Genetic resistance to gastro-intestinal nematode parasites in Red Maasai, Dorper and Red Maasai × Dorper ewes in the sub-humid tropics

R. L. Baker[1], D. M. Mwamachi[2], J. O. Audho[1], E. O. Aduda[1] and W. Thorpe[1]

[1]*International Livestock Research Institute (ILRI), PO Box 30709, Nairobi, Kenya*
[2]*Kenya Agricultural Research Institute (KARI), PO Box 16, Mtwapa, Kenya*

Abstract

Resistance to naturally acquired gastro-intestinal (GI) nematode parasite infections (predominantly Haemonchus contortus*) was studied in 166 Red Maasai, 230 Dorper and 294 crossbred (Red Maasai × Dorper) ewes in the sub-humid coastal region of Kenya. Live weights (LWT), blood packed-cell volume (PCV) and faecal egg counts (FEC) were recorded at mating, 3 months post mating, 1 week before lambing and 1, 2 and 3 months post lambing for four separate lambings that took place between 1993 and 1996. The Red Maasai ewes were more resistant to GI nematode infections than Dorper ewes as shown by their significantly lower FEC and significantly higher PCV at most of the sampling times over the reproductive cycle. The breed difference for FEC was significant in the lactating ewes but not in the non-lactating ewes. At most sampling times, the crossbred ewes were as susceptible as the Dorper ewes in terms of both PCV and FEC, particularly at the 1 and 2 month post-lambing samplings. Resistance was also manifested by a lower proportion of ewes having to be treated with an anthelmintic and a lower mortality rate in the Red Maasai than the Dorper. The Red Maasai ewes were significantly lighter by about 1 to 2 kg than the Dorper ewes at all sampling times. There was a significant increase in FEC and decrease in PCV over the first 2 months of lactation in lactating ewes compared with non-lactating ewes. This peri-parturient increase in FEC occurred in both breeds and the crossbreds but was more marked in the susceptible Dorper ewes.*

Keywords: *genetic resistance,* Haemonchus contortus, *humid tropics, sheep.*

Introduction

There is evidence that the indigenous Red Maasai sheep of East Africa are resistant to naturally acquired and artificial infections with gastro-intestinal (GI) nematode parasites and in particular to the highly pathogenic abomasal worm *Haemonchus contortus* (Preston and Allonby, 1978 and 1979; Baker *et al.*, 1994 and 1998b; Mugambi *et al.*, 1996 and 1997; Wanyangu *et al.*, 1997).

Lambs are usually more susceptible to infections with GI nematode parasites than mature sheep. However, it is well documented that lactating ewes are more susceptible than non-lactating ewes, mature rams or wethers (reviewed by Barger, 1993). This phenomenon usually gives rise to increases in faecal egg output in lactating ewes and is commonly known as the peri-parturient rise (PPR) in egg count. The cause of the PPR has been variously ascribed to poor nutrition, stress, lack of antigenic stimulation and hormonal suppression of immunity, of which the latter is considered to be the most likely cause (Barger, 1993).

A few studies have shown that breeds or selection lines that are relatively resistant to GI nematodes as lambs also show resistance in mature animals, particularly in lactating ewes. This results in either a reduced PPR, or absence of the PPR in lactating ewes in resistant breeds or resistant selection lines within breeds (Donald *et al.*, 1982; Courtney *et al.*, 1984; Zajac *et al.*, 1988; Woolaston, 1992; Romjali *et al.*, 1997; Morris *et al.*, 1998).

This paper reports a 5-year study (four lambings) investigating genetic resistance to GI nematode parasites in Red Maasai, Dorper and Red Maasai × Dorper sheep in sub-humid coastal Kenya. Both

Table 1 *Number of ewes in the study at mating, lambing and weaning by breed and year*

Effect	No. of ewes mated	No. of ewes at lambing			No. of ewes at weaning			
		Experimental		Control	Experimental			Control
		Lambed	Non-pregnant	Non-pregnant	Lactating	Lamb(s) died	Non-pregnant	Non-pregnant
Breed								
Dorper (D)	442	248	115	23	151	40	88	19
Red Maasai (R)	463	310	114	36	249	41	104	32
R × D	786	549	151	46	422	75	135	45
Year								
1992/1993	499	350	84	43	306	27	85	44
1993/1994	447	250	125	25	177	31	95	21
1994/1995	404	279	85	21	173	54	66	19
1995/1996	341	228	86	16	166	44	81	12
Overall total	1691	1107	380	105	822	156	327	96

pregnant/lactating and non-pregnant/non-lactating ewes were included in the experiment permitting the PPR in faecal egg counts to be investigated. Some preliminary results of this study have been reported by Baker *et al*. (1994 and 1998b)

