Methodological illustration of genotype x environment interaction (GxE) phenomenon and its implications: A comparative productivity performance study on Red Maasai and Dorper sheep breeds under contrasting environments in Kenya.

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Introduction

The greatest desire and goal of an animal breeder is to match the genetic potential of a given livestock breed type to the prevailing or anticipated production environment. The environment may in this case, refer to the production system, climate or could be broad enough to include the entire continuum from production system (management, type of feed, feeding, housing health management etc) to animal product market requirements. More often, one livestock breed (A) may out-perform another breed (B) in a given environment (Y), but not in another environment (Z). Alternatively, whereas breed (A) may out perform breed (B) in both environments Y and Z, the magnitude of performance differences in each of the two environments might be quite different. Besides, the differences may significantly vary from one another. This phenomenon is what is generally referred to as genotype by environment interaction (G x E).

When faced with alternative breed and production environment choices, the need to ascertain the existence, non-existence and extent (magnitude) of G x E is usually critical. Decisions on breed choices when production environments vary widely without due regard to G x E can lead to expensive failures (Cunningham and Syrstad 1987; Madalena et al. 1990a; 1990b; Payne and Hodges, 1997). Breeding programmes that involve introduction of exotic breeds to local environments, as replacement to indigenous breeds that were hitherto often thought to be inferior to the exotic ones are the most common culprits when it comes to ignoring G x E (Devendra and Burns 1983; Cunningham and Syrstad 1987; Madalena et al. 1990a; 1990b; Payne and Hodges 1997; Saithanoo et al. 1993; Nepane 2000; Workneh et al. 2002).

While the need to first verify the existence and extent of G x E prior to wider introduction and commercial use of an exotic livestock breed may seem to be a matter of common scientific sense, this is invariably the case. In developing countries, common examples exist where technical assistance from developed countries that are associated with exotic breeds introductions have not been subjected to rigorous scrutiny and well thought out utilization programmes (Devendra and Burns 1983; Payne and Hodges 1997; Saithonoo et al. 1993; Workneh et al. 2002). On the other hand, whereas verification of G x E may on the surface appear to be a simple comparative breed characterization exercise, in practice it is invariably that simple to carry out appropriately. In order to accurately evaluate breeds and fully demonstrate G x E, the study design must be appropriate, the information collected sufficient and reliable (Gibson and Cundiff 2000). To be able to make the right breed or genotype choices and/or their combinations, use should be made of results obtained from G x E evaluation studies that are not only comprehensive, but in which sufficient accounts are given to the various traits that contribute to overall productivity under the production environments of interest.

Helminths constitute one of the most important constraints to ruminant livestock production in the tropics (Fabyi 1987). Widespread infection with internal parasites in grazing animals, associated production losses, anthelmintic costs, the proportions and deaths of infected animals are some of the major concerns. In environments where helminths are endemic and rates of infestations risk are high, it would be therefore desirable to investigate the extent to which livestock, especially the sheep and goat breeds differ in their ability to resist and/or tolerate helminthes. In such studies, particular attention should be paid to the various component traits (reproduction, survival, growth and milk yield) of productivity and efficiency that are usually affected by helminthosis, the magnitude of such effects to the each of component traits, for the respective genotypes and prevailing environments.

The problem

It is a well-established fact that, because different breeds have been developed under different levels of parasite challenge, they have evolved to have genetic ability to resist or tolerate disease (Baker 1995; Preston and Allonby 1978; Preston and Allonby 1979; Wanyangu et al. 1997; Baker et al. 1999 and 2003). However, the phenomenon has not been widely exploited in livestock breeding, especially in making breed choices in, and for environments where the parasites/diseases are endemic, like the humid tropics. Several factors could be attributed to such omissions. One is that the concept of genotype by environment (G x E) interaction is often seen as being rather difficult to demonstrate quantitatively with respect to traits such as resistance/tolerance to parasites and the diseases they cause. This is because; first, the parasites, especially at lower levels of challenge, often cause qualitative rather than quantitative damages; second, their effects are usually impacted at various levels, and most of the time, such effects are difficult to clearly separate and globally quantify. For example, for sheep production in the tropics, helminthosis may lead to, poor ewe condition during pregnancy and the subsequent lactation periods hence, poor nursing ability which in turn results in low lamb weaning weights at the ewe flock levels.

Using only the breeds' comparative total weight of young weaned per ewe lambing, to assess the extent to which a given breed tolerates/resists helminths would therefore be insufficient. This is because helminthosis affects ewe fertility and the lambs rearing ability during the subsequent parities as well. Furthermore, helminthosis also causes ewe and lamb mortality (Wanyangu et al. 1997; Baker et al. 1999; Nguti et al. 2003). In addition it reduces ewe fertility and lengthens lambing intervals among the surviving ewesand also causes delayed reproduction (older age at first lambing) among the ewe lambs that survive. Also, delayed market age and size for castrates are common consequences of this condition. All these effects additively impact on the overall individual animal and flock productivity and should be critically considered before passing judgment as to the suitability or superiority of a given sheep breed or genotype for a given production environment/system, especially when considering breed introductions or replacement strategies and options.

