Optimisation of breeding schemes for litter size, lambing interval, body weight and parasite resistance for sheep in Kenya

Else Verbeek[1,3], Egbert Kanis[1], Rawlynce C Bett[2] and Isaac S Kosgey[3]

[1]Animal Breeding and Genetics Group, Wageningen University and Research Center,
P.O. Box 338, 6700 AH Wageningen, The Netherlands
[2]Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences (SLU), Animal Science Center (HVC), Undervisningsplan 4 A, P.O. Box 7023, 750 07 Uppsala, Sweden
[3]Department of Animal Sciences, Egerton University,
P.O. Box 536, 20115 Egerton, Kenya
isaac_kosgey@yahoo.co.uk / isaacs.kosgey@gmail.com

Abstract

The current study optimised breeding schemes for litter size (LS), lambing interval (LI), body weight (BW) and gastrointestinal parasite resistance for sheep in Kenya. Selection for the breeding goal traits was performed in a conventional way using information on phenotypes only. For gastrointestinal parasite resistance, information on genetic makers was used, with faecal egg count (FEC) as an indicator trait. Selection for parasite resistance was partly based on field measurements and the possibilities for marker-assisted selection (MAS) were explored. Several selection schemes were defined based on whether a classical selection only was used (Latin number 1), a quantitative trait loci (QTL) for FEC was assumed to be available (2), that the correlation between FEC and BW was assumed to be positive (unfavourable-Roman I) or negative (favourable- II) and finally how FEC was included in the index (i.e., no inclusion (A), with FEC (B) or with FEC QTL (C-F)). The schemes with overlapping generations were evaluated using the computer program SelAction. Rams, ewes and total selection responses in US dollars ($) per animal, and rams' and ewes' accuracies for each scheme with a favourable or unfavourable correlation were estimated.

The differences in total selection responses between schemes that did not include FEC in the selection index resulted in a response of $0.16 in scheme 1AI and $0.20 in scheme 1AII. In schemes 1BI and 1BII, FEC was included in the index. The responses in scheme 1BI and 1BII were $0.165 and $0.217, respectively. The increase in response in schemes II compared with schemes I was due to a favourable correlation between BW and FEC. The different FEC index traits had a different effect on economic response. It should be noted that increased emphasis on selection for FEC will reduce the relative responses to the breeding goal traits BW, LS and LI. Consequently, the goal of selection for FEC should be to maintain acceptable levels of gastro-intestinal parasite resistance as well as sufficient improvement of LS and BW.

Keywords: Breeding programs; gastro-intestinal parasite resistance; sheep; Kenya

Introduction

Selection for disease resistance should be an important component of small ruminant breeding programs in the tropics because of its large negative impact on production. Of paramount importance is gastro-intestinal parasite resistance, which is defined as the enhanced ability to prevent establishment of nematode larvae and promote the elimination of any that do establish. Gastro-intestinal parasite resistance can only be measured indirectly by methods like faecal egg count (FEC), in which the number of nematode eggs in the faeces of the sheep are counted (Douch et al 1996). There are several limitations to the use of FEC as a field indicator for gastrointestinal parasite resistance. If a genetic marker for FEC would be available, selection for FEC could avoid the cost and difficulty of field measurements and be ethically more acceptable. Genetic markers could be used to identify specific regions on chromosomes, known as Quantitative Trait Loci (QTL). A quantitative trait is usually affected by a large number of genes from which a QTL constitutes only one or some of the genes that affect the phenotype. The other relevant genes are called polygenes. Both the QTL and the polygenes determine the total genetic variation of the particular trait. However, the actual QTL of an animal cannot be observed directly and, therefore, a marker linked to the genotype is required to obtain information on the QTL. The distance between the genetic markers and the QTL is a function of the recombination fraction between them. The closer the distance between marker and QTL the more certainty about the genotype at the linked QTL. Although QTL effects do not explain all the genetic differences between animals and cannot be observed directly, they could be useful in estimating the true genotype of the animal and, subsequently, increase the accuracy of the estimated breeding value. At this moment, no genetic marker for FEC is available, but optimistic results for detection of a QTL have been found (Schwaiger et al 1995). The breeding program was designed for Kenyan smallholder farmers in particular. The aim of this study was to optimize breeding schemes for litter size (LS), lambing interval (LI), body weight (BW) and gastro-intestinal parasite resistance.