Material and methods

Experimental site

This study was carried out at the Diani Estate farm located 20 km south of Mombasa in the sub-humid coastal region of Kenya. Rainfall is bimodally distributed with rainy seasons in March-June and October-December. Rainfall data were collected daily at Diani Estate and over the 5-year study period (1992-96); the average annual rainfall was 819 mm. The monthly mean maximum temperatures varies between 28 and 33°C, while relative humidity varies between 0·60 and 0·90 (Jaetzold and Schmidt, 1983). The soils on the farm are sandy, well drained and are characterized by very low levels of nitrogen and phosphorus, organic matter, cation exchange and water-holding capacity. The vegetation is composed of natural pasture and bush, with *Heteropogon contortus* and *Hyparrhenia rufa* the predominant perennial grass species.

Experimental design and data recorded

Over the study period, 442 Dorper, 463 Red Maasai and 786 Red Maasai × Dorper (R × D) matings occurred from 230 Dorper, 166 Red Maasai and 294 R × D ewes. The number of ewes recorded at mating, lambing and weaning by breed, year, their reproductive status (pregnant or non-pregnant) and physiological status post lambing (lactating and non-lactating) are shown in Table 1. Each year a small group of ewes (average number 22, ranging from 16 to 43) was deliberately not mated to compare their performance as non-pregnant or non-lactating controls with the non-pregnant/non-lactating experimental ewes.

Red Maasai sheep are a fat-tailed, hair breed which are principally associated with the Maasai tribe and are found in northern Tanzania and south-central Kenya. The Dorper breed was developed in South Africa in the 1940s at the Grootfontein College of Agriculture by interbreeding F1 crosses between the Black Head Persian and Dorset Horn breeds. The Dorper has a reputation for adaptability to harsh, arid conditions and was first imported into Kenya from South Africa in the 1960s. The Dorper and Red Maasai × Dorper (sire breed × dam breed) ewes were already present at Diani Estate at the start of the experiment in 1991. The Dorper flock was established by Baobab Farm by backcrossing purebred Dorper rams over a flock of about 300 Black Head Persian ewes starting in the late 1970s. The Dorper rams were purchased from the two to three flocks in Kenya that had established their flocks by importing purebred Dorper ewes and rams from both South Africa and Zimbabwe. It is estimated that the Dorper ewes used in this experiment were at least third generation backcrosses (i.e. 15/16 Dorper). The R × D crossbred ewes were bred by Baobab Farm between 1986 and 1990 for another experiment that investigated various management interventions to control endoparasite infections using both Dorper and R × D sheep (Bullerdiek, 1996). About 100 Red Maasai ewes were purchased from pastoralists in south-central Kenya in 1992. They were purchased from as wide a range of flocks and owners as possible to ensure that they were a representative genetic sample of the breed. They were not selected on any particular phenotypic characteristic, except that healthy, reasonable condition sheep were purchased.

Each year the three ewe genotypes (Dorper, Red Maasai, R × D) were mated to 12 Dorper and 12 Red Maasai rams in single-sire mating groups in a complete diallel design (Baker *et al.*, 1994 and 1998b) for a 6-week period. About seven or eight new rams of each breed were used at each mating so that 27 different Red Maasai rams and 29 different Dorper rams were used over the entire study. All Dorper and Red Maasai rams purchased were as unrelated as possible to ensure a representative genetic sample. The complete experiment included six crops of lambs (Baker *et al.*, 1998b), but the mating/lambing data of 1990/91 and 1991/92 are not included in this paper as the experimental protocol for sampling the ewes was different in these 2 years. In particular, the non-pregnant and non-lactating ewes were not sampled, which precluded any estimation of the PPR.

Each year, all ewes had live weights (LWT), faecal egg counts (FEC) and blood packed cell volume (PCV) recorded at mating, 3 months post mating, 1 to 2 weeks before lambing (hereafter called the lambing sampling), and 1, 2 and 3 (weaning) months after lambing. At the sampling times at mating, 3 months post mating and lambing all ewes were sampled in one group on 1 day. At the three post-lambing samplings there were usually two sampling dates to account for the 5- to 6-week spread in lambing. Faecal egg counts were determined using the modified McMaster method (Ministry of Agriculture, Fisheries and Food, 1977) with a lower limit of detection of 50 eggs per gram (epg) of faeces. PCV was measured by the microhaematocrit method. At each sampling time bulked faecal samples by breed were cultured and the larvae identified (Hansen and Perry, 1994).