Because a parasite such as *H. contortus* affects the various traits and sheep breeds differently, resistance of the host animal also manifests itself equally differently among the breeds and traits. It would be therefore prudent to undertake breed evaluation studies that fully bring out the existence and extent of genotype by environment interaction under relevant conditions (i.e. those that are as similar to the natural grazing patterns as possible). Results of such studies would then be used for making knowledge-based, hence better breed choices and formulation of appropriate and sustainable breeding programmes. In turn, participating farmers would realize their breeding goals and optimal benefits.

However, studies involving tropical sheep and goat breeds that are designed to reliably quantify the magnitude and direction of G x E are very scarce. The few that are documented have not been comprehensive enough, having generated insufficient information. For example, many studies in which temperate exotic and tropical sheep and goat breeds and their crosses have been evaluated or compared in tropical Africa and Asia, and under smallholder farmer conditions, hardly looked at the efficiency with which the final product (total weight of meat or milk off take) was converted from the unit input (the carrying capacity unit per year), (Chemitei 1978; Preston and Allonby 1978; Preston and Allonby 1979; Devendra and Burns 1983; Agwenyi 1986; Ruvuna et al. 1988a; 1988b; Ruvuna et al. 1989; Inyangala et al. 1992; Ruvuna et al. 1992a; 1992b; Ruvuna et al. 1995; Wanyangu et al. 1997; Okeyo et al. 2001; Workneh et al. 2002; Neopane 2000). Neither did such previous studies comprehensively look at the G x E issue with respect to the resistance to *H. contortus*, especially with regard to the differential predisposing environmental conditions and the resulting relative productivity and efficiency of the two breeds. The set of studies, which are subject of this case study, are exceptions to most of the previous ones and therefore have made very valuable contributions in this area (Baker 1998; Baker et al. 1999, 2002 and 2003).

There is therefore need to undertake studies that employ a variety of analytical tools and methods in order to give a more complete picture as to how various breeds perform under contrasting local production systems or environments. Such methodologies need to adequately take into account, all aspects of reproductive, survival (both young and adult) and growth to market weight. In order to achieve this, study designs must be comprehensive and appropriate analytical statistical methods employed on the results to fully demonstrate the G x E effects.

For example, given the discrete nature of survival data, in order to correctly estimate mortality rates across breed groups, age groups, years, seasons etc., including any interaction effects between these causal factors, the data must be transformed into logit form to normalize the variances and thus avoid biases when least squares analyses are to be run on the original observations as such. It is only then that the mean rates obtained from such analyses can be reliably factored in to subsequently estimate mean breed productivity and efficiency values. Besides, when dealing with traits such as parasite tolerance that are usually measured indirectly through the use of faecal egg count (FEC) and blood packed cell volume (PCV), due care need to be further taken to transform the observed values accordingly before running the desired analyses to normalize the variances, given that faecal eggs counts, by their very nature, exhibit skewed distribution (Baker et al. 1999 and 2003).

This case study briefly describes and presents results from a series of studies that were carried out in two contrasting locations in sub-humid (1991 to 1996) and semi arid (1998 to 2000) regions of Kenya by ILRI scientists. The design, data collection and use of various combinations of analytical methods and statistical procedures to fully bring out and indeed, reliably illustrate the components of the G x E concepts and implications are highlighted. In particular, this case study illustrates and demonstrates how *sufficient, relevant and reliable breed characterization data (information)* can be used as powerful decision making tools when designing sustainable genetic improvement programmes for indigenous and exotic livestock breeds under varying production systems and/or environments. Two sheep breeds (the Red Maasai and Dorper) kept under contrasting production environments in Kenya are used. An environmentally important adaptive trait-tolerance and resistance to a notorious tropical gastro-intestinal parasites (*H. contortus*) is used here to illustrate how one single factor can ultimately influence magnitude of G x E in many different ways. Haemonchosis, which is a complex phenomenon that is exhibited at different traits levels of an infested animal's life, is the main determinant of, or driving force behind the observed G x E interaction. The background to the set of studies was given elsewhere by Baker (1998).

Experimental sites and protocols

Experimental sites

The first study was undertaken at Diani Estate of Baobab Farm Ltd., in the humid coastal region of Kenya (Baker 1998; Baker et al. 1999 and 2003). Red Maasai (R), Dorper (D) and their crosses were evaluated at this site between 1991 and 1996. The second study was initiated in 1997 at Kapiti Plains in the semi-arid highland region of

Kenya to generate double-backcross resource families (Mugambi et al. 2003). Six F_1 (Red Maasai/Dorper) rams were mated to both Red Maasai and Dorper ewes. However, this study focuses mainly on the purebred Red Maasai and Dorper sheep. Matings continued at 6-monthly intervals until by December 2000 six lamb-crops, about 200 backcross lambs per family had been produced. In addition, in each lamb crop small numbers (20-30) of purebred Red Maasai and purebred Dorper lambs were also produced and over the 6 lamb crops 15 Red Maasai and 16 Dorper rams were used. The mating design is given in Table 1a, while a summary of the statistical methods employed during the study are given in Tables 1b.