Materials and methods

Population structure

Figure 1 is a schematic representation of the flock dynamics in the closed nucleus. A nucleus is assumed with 774 dams and 15 sires (mating ratio 1:52). These animals have to produce their own replacements and should provide the commercial population with high quality breeding stock. Near the equator, all year round breeding is possible although there might be some seasonal differences in ovulation rates (Turner 1985). Age at birth of first progeny of the dam is 24 months and from that moment on, every eight months 1.2 lambs are born. Assumed is that only one lamb per ewe is weaned. This means that every ewe will produce three weaned lambs in two years, 50% male and 50% female. Dams are used for five lambings and are 56 months old when they give birth to their fifth lamb. Weaning age of the lambs is three months, which means that the dams will be part of the nucleus until 59 months of age. Ewe mortality is assumed to be 10% every lambing period of eight months. The sires are used for one breeding cycle only and

are sold to the commercial population afterwards. High quality lambs that are not selected and the dams that have reached the maximum of five lambings but are still performing above average could also be sold to the commercial population.

Figure 1. Flock dynamics in the closed nucleus

Per eight months, 189 females and 15 males are needed for the replacement of the first age class. Information on LI is only available when the dams have had at least two lambings. Consequently, all progeny born from all nucleus ewes that had at least two lambings are selection candidates and are selected by truncation on the index. It is assumed that ten percent of the dams (19 dams) die or are culled between their first and second lambing and, therefore, only 774-19= 755 dams will produce selection candidates. There are in total 0.7 x 755 x 0.5 = 265 female and 265 male lambs available for selection, assuming that 70% of the lambs weaned survive until 12 months of age. Assumed is also that only 90% of the selected sheep at 12 months of age will survive until the age of 24 months when their first progeny is born. One hundred and eighty nine replacement females and 15 males are required at 24 months and, therefore, 210 females and 17 males have to be selected at 12 months of age.

Definition of the breeding objective

Breeding goal traits

For practical reasons, the breeding goal traits and selection index traits are defined exactly the same. The breeding objective traits are shown in Table 1.

Table 1. Traits in the breeding objective and selection criteria

Trait	Unit	Abbreviation
Breeding objective		
Litter size	Average number of lambs weaned per ewe over parities 1 and 2	LS
Lambing interval	Time (days) between 1st and 2nd parity	LI
Body weight	Individual live weight (kg) at 12 months of age	BW
Faecal egg count	Number of parasite eggs per gram of faeces at 5 and 12 months	FEC
Selection criteria		
Females only		
Litter size	Average number of lambs weaned per ewe over parities 1 and 2	LS
Lambing interval	Time (days) between 1st and 2nd parity	LI
Males only		
Faecal egg count	Number of parasite eggs per gram of faeces at 5 and 12 months	FEC
Faecal egg count, QTL	Quantitative trait loci	FECQTL
Both males and females		
Body weight	Individual live weight (kg) at 12 months of age	BW

The selection index

Fertility traits

To get information on LS and LI, it would be necessary to record these traits during the dam's entire reproductive life. However, this means that information will only be available at the end of the dam's life span and it will take a lot of effort and costs to record all lambings. Another possibility is to include only the dams' information on first and second lambing LS and LI, which will reduce the generation interval. At the time the male and female selection candidates born from a first parity ewe are 12 months old, their dams will have their second lamb weaned and this information could be included in the index of both the male and female selection candidates. To measure LS and LI, the surviving lambs of every ewe should be counted at weaning, and this information has to be included in the selection index. Equally, the date of lambings and the exact number of days between the two successive lambings have to be recorded for every ewe. Fertility traits included in the index are shown in Table 1.

Body weight

Selection for a heavier body weight is a way to increase the households' nutrition or income. Small ruminants are rarely slaughtered at weaning, so body weights at 6, 8 or 12 months will be more important criteria for selecting replacement animals. Additionally, weaning weight is not a reliable indicator for future performance in unstable environments. Consequently, in this study,

the trait is defined as 12-month live body weight. Body weight will be measured on both males and females only once at 12 months of age using a balance (Table 1).

Faecal egg count

It will be possible to include two classical measurements of FEC in the index. However, the first measurement should not take place before the age of 4 months. The reason is that there is a possibility that genetically acquired resistance becomes only apparent at four months of age (Stear and Murray 1994). The FEC will be measured at 5 and 12 months of age. The average value of these will be included in the index. To reduce the costs of the breeding program, FEC will be measured only in males. In case that a QTL for FEC is available, this information will be included in the selection index (Table 1).