In the first 2 years of the study (i.e. 1992/93 and 1993/94), if at any sampling time the FEC was greater than 4000 epg and/or if the PCV was less than 15% for an individual ewe, anthelmintic treatment was given to that individual ewe using either injectable Ivermectin or Levamisole and the treatment date recorded. In the last 2 years of the study (i.e., 94/95 and 95/96) anthelmintic treatment of individual ewes took place when the FEC was greater than 3000 epg and/or if the PCV was less than 20%. The only time all ewes in the flock were given a strategic anthelmintic treatment was at weaning to prepare them for the next mating, which usually took place about 1 to 2 months after weaning.

All ewes were sprayed with an acaricide (Triatix, Coopers, Kenya) every 2 weeks to control tick infestations and prevent tick-borne diseases. Whenever the PCV fell below 20%, infections with trypanosomes were monitored using the dark ground/phase contrast buffy coat technique (Paris *et al.*, 1982). This was to ensure that the anaemia being measured by PCV was due to *Haemonchus contortus* rather than to trypanosomosis, which also causes anaemia. While there have been reports of trypanosomosis in cattle on the same farm, no cases were diagnosed in the sheep during this study.

Statistical analyses

The traits analysed at each sampling time were LWT, PCV, FEC, percentage of ewes treated with an anthelmintic at each sampling time and the total number of anthelmintic treatments for each ewe each year. Because of a skewed distribution, FEC was analysed using a logarithmic transformation (LFEC, $\log_{10}$ (FEC + 25)). The results were back-transformed by taking anti-logarithms of the least-squares means (LSM) and presented as geometric means (GFEC). All statistical tests for FEC were applied to the transformed data.

LWT, PCV, LFEC and the total number of treatments with an anthelmintic each year were analysed using least-squares analysis of variance (Harvey, 1990; Statistical Analysis Systems Institute, 1989). The statistical model that was fitted varied with sampling time. At mating, 3 months post mating and at lambing the model fitted included the fixed effects of year (four classes), ewe breed (three classes), ewe age (four classes; 2, 3, 4, 5+ years) and physiological status (pregnant or non-pregnant experimental ewes and the non-pregnant controls). To ascertain which ewes were pregnant and non-pregnant at mating and at 3 months post mating it was necessary to make this classification retrospectively once lambing had been completed. However, some ewes died between mating and lambing (Table 1) and for the mating and 3 months post mating analyses it was necessary to add to the physiological status classification another class for ewes that died prior to lambing. At the three post-lambing sampling times the model fitted was the same except that the physiological status effect was modified to reflect the lactation status of the ewe (i.e., lactating or non-lactating (because the lamb(s) died) and non-pregnant/non-lactating experimental ewes and the non-lactating controls). At each sampling time, the first order interactions among the main effects were investigated in preliminary analyses; when significant ($P < 0{\cdot}05$) they were included in the final statistical model.

The analyses at each sampling time included all ewes alive at that sampling time regardless of whether

Table 2 *Least-squares means (LSM) and residual standard deviations (r.s.d.) at the different sampling times for ewe live weight (LWT, kg), packed cell volume (PCV, percent) and logarithm transformed FEC (LFEC, $\log_{10}$ (FEC (epg) + 25))*

Sampling time	LWT		PCV		LFEC	
	LSM	r.s.d.	LSM	r.s.d.	LSM	r.s.d.
Mating	27·7	3·9	26·0	3·6	2·55	0·60
3 months post mating	30·2	4·2	27·0	3·5	2·64	0·57
Lambing	29·2	4·0	24·7	3·5	2·55	0·69
1 month after lambing	28·0	3·4	23·8	3·6	2·77	0·57
2 months after lambing	27·7	3·5	24·3	4·0	2·76	0·69
3 months after lambing (weaning)	28·2	3·5	25·8	3·9	2·34	0·69

animals had been treated at the previous sampling time or not. In some years and at some sampling times (particularly at the samplings 1 and 2 months after lambing) a high proportion of sheep were drenched individually based on the PCV and FEC thresholds (Table 4). The consequences of this were investigated in additional analyses where the effect of treatment at the previous sampling (treated or not treated) was added to the statistical model for analyses of FEC, PCV and LWT. This effect was only significant occasionally and even when it was significant made little difference to the breed and physiological status effects.

The proportion of ewes treated with an anthelmintic at each sampling time was analysed by logistic-binomial regression using the generalized linear model procedure of GENSTAT (Payne *et al*., 1997), fitting the main effects of year, breed and physiological status. Ewe attrition and mortality were also analysed by logistic-binomial regression fitting the main effects of year and breed.

