line)
3. FEC= Faecal Egg Count (egg per gram); LSA = Lymphocyte Stimulation Assay; NIL= Number of Infective Larvae ingested
4. A= Artificial; N= Natural
5. *Tc= Trichostrongylus colubriformis; Hc= Haemonchus contortus;*
   Oc= Ostertagia (Teledorsargia) circumcincta; Tsp= *Trichostrongylus* species; *Osp = Ostertagia* species

Appendix 8: Heritability(h^2) estimates for measures of resistance to ticks in cattle.

Trait	Parameter	Estimate	Breed	Number of sires	Infection	Reference
TC	h^2	0.42	var	6	A	Heweston, (1968)
TC	h^2	0.58	AX	DO	A	Seifert,(1971.)
		0.10	BX	DO		
		0.10	HS	DO		
TC	h^2	0.39	AIS	49	N	Wharton (1970)
TC	h^2	0.00	BX	36	N	O'Rourke, (1989)
TC	h^2	0.37	AX	71	N	Mackinnon *et al.*(1991)
TC	h^2	0.35	AXBX	1329	N	Mackinnon *et al.*(1991
TC	h^2	0.34	AX,AXBX	20	N	Mackinnon *et al.*(1991
TC	h^2	0.20	Friesian	-	N	Madalena, *et al.* (1985)

VAR= various breeds
HS= 50% Hereford x 50% Short horn
AX= 50% Africander x 25% Hereford x 25% Shorthorn
AXBX = 25% Hereford x 25% short horn x 25% Brahman x 25% Africander
BX= 25-75% Brahman or Sahiwal with remaining for Bos taurus
DO = Dam - Daughter regression
A - Artificial infection
N - Natural infection
Source Davis , (1993)

Appendix 9 Genetic(rg) and phenotypic(rp) correlation estimates between faecal egg count(FEC) or antibody Elisa assay (ELTC) and production traits in sheep

Source[1]	Trait1	Trait2[2]	rg±se	rp	Reference
Merino random bred flock (UNE) *Hc* infection	SqrtFEC (5 wk)	LWG(UNI)	-0.29±.26		Albers *et al.*(1987) (Sire model)
		WGR(UNI)	-0.02±.32		
		FD(UNI)	-0.26±.27		
		LWG(INF)	-0.68±.34		
		WGR(INF)	-0.66±.28		
		FD(INF)	-0.41±.24		
Merino random bred flock(CSIRO) *Hc* infection	LogFEC	CFW	0.10±31	0.12	Piper (1987) (Sire model)
		FD	-0.15±.26	-0.05	
		HBW	-0.42±.46	0.03	
Same as above (more relatives)	LogFEC	CFW	0.14	0.03	Woolaston (1990) (Animal model)
		FD	-0.14	-0.08	
		HBW	-0.15	0.01	
Merino *Hc* sel. lines (CSIRO)	Sqrt FEC (Control line)	CFW	-0.05	-0.06	Woolaston *etal.*,(1991) (Animal model)
		FD	0.11	-0.05	
		HBW	0.08	-0.08	
All lines, animal model		EL/EJ	-0.22		
Merino Random-bred Flock(Victoria) *Osp*-natural infection	LogFEC	CFW	0.22	-0.05	Cummins *et al.* (1991) (Sire model)
		FD	0.00	-0.09	
		WW	-0.20	0.02	
		HBW	-0.02	-0.17	
Romney lambs in New Zealand (Wallaceville) Natural Infection *(Tsp,Osp)*	LogFEC	LWG(INF)	0.02±.25	-0.09	Baker *et al.*(1991) (Sire model)
		Dag Score	-0.26±.24	-0.09	
Romney lambs in New Zealand (Wairunga) Natural infection *(Tsp,Osp)*	LogFEC	WW	-0.05±.22	-0.01	Bisset *et al.*(1992) (Sire model)
		BW(8mo)	-0.29±.22	-0.05	
		LWG(INF)	-0.36±.23	-0.05	
		HFW	-0.15±.18	-0.02	
		Dag Score	0.44±.19	0.11	
Romney lambs in New Zealand (5 N.I flocks) Natural infection *(Tsp,Osp)*	LogFEC	LGW	-0.24±.17	-0.02	Bisset *et al.*(1994) (Sire model)
		Dag Score	0.28±.16	-0.12	
		HBW	-0.46±.13	-0.08	
		HFW	-0.49±.12	-0.07	

Appendix 9. (Cont') Genetic(rg) and phenotypic(rp) correlation estimates between faecal egg count(FEC) or antibody Elisa assay (ELTC) and production traits in sheep

Source[1]	Trait1	Trait2[2]	rg±se	rp	Reference
Romney lambs in New Zealand (Wallaceville) Natural infection *(Tsp,Osp)*	LogFEC	LWG	-0.30	-0.12	Douch *et al.*(1995) (Sire model)
		Dag Score	-0.03	-0.13	
Apex Coopworth flocks, New Zealand *(Osp+Tsp)*	LogFEC (5mo)	WW	0.25±.15	-0.003	McEwan *et al.*(1994) (Sire model)
		WT(8mo)	0.15±.14	-0.04	
		HFW	0.14±.15	-0.04	
	LogFEC (7mo)	WW	0.21±.14	0.04	
		WT(8mo)	0.18±.13	-0.006	
		HFW	0.16±.14	-0.013	
	LogELTC (7mo)	WWT	0.10±.14	0.03	
		WT(8mo)	0.30±.12	0.12	
		HFW	0.03±.12	0.08	
Southern Romney Development Group flocks, New Zealand *(Osp+Tsp)*	LogFEC (5mo)	WW	0.06±.23	-0.01	McEwan *et al.*(1995) (Sire Model)
		WT(8mo)	0.24±.20	-0.03	
		HFW	0.02±.22	-0.02	
	LogFEC (7mo)	WW	-0.03±.21	-0.02	
		WT(8mo)	0.04±.18	-0.03	
		HFW	0.25±.18	0.02	
	LogELTC (7mo)	WW	0.45±.20	0.03	
		WT(8mo)	0.26±.18	0.06	
		HFW	0.16±.20	0.04	

1. *Hc= Haemonchus contortus; Osp= Ostertagia* species; *Tsp= Trichostrongylus* species
2. CFW = Clean Fleece Weight; FD= Fibre Diameter; HBW= Hogget(Yearling) Body Weight; WW = Weaning weight; LWG = Live Weight Gain; WGR = Wool Growth; (UNI) = Uninfected with parasites; (INF)= Infected with parasites; BW = Body Weight; HFW = Hogget Fleece Weight; EL/EJ = Ewes lambing/ Ewes joined(mated); Dag score = degree of breech soiling by faeces