Table 1b: *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-preg.	Non-preg.	Lactating	Lamb(s) Died	Non-preg.	Non-preg.
Breed								
Dorper (D)	442	248	115	23	151	40	88	19
Red Maasai ®	463	310	114	36	149	41	104	32
RxD	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**

Experimental protocol.

The predominant GI parasites at both experimental sites were *H. contortus* and *Trichostrongylus spp.* The experimental protocol to assess resistance to GI parasites at Diani Estate was described in detail by Baker (1998) and Baker et al. (1999 and 2003). Briefly, all lambs were weighed at birth and had live weight (LWT), faecal egg count (FEC) and blood packed cell volume (PCV) recorded at 1, 2, and 3 months of age, then treated with an anthelmintic and weaned. They were then grazed on pasture until a monitor group of about 40-50 lambs, which were sampled every week, reached an average FEC of about 1500-2000 eggs per gram (epg). When this threshold mean FEC was reached all animals in the grazing group were weighed and FEC and PCV recorded on two consecutive days. Then all lambs were drenched and the procedure repeated until they reached about a year of age. The experimental protocol for lambs at Kapiti was identical from birth to weaning. After weaning the lambs were subjected to just one pasture challenge (lambs 4 to 6 mo of age) and then an indoor trickle challenge for about 5-7 weeks with *H. contortus*. The ewes at both sites had LWT, PCV and FEC recorded six times during the reproductive cycle: at mating, 3 months after mating, 2 weeks before lambing and 1, 2 and 3 months after lambing.

Statistical analysis.

The breed effects reported in this paper for lambs were derived from least squares analysis of variance of single-born lambs fitting, when significant ($P<0.05$), main effects for year of birth (Diani data), lamb crop (Kapiti data), breed/crossbreed, sex, age of dam, age of lamb (birth date for analysis of birth weight) as a linear covariate and any significant interactions. Breed effects for ewes were derived from analyses of variance fitting breed, year of birth or lamb crop, ewe age and any significant interactions. Faecal egg counts were logarithm transformed ($\log_{10}$ (FEC+25)) to normalize the variance (Table 1b).

Fitting of different ewe reproductive status (pregnant and non-pregnant) and physiological status (lactating and non-lactating) was made in order to factor out the known biological effects that would influence the response variables of interest (LWT, FEC and PCV) at mating, 3-months post-mating, 1-2 weeks pre-lambing and every month post-lambing (Table 1b). Also, based on the previous experimental evidence, the FEC and PCV were monitored for different age groups of the lambs (1-month- weaning; weaning to 6-months and 6-month to 1 year) of age.

Table 1c: The statistical transformations and linear models applied to the data and traits of interest

Experimental Group/ Parameter	Data and Transformation made	Independent fixed effects & Covariables (Co)							
		Year	Breed/ cross	Sex	Reprod. status	Physiol. Status-L	Dam age class	Lamb age (Co)	Interactior

Mature ewes									
LWT (kg)	None	✓	✓	NA	✓	✓			
PCV	None			NA					
FEC	Log_{10}(FEC+25)	✓	✓		✓	✓			
% Ewes treated	Logistic-bionomial.	✓	✓	NA					
Total No. of treatments/ewe/yr	Logistic-bionomial.	✓	✓						
Mortality rate%	Logistic-bionomial.	✓	✓						
Lambs									
LWT (kg)	None	✓	✓	✓	✓	NA	✓	✓	✓
PCV	None					NA			
FEC	Log_{10}(FEC+25)	✓	✓	✓	✓	NA	✓	✓	✓
*Mortality rate%	Log_e(y/1-y)	✓	✓	✓	✓		✓	✓	✓

LWT= Live weight (kg); FE = Faecal egg count (eggs/gram); PCV = Blood packed cell volume
*Mortality (y=0 (Died); y=1 (survived)
NA= Not applicable.

Results and discussion

The results of the ewe live weight, packed cell volume (PCV), faecal egg counts (FEC) and reproduction data for the two sites are summarized in Table 2, illustrated in Figure 1a and 1b and discussed in detail elsewhere by Baker et al. (1999). Table 3 summarizes the results for the same traits for the lambs, including lamb mortality (%), while Table 4 gives the overall flock productivity and efficiency for the two breeds in the two sites (environments).

Table 2: *Least squares means for ewes of the Red Maasai (RM) and Dorper breeds for live weight (LWT, kg), packed cell volume (PCV, %), the anti-log of logarithm faecal egg count (ALFEC, eggs per gram) and reproduction at the two experimental sites*

Traits	Kenya - humid[A] (1991 – 1996)		Kenya – semi-arid[A] (1998 – 2000)	
	RM	**Dorper**	**RM**	**Dorper**
No. ewes mated (EM)	442	807	1015	1055
LWT-mating	27.7[a]	30.6[b]	30.2[a]	46.1[b]
PCV-mating	26.1[a]	24.6[b]	33.3[a]	31.4[b]
ALFEC-mating	378[a]	525[b]	204[a]	178[a]
PCV – lactating ewes	24.0[a]	22.2[b]	28.3[a]	26.0[b]
ALFEC – lactating ewes	692[a]	988[b]	2187[a]	3090[b]
EL/EM[B]	0.80[a]	0.65[b]	0.78[a]	0.73[b]
LB/EL[B]	1.02[a]	1.02[a]	1.01[a]	1.16[b]
LW/LB[B]	0.93[a]	0.73[b]	0.95[a]	0.89[b]
LW/EM[B]	0.71[a]	0.48[b]	0.73[a]	0.70[a]
Annual mortality	0.05[a]	0.27[b]	0.068[a]	0.081[a]

[A] Means with different superscripts are significantly different (P<0.05).
[B] EL = ewes lambing; LB = lambs born; LW = lambs weaned.