Analyses were carried out to estimate the repeatability of LWT, PCV and LFEC among measurement times pooled within years. A mixed model was fitted with year-breed-physiological status (YBP) and measurement time (six classes) as fixed effects and ewes nested within YBP as a random effect. Repeatabilities were also estimated for just the pregnant/lactating ewes from lambing to weaning (four sampling times), excluding all ewes that had been treated with an anthelmintic at any of these measurement times, except at weaning when all ewes were strategically drenched.

Results

LSM and residual standard deviations for LWT, PCV and LFEC at the six different sampling times are shown in Table 2. LFEC increased markedly at the samplings at 1 and 2 months after lambing, at which stage there was also a decline in PCV. The average coefficient of variation (residual s.d./LSM) over the six sampling times was 0·13 for LWT, 0·15 for PCV and 0·25 for LFEC.

The larval differentiation from bulked cultures from each breed/genotype and at each sampling time showed that the predominant larvae were *Haemonchus contortus* (mean 70%, range 50 to 89%), *Trichostrongylus* spp. (mean 22%, range 9 to 37%) and *Oesophagostomum* spp. (mean 8%, range 0 to 21%).

Breed effect

The Dorper ewes were consistently and significantly heavier than the Red Maasai ewes over the different sampling times ($P < 0\cdot01$), while the R × D ewes were either intermediate in weight between the two purebreds, or at three of the sampling times not significantly different in weight to the Dorpers (Table 3). The interactions of breed by year or breed by physiological status were not significant for LWT at any of the sampling times.

The Red Maasai ewes were more resistant to endoparasites than the Dorper ewes as shown by their higher PCV and lower GFEC at most of the sampling times (Table 3). PCV was significantly higher in Red Maasai ewes than in Dorper ewes at all sampling times, except at 1 month post lambing. At this sampling, there was a significant breed by physiological status interaction with lactating Red Maasai ewes having a significantly higher PCV ($P < 0\cdot05$) than lactating Dorper ewes (23·3% *v*. 22·1%, respectively), while there was no significant breed difference in PCV for the control non-lactating ewes (26·9% *v*. 27·0%, respectively). The R × D ewes were intermediate in PCV between the purebreds at the lambing sampling but were not significantly different from the Red Maasai ewes at the mating, 3 months post mating and weaning samplings, while at the samplings 1 and 2 months post lambing they had the lowest PCV.

The difference in GFEC between the Dorper and Red Maasai ewes was significant at some but not all the sampling times (Table 3). This was partly due to a significant breed by physiological status interaction post lambing, as illustrated in Figure 1. There was no interaction at the mating and 3-month post-mating samplings; GFEC in Red Maasai ewes was significantly lower than in Dorper ewes in both pregnant experimental ewes and in the non-pregnant control ewes ($P < 0\cdot05$). At the lambing and at the

Table 3 *Least-squares means by breed and physiological status for ewe live weight (LWT, kg), packed cell volume (PCV, percent), and the geometric mean of faecal egg count (GFEC, eggs per gram) at the six sampling times*

					Physiological status			
		Breed			Experimental ewes			Controls Non-pregnant
Sampling time	Trait	Dorper (D)	R × D	Red Maasai (R)	Pregnant		Non-pregnant	
Mating	LWT	28·8^{a}	27·5^{b}	26·8^{b}	28·1^{a}		28·1^{a}	26·8^{b}
	PCV	24·6^{a}	25·5^{b}	26·1^{b}	26·6^{a}		25·9^{b}	26·0^{ab}
	GFEC	525^{a}	376^{b}	378^{b}	327^{a}		366^{a}	365^{a}
3 months post mating	LWT	31·6^{a}	30·5^{b}	27·5^{c}	32·2^{a}		30·2^{b}	29·7^{b}
	PCV	24·6^{a}	26·7^{b}	26·3^{b}	27·7^{a}		26·1^{b}	27·6^{a}
	GFEC	651^{a}	512^{b}	412^{c}	405^{a}		446^{a}	436^{a}
Lambing	LWT	30·2^{a}	30·1^{a}	27·5^{b}	30·9^{a}		28·1^{b}	28·7^{b}
	PCV	23·7^{a}	24·7^{b}	25·8^{c}	24·4^{a}		24·2^{a}	25·6^{b}
	GFEC	354^{ab}	437^{a}	288^{b}	363^{a}		347^{a}	347^{a}
						Non-lactating		Controls Non-lactating
					Lactating	Lamb(s) died	Not lambed	
1 month post lambing	LWT	29·1^{a}	27·8^{b}	27·1^{c}	26·4^{a}	27·9^{b}	28·0^{b}	29·8^{c}
	PCV	24·0^{a}	23·0^{b}	24·5^{a}	22·4^{a}	22·6^{ab}	24·0^{b}	26·4^{c}
	GFEC	589^{a}	741^{ab}	457^{abc}	912^{a}	692^{ab}	490^{b}	380^{bc}
2 months post lambing	LWT	28·5^{a}	28·0^{ab}	26·7^{b}	26·1^{a}	27·1^{b}	28·8^{c}	28·9^{c}
	PCV	23·7^{a}	23·5^{a}	26·0^{b}	21·1^{a}	24·0^{b}	25·9^{c}	26·1^{c}
	GFEC	646^{a}	676^{a}	437^{b}	1000^{a}	490^{b}	603^{b}	372^{c}
3 months post lambing	LWT	28·8^{a}	28·5^{a}	27·4^{b}	26·3^{a}	27·5^{b}	29·5^{c}	29·6^{c}
	PCV	24·9^{a}	26·0^{b}	26·6^{b}	23·6^{a}	26·1^{b}	26·7^{b}	27·1^{b}
	GFEC	251^{a}	229^{a}	182^{a}	339^{a}	234^{b}	178^{b}	166^{b}