Economic values

After definition of the breeding objective, economic values have to be derived. The economic value is defined as the effect on the objective function (i.e., profit) of a marginal (one unit) change in the genetic level of that trait, while keeping all other traits that are included in the breeding objective constant (Hazel 1943). Because detailed economic assessments of costs and returns in the tropics are rare, many breeding objectives have been defined in biological terms (Franklin 1986; Kosgey et al 2003). This means that instead of using economic weighting factors to define the aggregate genotype, weighting factors based on biological efficiency are used, and costs and returns are expressed in units of energy and/ or protein. But because it is not possible to express all costs and revenues in terms of energy and protein, this method is not ideal. However, studies by Kosgey et al (2003 and 2004) have calculated several economic values applicable on Kenyan small ruminant production systems using a profit function. A profit function is a single equation that describes the change in net economic returns as a series of physical, biological and economic parameters. Gicheha et al (2005) used a profit function to calculate the economic value for FEC.

Economic values for BW, LI and LS in this study are taken from Kosgey et al (2004). However, the economic values for LI and LS had to be adapted to fit the definitions of this study while the economic value for BW (0.02$) could be taken directly. The economic value for FEC (-1.20$) is taken from Gicheha et al (2005). The economic values taken from the foregoing studies are suitable for smallholder conditions taking into account only tangible benefits from small ruminant production. All economic values are expressed per ewe per year. A short explanation on the calculation of the economic values will follow; more details are available from Gicheha et al (2005) and Kosgey et al (2003 and 2004).

In the studies by Kosgey et al (2003 and 2004), a deterministic model was used to describe the quantitative relationships between levels of genetic merit for the traits considered and levels of output of the farm. The total annual profit of the flock was derived as the difference between costs and revenues of the system and expressed in US dollars ($). Equations 1-9 presented below were used to calculate the economic values.

Equation 1 describes the annual profitability of the sheep flock (T_f):

$$T_f = [N_e \times (R_e - C_e)] - C_{FCF} \quad (1)$$

where N_e is the number of ewes in the flock per year, R_e the average revenue per ewe per year, C_e the average variable costs per ewe per year, and C_{FCF} the fixed costs per flock per year.

The revenue (R_e) was calculated from equation 2 as the sum of three revenues:

R_e = surplus yearlings meat revenues + cull-for-age ewes' and rams' meat revenues +

manure revenues (2)

The variable costs were calculated from equation 3 as the sum of three costs:

C_e = feed costs + management costs + marketing costs (3)

In many smallholder situations, feed availability is often scarce due to seasonal rain patterns or restriction of the available land for grazing. Consequently, the economic values were calculated with fixed feed resources. Management costs were calculated per adult animal. For healthcare, three components were considered; general drugs and veterinary services, anthelmintics and ecto-parasite control. Feeding management in the form of mineral supplements was also included. Labour requirements were calculated by assuming one shepherd per 100 head of sheep working for eight hours a day. Marketing costs were calculated by summing the average costs incurred between buying of a live animal and selling its carcass. This included costs for transport of a live animal to the market, auction, slaughter, and carcass inspection and transport.

The economic value for LS was modified and derived from the economic value of Kosgey et al (2004) designated here as LSK. The LSK was defined as "average number of lambs born over parities per ewe lambing per year". However, the definition of LS in this study is "average number of lambs weaned over parities one and two". The economic value of LSK ($12.94) should be multiplied by 1.5 to get the economic value for LS ($19.41) at time of birth. To get the economic value at time of weaning, the economic value for LS needs to be divided by the fraction of surviving lambs at weaning (3 months of age) which is 0.925. Therefore, the economic value for LS ($) is as shown in equation 4:

$$19.41/ 0.925 = 20.98 \quad (4)$$

The economic value for LI is derived from LSK (Kosgey 2004) as follows: every year an ewe gives birth to 1.5 lambs. This means that a lamb is born after 365/1.5 = 243.3 days. Reducing the lambing interval by one day will result in the birth of 365/ 242.3 = 0.031 more lambs. The number of more lambs born should then be multiplied with the value of one lamb, which is equal to the economic value of LS. Because the lambing interval has to be reduced, the economic value is negative. The economic value for LI ($) is calculated from equation 5 as:

$$- 0.031 \times 20.98 = - 0.65 \quad (5)$$

Economic values for FEC were taken directly from Gicheha et al 2005. The method used in that study was based on the method by Sivarajasingam (1995); in this method, and for a given set of assumptions, the breeding objective is matched to the expected responses in production traits, and responses in these traits maximized relative to overall gains. The breeding goal in the study by Gicheha et al (2005) consisted of FEC at 12 months of age and 12-month live body weight.