Table 2 and Figures 1 a and 1b clearly show that, from FEC and PCV results, the lactating Red Maasai ewes had significantly lower PPR and mean FEC and lower mean FEC, hence higher tolerance/resilience to the *H. contortus* parasite than their Dorper counterparts. However, among the controls, the picture was somewhat different, in that the non-drenched and open Red Maasai ewes, had higher FEC at lambing and thereafter till 2 months post-portem compared to the Dorper ewes. This shows that physiological status with respect to this trait is important.

The levels of tolerance/resilience for the two breeds differ, depending on the physiological status and the traits being considered. This particular component of the results demonstrates a level of G x E that is neither frequently documented nor given due attention. For example, at mating, the difference is smaller, and then it increases steadily post-mating, all through to 2 months into lactation, after which it decreases (Figures 1a and 1b). The fact that tolerance/resistance differs among ewes depending on both their physiological status (internal environment) and breed is itself of practical significance. It calls for strategic parasite infestation management or control among a relatively resistant breed. This would be even more crucial in situations where Dorper and Red Maasai ewe flock are raised and herded together.

The results from the controls alone give an incomplete picture, hence making any conclusions based on such information alone, inappropriate as the differences in mean productivity and efficiency of the ewe flock (Table 4), which takes into account the effects of the parasite on both the ewe and their lamb crops, gives a more complete picture (Figure 4).

Breed effects: Ewes

At the humid coast environment, the Red Maasai ewes had a significantly higher overall reproductive rate (LW/EM) than Dorpers while in the highlands there was no significant breed difference because Dorpers had much better reproductive performance than on the coast (Figure 2a).

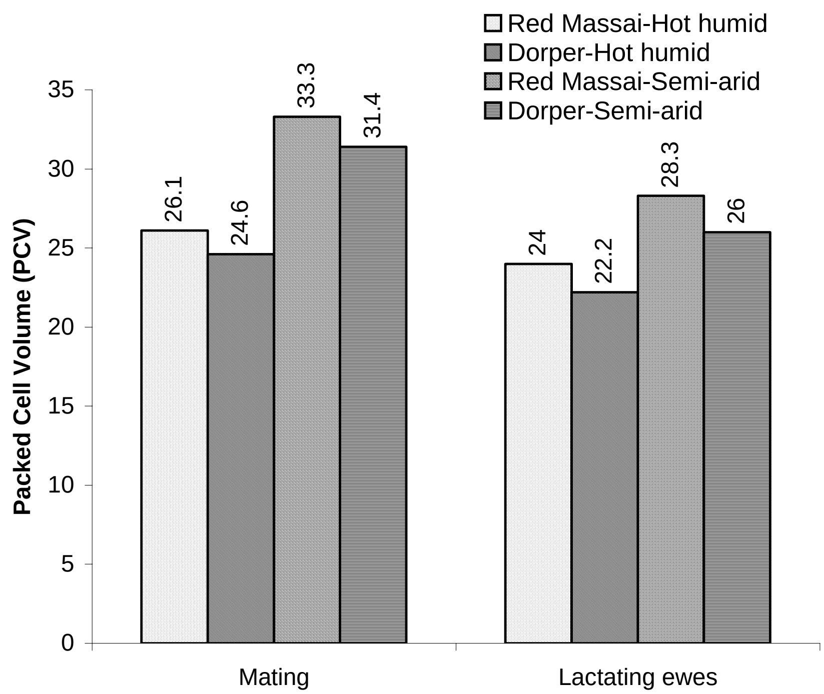

Figure 1a. Packed cell volume of blood from ewes at mating and lactation at the Hot-humid and Semi-arid sites.