^{a,b,c} Means within each row and classification (breed or physiological status) with a different superscript are significantly different (P < 0·05).

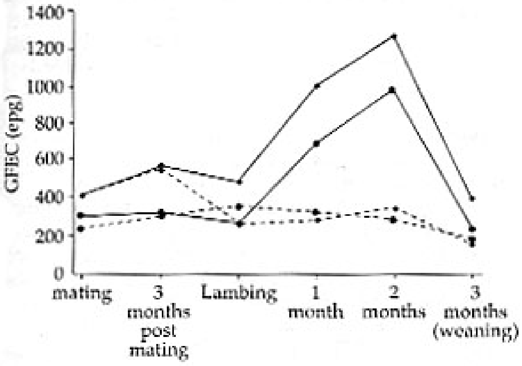

Figure 1 The periparturient rise in geometric mean of faecal egg count (GFEC) in lactating Red Maasai ewes (—●—), in lactating Dorper ewes (—•—) relative to the non-pregnant/non-lactating Red Maasai (- -●- -) and Dorper (- -•- -) ewes.

three post-lambing samplings, there was a significantly lower GFEC in the lactating Red Maasai than in the Dorper lactating ewes (P < 0·05) but no significant breed effect for the non-lactating control ewes. The breed differences in GFEC and PCV also resulted in a significantly higher proportion of Dorper ewes being treated with an anthelmintic (P < 0·05) at all sampling times except at mating and at 2 months post lambing and having significantly more anthelmintic treatments each year (P < 0·05) than the Red Maasai ewes (Table 4). The R × D ewes were not significantly different from the Dorper ewes in GFEC at the samplings post lambing.

The annual attrition rate in the number of ewes in the study over the four matings/lambings from mating to weaning was significantly higher (P < 0·01) in the Dorper ewes (0·324, s.e. 0·022) than in the R × D ewes (0·140, s.e. 0·012) or Red Maasai ewes (0·093, s.e.

Table 4 *Least-squares means (standard errors in parentheses) by year, breed and physiological status for the percentage of ewes treated with an anthelmintic at each sampling time and the total number of treatments*

	Percentage of ewes treated with an anthelmintic					
Effect	Mating (mtg)	3 months post mtg	Lambing (lbg)	1 month post lbg	2 months post lbg	Total no. of treatments
Year						
92/93	2·6 (0·7)	3·6 (0·8)	2·2 (0·7)	10·0 (1·4)	18·0 (1·8)	1·35 (0·051)
93/94	12·5 (1·5)	10·8 (1·4)	6·7 (1·2)	59·4 (3·4)	10·7 (1·7)	1·64 (0·054)
94/95	5·0 (1·1)	13·4 (1·6)	28·0 (2·2)	4·2 (1·1)	56·9 (2·2)	1·68 (0·062)
95/96	22·7 (2·3)	5·2 (1·3)	20·3 (2·2)	38·4 (2·8)	37·9 (2·9)	1·93 (0·071)
Breed						
Dorper (D)	12·4 (1·6)^a	13·7 (1·6)^a	21·4 (2·0)^a	24·0 (2·5)^a	30·8 (2·3)^a	1·74 (0·044)^a
Red Massai (R)	11·0 (1·3)^a	4·6 (1·0)^c	7·6 (1·1)^c	16·6 (1·5)^b	25·6 (1·8)^a	1·55 (0·044)^b
R × D	7·7 (0·9)^b	7·4 (0·9)^b	12·7 (1·2)^b	27·0 (1·4)^a	31·1 (1·5)^a	1·66 (0·036)^a
Status						
Pregnant/lactating	7·2 (0·8)^a	5·3 (0·7)^a	12·4 (1·0)^a	25·9 (1·2)^a	37·2 (1·4)^a	1·88 (0·024)^a
Lactating/lost lambs				29·7 (4·9)^a	23·7 (3·1)^b	
Non-pregnant	15·0 (1·5)^b	15·4 (1·7)^b	18·0 (1·8)^b	15·9 (2·4)^b	16·0 (1·9)^c	1·66 (0·036)^b
Controls	14·0 (3·5)^b	8·8 (2·8)^a	6·6 (2·7)^a	7·0 (3·5)^b	12·3 (3·4)^c	1·41 (0·077)^c

^{a,b,c} Means within each column and classification (breed or physiological status) with a different superscript are significantly different ($P < 0·05$).