Genetic and phenotypic parameters

Genetic and phenotypic parameters for LS, LI and BW were sourced from the literature (Kosgey et al 2004). The genetic parameters for FEC were also taken from the literature but were contradicting in many of the literature sources. The genetic and phenotypic parameters are presented in Table 2.

Table 2. Left side: heritabilities (diagonal), genetic correlations (below diagonal) and phenotypic correlations (above diagonal), favourable genetic and phenotypic correlations between FEC and BW in parentheses. Right side: population means, heritabilities, phenotypic standard deviations (σ_p) and economic values (EV) in US dollars ($)

Trait[a]	LS	LI	BW	FEC(x1000)	mean	σ_p	EV ($)
LS	0.10	0.10	0.26	0.10	1.00 animals	0.28	20.98
LI	0.11	0.07	0.50	-0.05	243.0 days	5.00	-0.65
BW	0.20	0.10	0.25	0.08(-0.08)	25.0 kg	2.87	1.02
FEC (x1000)	0.10	-0.05	0.30(-0.20)	0.25	1.40 eggs x 1000	1.50	-1.20

[a]see Table 1 for description of traits

The correlations between FEC and BW varied widely from positive to negative. The reason for this might be that correlations between FEC and BW estimated from a number of flocks could be influenced by genotype by environment interactions (Eady et al 1998). Consequently, the most positive literature correlations between FEC and BW (0.30 genetic and 0.08 phenotypic) were taken from Baker (1995) and the most negative correlations (-0.20 genetic and –0.08 phenotypic) were taken from Eady et al (1998) and Swan et al (1998). Information about correlations between LS and FEC and LI and FEC was scarce. Vanimisetti et al (2004) calculated the regression coefficients of the number of lambs born per 100 ewes lambing (NB) and fertility in autumn lambing (FF) on a standardized FEC (log (FEC + 25)). The regression of FF on FEC was not significant but the regression coefficient of NB on FEC was found significant ($P < 0.09$). However, the number of observations to estimate the correlations between FEC and fertility traits were not adequate. Woolaston et al (1991) studied the effects of FEC on reproductive rate and found that there were no adverse effects. A study by Morris et al (200) showed that a low FEC sheep line had more reproductive successes compared to a high FEC line. However, neither of these studies calculated a correlation between FEC and reproduction. Although both phenotypic and genetic correlations of FEC with LS and LI are missing, it can be assumed from the foregoing discussion that they will be close to zero. In the current study, it is assumed that the genetic and phenotypic correlations are equal: correlations between FEC and LS are assumed to be 0.1 and correlations between FEC and LI are assumed to be –0.05. These could be inaccurate assumptions and more research is needed to calculate more reliable values. However, the assumptions used will serve to compare the breeding schemes.

The correlations between FECQTL and production or fertility traits depend on the fractions of the additive genetic variance (σ_A^2) explained by the FECQTL. If FECQTL explains a proportion ρ^2 of σ_A^2 for FEC, the genetic correlation ($r_{gFEC,FECQTL}$) between FEC and FECQTL is calculated from equation 6 as:

$$r_{gFEC,FECQTL} = \rho \quad (6)$$

The phenotypic correlation ($r_{pFEC,FECQTL}$) between FEC and FECQTL is derived by equation 7 as:

$$r_{pFEC,FECQTL} = \rho \times h_{FEC} \quad (7)$$

where h_{FEC} is the square root of the heritability for FEC.

The correlations of FECQTL with the production/ fertility traits (i.e., LS, LI and BW) depend on the genetic correlation between FEC and the particular production/ fertility trait (PF) and the heritability of PF. The genetic correlation ($r_{gPF,FECQTL}$) between PF and FECQTL is calculated from equation 8 as:

$$r_{gPF,FECQTL} = \rho \times r_g \quad (8)$$

where r_g is the genetic correlation between FEC and PF.

The phenotypic correlation ($r_{pPF,FECQTL}$) between PF and FECQTL is derived from equation 9 as:

$$r_{pPF,FECQTL} = \rho \times r_g \times h_{PF} \quad (9)$$

where h_{PF} is the heritability of the production trait (PF).