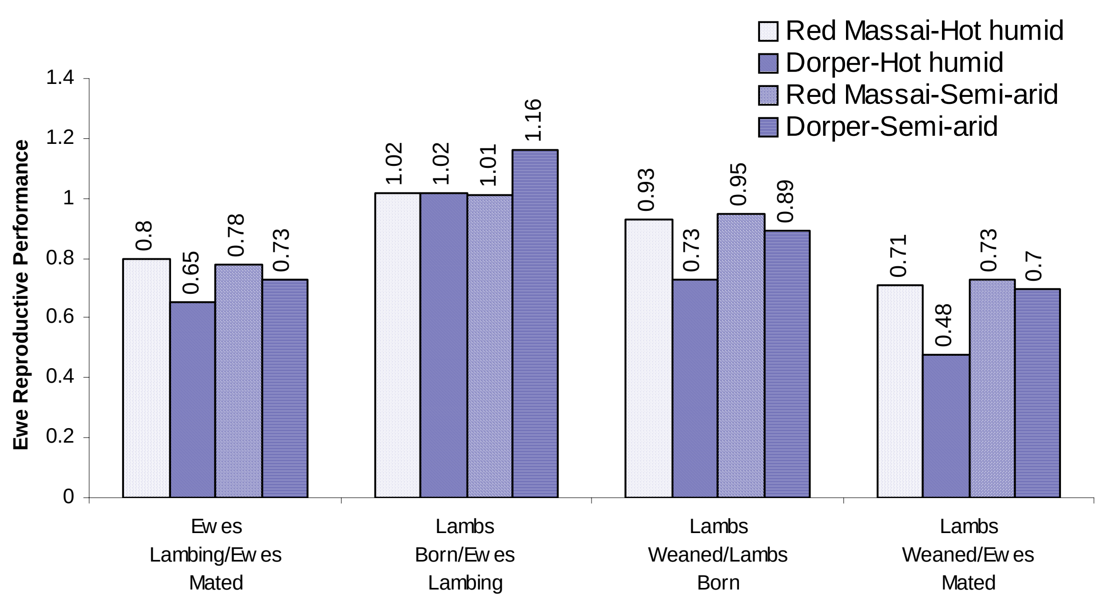

Figure 1b. Reproductive performance of ewes under Hot Humid and Semi-arid environments.

While the Dorper ewes were significantly heavier than Red Maasai ewes at both sites they showed their growth superiority much more clearly in the semi-arid conditions at Kapiti to which they were better adapted. This is another level of G x E, being exhibited in the form of differential growth potential by the two breeds in the two sites. Red Maasai ewes were significantly more resistant to GI nematodes than Dorpers at both sites as shown by their higher PCV and lower ALFEC (except at mating at Kapiti) both in dry ewes (at mating) and in lactating ewes.

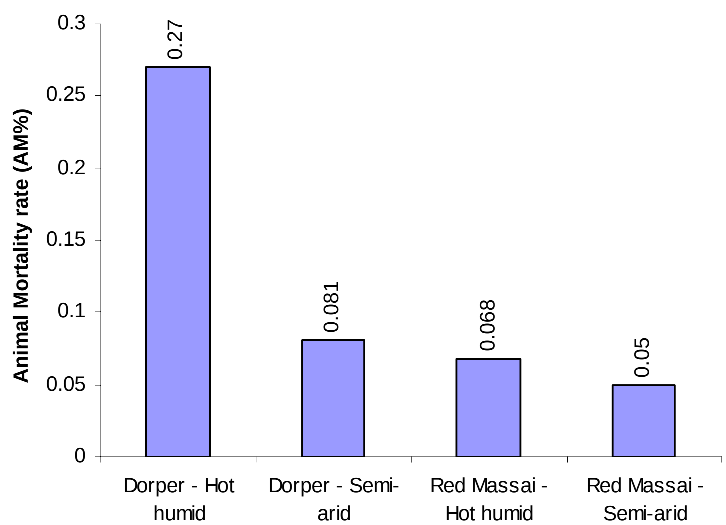

Figure 2. Annual mortality rate of Red Massai and Dorper lambs under the Hot-humid and Semi-arid environments

Breed effects: Lambs

Red Maasai lambs had a significantly higher PCV than Dorper lambs at 3 and 6 months of age at both sites (Table 3 and Figure 3a). Consistent breed differences for ALFEC were also found for 6-month-old lambs at both sites (Red Maasai having lower egg counts), but in 3-month-old lambs there was a significant breed effect for ALFEC at Kapiti but not at the coast (Figure 3b). Consistent with ewe performance, the LWT for Dorper lambs was higher at the drier Kapiti than at the more humid coast resulting in the Dorper lambs being about 50% heavier than the Red Maasai lambs at Kapiti but only 5-10% heavier at the coast (Figure 3c). Conversely, the Dorper lambs had a much higher mortality rate (28.3%) compared to Red Maasai lambs (9.9%) at the coast than at Kapiti, where the respective lamb mortality rates for the two breeds were 5.4% and 3.1% (Figure 3d).

Table 3: *Least squares means for single-born lambs by breed for live weight (LWT, kg), packed cell volume (PCV, %) the anti-log of logarithm faecal egg count (ALFEC, epg) and mortality (%)*

Traits	Kenya- humid[A]		Kenya – semi arid[A]	
	RM	D	RM	D
Number born	216	318	156	99
Live weight (LWT) at birth	2.3^{a}	2.5^{b}	2.9^{a}	4.1^{b}
Number weaned	182	226	152	95
LWT at 3 mo	10.1^{a}	11.0^{bc}	13.0^{a}	20.2^{d}
Packed cell volume (PCV)	27.8^{a}	24.2^{b}	35.1^{a}	33.3^{b}
ALFEC	676^{a}	832^{a}	741^{a}	1698^{b}
LWT at 6mo	13.0^{a}	14.2^{b}	15.2^{a}	24.5^{d}
PCV at 6mo	24.6^{a}	21.9^{b}	26.1^{a}	21.0^{c}
ALFEC at 6mo	1950^{a}	2818^{b}	$8{,}128^{a}$	14125^{c}
LWT at 12mo[B]	17.5^{a}	18.4^{b}	20.0	30.0
Mortality (%)				
Birth to 3mo	9.9^{a}	28.3^{b}	3.1^{a}	5.4^{a}
3mo to 12 mo	15.9^{a}	44.7^{b}	2.0^{a}	10.0^{b}