0·013). Part of this attrition was due to ewes not being sampled at weaning (0·128) or those that were sold, culled or stolen (0·079). For the remaining ewes (117 Dorper, 87 R × D and 26 Red Maasai) both the date of death and cause of death were recorded. Based on these ewes the annual mortality rates were significantly different among the three genotypes ($P < 0·05$), and were 0·270 (s.e. 0·020) for the Dorper, 0·112 (s.e. 0·011) for the R × D and 0·054 (s.e. 0·010) for the Red Maasai. Overall, the two most important causes of mortality were haemonchosis (0·374) and pneumonia (0·187). A higher proportion of Dorper (0·405, s.e. 0·044) and R × D (0·377, s.e. 0·050) ewes died from haemonchosis than Red Maasai ewes (0·228, s.e. 0·080) but this difference was not significant.

Physiological status and the peri-parturient rise in egg counts

Figure 1 clearly shows that the PPR rise in egg counts (GFEC) occurred in both the Red Maasai and Dorper lactating ewes and peaked at 2 months post lambing. The same was true in the R × D ewes (not included in this Figure). Most studies on the PPR in sheep have utilized non-pregnant ewes as the non-lactating group, which have been compared with the lactating ewes to establish the magnitude of the PPR in egg counts. In this study, we included a randomly chosen group of ewes which were not mated and which were specifically designated as a non-pregnant/non-lactating group. At most of the sampling times the experimental and the control non-pregnant and non-lactating groups were similar for LWT, PCV and GFEC (Table 3). However, the non-lactating experimental ewes had a significantly higher GFEC than the control ewes at the sampling 2 months post lambing. There was also a significant interaction ($P < 0·01$) for year by physiological status for GFEC at the samplings 1, 2 and 3 months post lambing. This resulted in different magnitudes of the PPR in the lactating experimental ewes relative to the non-lactating control ewes in the different years (seasons). At the 2-month post-lambing sampling the experimental non-lactating ewes had significantly higher GFEC than the non-lactating control ewes in 2 years ($P < 0·05$), while in the other 2 years there was no significant difference in GFEC. As was expected, the lactating ewes at the 1- and 2-month post-lambing samplings had a significantly higher proportion of ewes treated with an anthelmintic than the experimental or control non-lactating ewes (Table 4).

Repeatabilities and correlations

Repeatabilities pooled within year, breed and physiological status among sampling times from mating to weaning were 0·70 (s.e. 0·01) for LWT, 0·22 (s.e. 0·01) for PCV and 0·01 (s.e. 0·01) for logarithm transformed FEC (LFEC). The repeatabilities were also estimated separately for each breed/genotype but there were no significant differences in the estimates. The phenotypic correlations within sampling time were 0·38 for LWT and PCV ($P < 0·01$), −0·14 for LWT and LFEC ($P < 0·01$) and −0·31 for PCV and LFEC ($P < 0·01$). Repeatabilities for just the non-drenched, lactating ewes from lambing to weaning pooled within year and breed were 0·71 (s.e. 0·03) for LWT, 0·26 (s.e. 0·06) for PCV and 0·34 (s.e. 0·06) for LFEC.

Discussion

Breed differences for resistance to endoparasites

This study confirms earlier reports that Red Maasai sheep are more resistant to GI nematode parasites than Dorper sheep (Preston and Allonby, 1978 and 1979; Mugambi *et al.*, 1996 and 1997; Wanyangu *et al.*, 1997). The present study is part of a larger experiment at this research site (Baker *et al.*, 1994 and 1998b). The purebred and crossbred lambs generated by the ewes evaluated in this study were also evaluated for their resistance to GI nematode parasites (FEC and PCV) and for productivity (growth and mortality), from birth to about 1 year of age. The Red Maasai lambs were more resistant to endoparasites than the Dorper lambs as shown by their lower FEC (ability to control the worm burden and/or the worm fecundity), higher PCV (ability to control anaemia caused by *Haemonchus contortus* infections) and markedly lower pre-weaning and post-weaning mortality (Baker *et al*, 1998b). Significant breed differences in both FEC and PCV were apparent when the lambs were weaned at 3 months of age and persisted up to 1 year of age.