Heritabilities for FEC were also varying in the literature. Other studies have found a heritability for FEC ranging from 0.20 to 0.40 (e.g., Eady et al., 1998; Woolaston and Windon, 2001). To account as much as possible for the many environmental and biological factors influencing FEC, a relatively low heritability of 0.25 was assumed in the present study. Variances for FEC were taken from Vanimisetti et al (2004) and the FEC population mean from different sources (Woolaston and Windon 2001; Pollot and Greeff 2004). Heritabilities of BW, LS and LI were taken from Kosgey et al (2004) as were the population means. Variance for BW was also taken from Kosgey et al (2004), and variances LS and LI were adapted from Kosgey et al (2004) to suit the definitions of the current study.

Selection indices

Different selection strategies with overlapping generations were evaluated using the computer program SelAction (Rutten et al 2002). This program performs deterministic simulations to predict the rates of genetic gain by multi-trait pseudo-BLUP (Villenueva et al 1993). Reduction of variance (Bulmer 1971) and correction for finite population sizes and the correlation between index values of family members (Meeuwissen 1991) were taken into account. The program includes full pedigree information consisting of estimated breeding values (EBV) of the sire and

dam, and the mean EBV of the dams of each half-sib group. It is, therefore, an accurate approximation of stochastic simulation of BLUP selection. Selection response is predicted for the Bulmer equilibrium situation and the mating structure is assumed to be hierarchical and random(Rutten et al 2002).

A number of different selection schemes are simulated to determine the possible genetic improvement. Several selection indices are evaluated and all of these include the breeding goal traits LS, LI, BW and FEC. The population structure remains the same in all schemes. Information sources (Table 3) included in the index for both males and females are for LS and LI: EBV; for BW: EBV, own performance and (50 half-sibs x 0.7 surviving at 12 months of age = 35 half-sibs). For FEC males: EBV, own performance, and 16 male half sibs; for FEC females: EBV and 16 male half-sibs. Every scheme has a Latin and a Roman number (Table 4): Latin number 1 indicates that only classical selection is used while Latin number 2 means that a QTL for FEC is assumed to be available. Roman number I means that the correlation between FEC and BW are assumed to be positive, and schemes with a Roman number II indicate that the correlations are assumed to be negative. Letters are used to indicate how FEC is included in the index (i.e., no inclusion (A), FEC (B) or FECQTL (C-F)).

Table 3. Information sources

	Males[b]				**Females[c]**			
Traits[a]	**Own**	**EBV**	**35 HS**	**16 HS**	**Own**	**EBV**	**35 HS**	**16 HS**
LS		x				x		
LI		x				x		
BW	x	x	x		x	x	x	
FEC	x	x		x		x		x

[a]*See Table 1 for the description of traits*
[b]*EBV, estimated breeding values; HS, half-sibs*

Table 4. Selection indices

Correlations		**FEC included in the index[a]**					
FEC and BW[b]		**none**	**as FEC**	**as QTL with fraction of σ_A^2 explained[c]**			
r_P	r_g			0.2	0.4	0.6	0.8
0.08	0.30	1AI	1BI	2CI	2DI	2EI	2FI
-0.08	-0.20	1AII	1BII	2CII	2DII	2EII	2FII

[a]*See text for explanation of the indices*
[b]*See Table 1 for the description of traits; r_P, phenotypic correlation; r_g, Genetic correlation*
[c]*QTL, quantitative trait loci; σ_A^2, genetic variance*

In schemes 1, where only classic selection based on phenotypes is used, information on own performance, half-sibs and EBV is included in the index. Scheme 1AI is the basic scheme and does not include FEC in the selection index. The correlation between BW and FEC is positive. Scheme 1AII is similar to scheme 1AI except that negative correlations between BW and FEC are used. In schemes 1B, FEC is included in the selection index. The correlations between FEC and BW are assumed to be positive in scheme 1BI and negative in scheme 1BII. In schemes 2, it is assumed that a QTL for FEC is identified and marker-assisted selection (MAS) can be used. Selection for LI, LS and BW is in the classical way. The fraction additive genetic variance explained by the QTL is varied and the correlations between FECQTL and LS, LI, BW and FEC

are adapted according to formulae 1-4, as discussed previously. The correlations between BW and FEC will be varied in the different schemes from negative to positive. In scheme 2A, 2B, 2C, and 2D, the QTL will explain 20, 40, 60 and 80% of the additive genetic variance, respectively.