[A] RM = Red Maasai, D = Dorper. Means with different superscripts are significantly ***different (P<0.05).*** [B] ***LWT at 12 mo at Kapiti (semi-arid) interpolated from 9 mo LWT.***

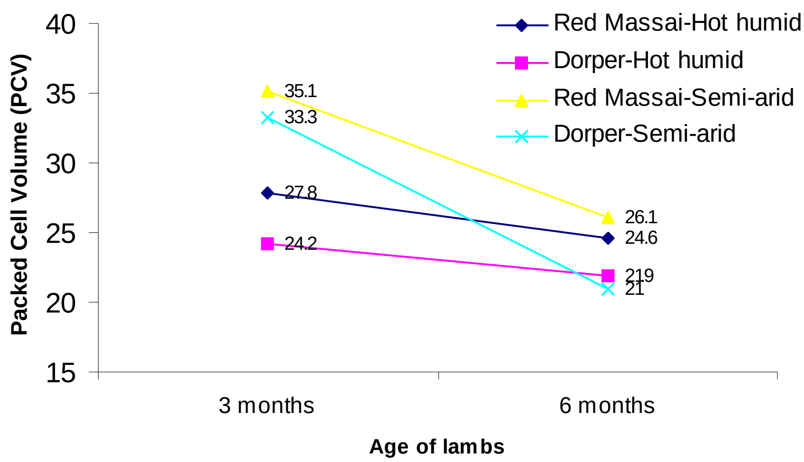

Figure 3a. The relationship between packed cell volume, lamb age, breed and environment under *Heamonchus* challenge.

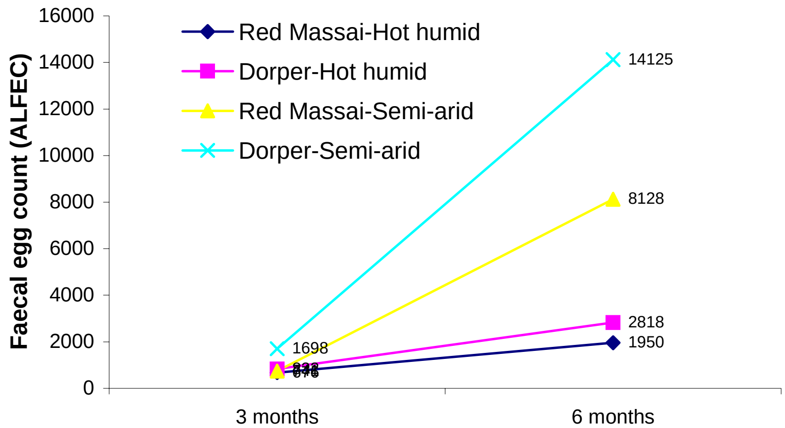

Figure 3b. Effect of lamb breed, age and environment on faecal egg count (ALFEC).

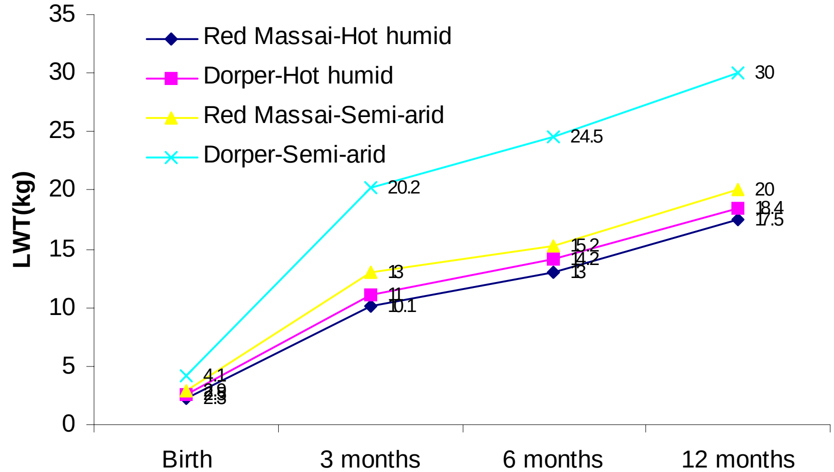

Figure 3c. Effect of lamb, breed, age and environment on lamb live weight.