Previous studies (Preston and Allonby, 1978 and 1979; Mugambi *et al.*, 1996 and 1997; Wanyangu *et al.*, 1997) which have investigated resistance to endoparasites in Red Maasai sheep, all concentrated on measuring the parasitological variables (e.g. FEC, PCV and worm burdens after necropsy) in experiments with small numbers of sheep for each breed. There was no attempt made to carry out a more comprehensive evaluation where breed resistance is related to total flock productivity and potential economic returns to smallholder farmers, which has been an important objective of the present study. The ewe reproduction and productivity data will be published separately but preliminary analyses have been completed (Baker *et al.*, 1998b; Baker, 1998). These clearly show that the combined effects of a higher reproductive rate, lower lamb and ewe mortality and similar yearling live weights, result in an approximately three-fold increase in the number or weight of yearling sheep available for sale in a purebred Red Maasai *v.* a purebred Dorper flock (Table 5). There is therefore a very clear economic advantage for farming the more resistant Red Maasai sheep rather than the Dorper in coastal Kenya and other humid/sub-humid regions of East Africa.

The previous evaluations of Red Maasai and Dorper sheep have all been undertaken in either the cool highlands (close to Nairobi) or semi-arid highlands (Naivasha) of Kenya. There is no evidence for breed by environment interaction for resistance to endoparasites as the Red Maasai are consistently the more resistant breed in each of these environments. However, there is evidence for a breed by environment interaction for lamb growth, mature size and ewe reproduction, where the Dorper sheep perform better and grow faster than the Red Maasai in the drier, less humid climates (Inyangala *et al.*, 1992; Kiriro, 1994). Dorper sheep are not well adapted to a sub-humid environment and their low reproductive performance and high ewe and lamb mortality at Diani Estate resulted in the purebred Dorper flock being difficult to sustain (Table 5).

Table 5 *Productivity of flocks of purebred Dorper and purebred Red Maasai sheep at Diani Estate, Mombasa, Kenya (1991-1996)*

Trait	Dorper	Red Maasai
Production		
No. of ewes mated (1991-96)	853	457
Ewes lambing per ewes mated	0·66	0·75
Prolificacy (lambs born/ewes lambing)	1·02	1·02
Lamb mortality (birth-yearling)	0·66	0·28
Yearling live weight (kg)	19·7	18·4
Offtake (1 year)†		
No. of sheep	11	35
Total live weight (kg)	217	644

‡ Offtake based on a 100-ewe flock with a 20% female replacement rate and all male progeny and non-replacement females alive at one year of age making up the potential offtake.

Repeatabilities

The objectives of this experiment were to quantify both between- and within-breed genetic resistance to endoparasites. There was insufficient pedigree information for the ewes to enable estimation of heritabilities and genetic correlations. However, it was possible to estimate repeatabilities among the measurement times for the ewes and the estimates were high for LWT (0·70, s.e. 0·01), moderate for PCV (0·22, s.e. 0·01) and not significant for LFEC (0·01, s.e. 0·01). However, the repeatability of LFEC from lambing to weaning for just the undrenched, lactating ewes was 0·34 (s.e. 0·06). The effect of drenching at any sampling time is clearly shown in Table 4 in terms of the percentage of ewes drenched in the different years at different sampling dates. This moderate within-year repeatability for LFEC in undrenched lactating ewes is similar to the high estimate reported for undrenched, lactating Romney ewes in New Zealand of 0·50 (s.e. 0·04) (Morris *et al.*, 1993). Moderate to high repeatabilities for LFEC have also been reported by Doligalska *et al.* (1997) in natural pasture infections of undrenched Wrzosowka ewes in Poland. This Polish study also clearly showed that repeatabilities were higher between measurements taken close together in time (1 to 2 weeks) than when samples were taken at intervals of 3 to 4 months. Heritabilities for LFEC and PCV for the lambs in this study have been estimated (Baker *et *al.*, 1998b; Baker, 1998) and were found to increase from non-significant estimates in weaner lambs to moderate estimates (0·10 to 0·20) in lambs from 6 to 12 months of age.

The peri-parturient rise in egg counts

This study has shown that the PPR in FEC occurs in both Dorper and Red Maasai sheep as has been well documented in other sheep breeds in temperate (Barger, 1993) and tropical climates (Romjali *et al.*, 1997). The significant difference in the magnitude of the PPR between the Dorper and Red Maasai lactating ewes (Figure 1) was consistent with the results reported by Wanyangu *et al.* (1997). Because a significantly higher proportion of Dorper ewes were treated with an anthelmintic than the Red Maasai ewes at the lambing and the 1-month post-lambing samplings, the difference between the two breeds in the PPR shown in Figure 1 is an underestimate.