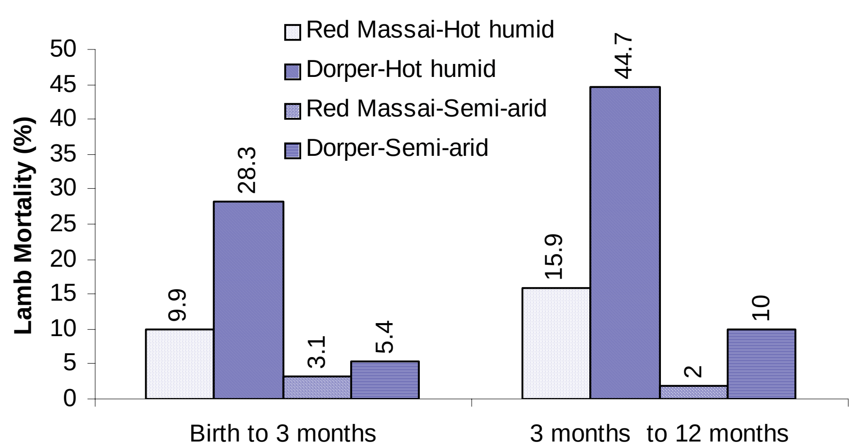

Figure 3d. Lamb mortality rate by breed, age group.

Breed effects: Flock productivity and efficiency

Flock productivity (Table 4 and Figures 4a, b and c) was derived from the parameters in Tables 2 and 3. Productivity was computed as the number or weight of yearling sheep for sale based on a 100-ewe flock with a 20% female replacement rate with all the male progeny and non-replacement females alive at one year of age making up the potential offtake. At the coast the Red Maasai sheep were about 3-fold more productive than Dorper sheep in terms of either the number of sheep for sale or weight of sheep for sale (Figure 4a). The Dorper sheep were non-sustainable at the coast at a 20% replacement rate so the 3-fold difference in off-take is in fact, an under-estimate. However, in the drier but higher rangelands (Kapiti) there was a much smaller advantage for the Red Maasai over the Dorper in terms of number of sheep for sale (20%) (Figure 4a), while in terms of weight of sheep for sale, the Dorpers were more productive than the Red Maasai by 25% (Figure 4b).

Efficiency was estimated as kg total offtake per Carrying Capacity Unit (CCU) per year (Figure 4c), using the livestock production efficiency approach (James and Carles 1996). The Red Maasai were about 5 fold more efficient than the Dorper at the coast and the negative efficiency value for the Dorpers indicates that they were not sustainable in this humid environment (Table 4). In contrast, there was no significant difference between the breeds for efficiency in the semi-arid environment (Figure 4c).

Table 4: *Flock productivity and efficiency of the Red Maasai (RM) and Dorper breeds*

Traits	Kenya - humid (1991 – 1996)		Kenya – semi-arid (1998 – 2000)	
	RM	Dorper	RM	Dorper
Productivity - offtake				
No. sheep for sale	40	13	48	40
Weight of sheep (kg)	700	239	960	1200
Efficiency				
Kg/CCU[A]/year	153.9	-36.5	164.8	167.5
Ratio	5.2	1.0	5.5	5.6

[A] One CCU = 100 mega joules of metabolisable energy per day.

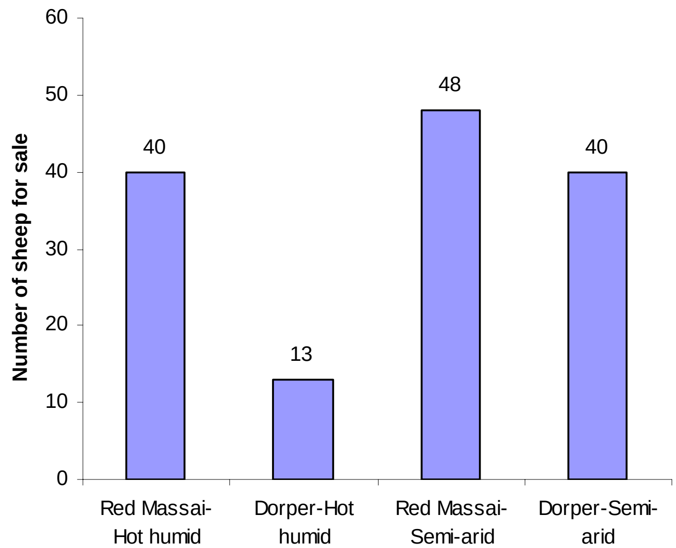

Figure 4a. Effect of breed and environment on number of sheep available for sale.

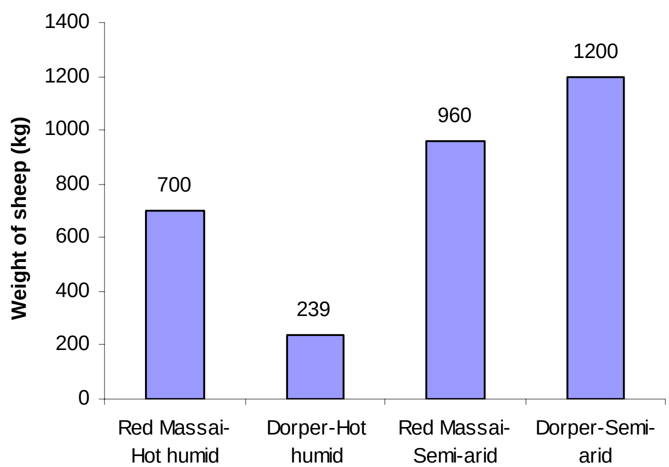

Figure 4b. Effect of breed and environment on sheep productivity

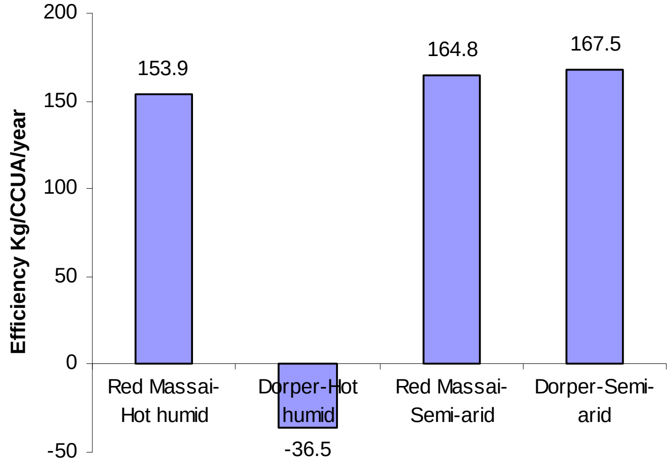

Figure 4c. Effect of breed and environment on flock efficiency.

Earlier comparative studies involving the two breeds by Chemitei (1978) concluded that the Dorper was more productive than the Red Maasai. Such results were however based in research station environments, and did not take into account the differential lamb and ewe mortality rates in the two breeds, hence underestimated the true differences between these breeds in terms of productivity. Such results, could have led to undue promotion of the Dorper breed, even in production environments where it is less suited compared to the Red Maasai.

Besides, the series of studies undertaken by Kingoku et al. (1975), Chemitei (1975) and (1978) were based on flocks that were regularly drenched, although, parasitic challenge from resistant *H. contortus* strains could still have had some differential effect on both breeds, particularly with regard to the studies by Chemitei (1978), given the fact that O'lmagogo station in which the study was conducted was a much wetter site, hence much greater impact of *H. contortus* challenge on mortality and flock productivity would have been expected, especially among the Dorpers.

It should be noted however, that as of 1978, no widespread cases of resistance to the anihelmintic in use then by *H. contortus* had been reported in Kenya. Nevertheless, a more critical look at the most of these earlier comparative studies (Kingoku et al. 1975, in drier environments; Chemitei 1975; 1978, in wetter environments) and when the reported relative mortality rates and growth performance among lambs and ewes for the two breeds were factored-in and the reported productivities re-calculated, it can be safely be concluded that, generally in wetter environments, the Red Maasai was indeed more productive than the Dorper and vice versa. This could explain the fact that despite their rigorous introduction campaigns in the more wet and humid Nyanza's Macalder station by Kenya's Ministry of Agriculture, the Dorper flock never survived there.

Conclusions and implications

C*onclusions*

Important shortcomings of much of the published literature on breed comparisons for resistance to GI nematodes in sheep and goats are that the most of the previous experimental designs were inadequate (small numbers of animals per breed, inadequate sampling, etc.) and there was no attempt to relate parasitological parameters for resistance to breed overall productivity or efficiency (Baker, 1998). Through appropriate experimental designs and by employing various analytical methods both these issues have been addressed in the studies presented here.

The results of the series of experiments show that there were important but differential breed by location (environment) interactions for LWT, mortality rates and reproduction rates. When all these parameters were combined it was found that the indigenous Red Maasai sheep were 3- to 5-fold more productive and efficient than Dorper sheep in the humid coastal environment (Table 4). In the semi-arid environment Dorper sheep were slightly more productive than the Red Maasai, but there was no significant difference in flock efficiency between the breeds.

Implications

Because G x E phenomenon is exhibited at different levels: 1) reproduction; 2) growth; 3) mortality; 4) product quality and 5) overall flock/herd productivity/or efficiency), due care should be taken to make farmers be aware of all these, so that they can make knowledge-based breed or breed combination choices, depending on their production systems, environment, including the existing market policies. Because, butchers and meat consumers might be willing to pay a premium or lower price/kg of mutton depending on whether it is of Dorper or Red Maasai, studies should be undertaken to quantify these. Results from such studies would give an even more complete breed comparative picture in a market oriented mutton production system.

Researchable areas and questions

1. Given the current body of knowledge, how can the contrasting merits of these two breeds be optimized in production systems under conditions similar to those where the study was undertaken?

2. What other studies would one undertake to help complete the story with due regard to production to consumption processes as to the relative merits of the two breeds?

3. What are the alternative methods that one would employ to demonstrate the existence or lack of G x E interaction for other ruminant livestock species and types under field conditions?

4. What additional practical challenges are presented in terms of experimental design and performance recording of traits such as tolerance/ resistance to parasites, given that the dead lambs and ewes, although dead, will have nevertheless caused undue challenge to the surviving individuals, through heavier pasture contamination by having released a much larger parasite egg numbers before they actually succumb to the parasite challenge and die, than would otherwise be the case if only the tolerant individuals grazed such pastures?

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