Other studies have also shown breed differences in the magnitude of the PPR. In the USA, Courtney *et al.* (1984) found that spring-lambing domestic ewes (Rambouillet or Finnish Landrace-Dorset × Rambouillet) exhibited a marked PPR in FEC (the challenge was primarily *Haemonchus contortus*), while imported hair breed ewes from the Caribbean (St Croix and Barbados Blackbelly) and the indigenous Florida Native ewes exhibited little or no PPR. When winter-housed, pregnant Florida Native (resistant breed) and Dorset × Rambouillet (susceptible genotype) ewes were studied through pregnancy and parturition/lactation, both FEC and total worm counts were significantly lower in the Florida Native ewes. Breed differences were apparent for worm numbers of *Haemonchus contortus*, *Ostertagia circumcincta* and *Trichostrongylus axei* (Zajac *et al.*, 1988). The PPR was studied in four sheep breeds and crosses in the hot, humid conditions of North Sumatra in Indonesia (Romjali *et al.*, 1997). The predominant parasite was *Haemonchus contortus*. The indigenous Sumatra thin tail sheep had the highest PPR while the PPR was significantly lower in Barbados Blackbelly × Sumatra crossbred ewes.

The Indonesian study (Romjali *et al.*, 1997) and other studies (Gruner *et al.*, 1992; Woolaston, 1992; Tembely *et al.*, 1998), showed a significant effect of litter size on the PPR with ewes suckling twins having a significantly higher FEC than those suckling singles. The effect of litter size could not be investigated in the present study because the prolificacy in this environment for both breeds was low (Table 5) and the few twins that were born mostly died soon after birth. However, in the goats that were also evaluated at Diani Estate and which had a higher prolificacy than the sheep (Baker *et al.*, 1998b), there was an effect of litter size on FEC. There was also a significantly higher PPR in Galla than in Small East African lactating does (Baker *et al.*, 1998a).

Experimental design

The experimental design used in this study probably resulted in an underestimation of the true genetic difference in resistance to endoparasites between the three genotypes. All the ewes were grazed together and managed uniformly to meet the requirements of a valid breed comparison for the production traits. If, however, they had been grazed in separate paddocks at the same stocking rate the Red Maasai ewes and lambs would have had a lower exposure to endoparasites than they experienced in this study. This may also have important effects on the epidemiological parameters and anthelmintic treatment (drenching) requirements in farming systems which utilize resistant *v.* susceptible genotypes (Bishop and Stear, 1997). Preliminary experimental evidence to support this contention is accruing from the establishment of a nucleus flock of Red Maasai sheep at another farm in coastal Kenya (R. L. Baker *et al.*, unpublished). In this flock drenching of individual Red Maasai sheep occurs only when the PCV of lambs post weaning falls below 16% and the PCV of ewes falls below 13%. A flock of about 100 ewes has been established and after 2 years only two ewes and four lambs have been drenched. The pre-weaning mortality from the first crop of 82 lambs born was 5% compared with 10% in the Red Maasai lambs in the Diani Estate experiment (Baker *et al.*, 1998b). Mugambi *et al.* (1997) compared the resistance to endoparasites of 15 yearling sheep of each of four breeds (Red Maasai, Blackheaded Somali, Dorper and Romney) with each breed grazing a separate paddock for 1 year with no anthelmintic treatment. In this study the Red Maasai was clearly the most resistant breed both in terms of maintaining the lowest FEC, the highest PCV and the lowest mortality. The FEC in the Red Maasai sheep remained below 1000 epg throughout the 1-year study.

Conclusion

In conclusion, Red Maasai sheep are resistant to infections with GI nematode parasites and particularly *Haemonchus contortus*. In addition, Red Maasai sheep have the ability to maintain good levels of production when under severe and persistant endoparasite challenge. Based on these results, ILRI has now initiated a new experiment to generate six large double backcross resource families utilizing the resistant Red Maasai and the susceptible Dorper sheep. These will be used to identify genetic markers linked to quantitative trait loci that control resistance to infections to GI nematode parasites and particularly *Haemonchus contortus*.

Acknowledgements

We are extremely grateful to Dr Rene Hailer, Managing Director, Baobab Farm for provision of land, animals and facilities at Diani Estate for this research. We also wish to thank Dr J. Rowlands for statistical advice and useful comments on an earlier version of the manuscript. This is ILRI publication no. 98071.

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(*Received* 10 *December* 1998 — *Accepted* 24 *February* 1999)