Results

Effects of correlations

The rams', ewes' and total selection responses are expressed in US dollars per ewe per year and presented in Table 5. The rams were responsible for the largest part of the response while the ewes contributed only slightly. The reason for the approximately equal response in the dam index throughout schemes 1AI-2FI and schemes 1AII-2FII, was probably due to the fact that selection is focused on the males. The only difference in the dam index can be seen in schemes II compared to schemes I. The differences in responses were 25, 22, 19, 19, 19 and 19% between schemes 1AII and 1AI, 1BII and 1BI, 2CII and 2CI, 2DII and 2DI, 2EII and 2EI and 2FII and 2FI, respectively. The differences between the sire and dam selection responses were mainly due to differences in selection intensity and accuracy. The higher the selection intensity and the higher the accuracy, the more genetic progress can be made. The accuracy increased when classic selection for FEC was used compared to no inclusion of FEC in the index. Using a QTL explaining 0.2 of the σ_A^2 reduced the accuracy slightly. Increasing the fraction of the σ_A^2 explained by the QTL caused an increase in accuracy except for the dams in schemes II. The reason for this was unknown.

Table 5. Rams', ewes' and total selection responses (ΔG) in US dollars ($) per ewe per year, and rams' and ewes' accuracies (R_{IH}) for each scheme with a negative (-) or positive (+) correlation (r_g)

Scheme[a]	r_g	Index FEC[a]	ΔG			R_{IH}	
			Rams	Ewes	Total	Rams	Ewes
1AI	+	none	0.13	0.02	0.16	0.31	0.31
1AII	-	none	0.17	0.03	0.21	0.37	0.37
1BI	+	FEC	0.14	0.03	0.17	0.33	0.32
1BII	-	FEC	0.19	0.03	0.22	0.40	0.38
2CI	+	QTL 0.2	0.14	0.03	0.16	0.32	0.32
2CII	-	QTL 0.2	0.18	0.03	0.21	0.39	0.37
2DI	+	QTL 0.4	0.14	0.03	0.17	0.33	0.32
2DII	-	QTL 0.4	0.19	0.03	0.22	0.41	0.37
2EI	+	QTL 0.6	0.14	0.03	0.17	0.33	0.32
2EII	-	QTL 0.6	0.20	0.03	0.23	0.42	0.37
2FI	+	QTL 0.8	0.15	0.03	0.17	0.34	0.33
2FII	-	QTL 0.8	0.21	0.03	0.24	0.44	0.37

[a]*See text for description of indices and explanation of schemes*

In the last section of Table 6, the differences in total selection responses between schemes I and schemes II are shown. Schemes 1AI and 1AII did not include FEC in the selection index, resulting in a response of $0.16 per ewe per year in scheme 1AI and $0.21 per ewe per year in

scheme 1AII. In schemes 1BI and 1BII, FEC was included in the index. The responses in scheme 1BI and 1BII were \$0.17 and \$0.22, respectively. The differences between schemes 1AI and 1AII; and between 1BI and 1BII were, correspondingly, 30 and 31%. The increase in response when MAS was used in schemes II compared to schemes I was also obvious. The differences between schemes 2CI and II, 2DI and II, 2EI and II and 2FI and II were, respectively, 32, 35, 36 and 38%. The increase in response in schemes II compared with schemes I was due to a negative correlation between BW and FEC.

Table 6. Selection responses in US dollars (\$) per animal per year

Index FEC[a]	Positive correlations			Negative correlations			Differences between schemes with positive and negative correlations:	
	Scheme[a]	Response:		Scheme[a]	Response:			
		Total (\$)	%		Total (\$)	%	\$	% difference
None	1AI	0.16	100	1AII	0.21	100	0.05	30.4
FEC	1BI	0.17	105	1BII	0.22	106	0.05	31.3
QTL 0.2	2CI	0.16	103	2CII	0.21	104	0.05	32.1
QTL 0.4	2DI	0.17	104	2DII	0.22	108	0.06	34.5
QTL 0.6	2EI	0.17	106	2EII	0.23	110	0.06	35.9
QTL 0.8	2FI	0.17	108	2FII	0.24	115	0.07	38.2

[a]*See text for description of indices and explanation of schemes*

Effects of FEC index traits used

The different FEC index traits (i.e., no inclusion of FEC, FEC phenotypic and use of a QTL) all had a different effect on the economic response. Schemes 1AI and 1AII (no inclusion of FEC in the index) are the basic schemes to which the other schemes are compared. Table 6 presents the results where the change in total response (%) is compared to the basic schemes. The change in response was calculated separately for the schemes with a positive correlation between BW and FEC (schemes I) and for schemes with a negative correlation (schemes II).

In case of a positive correlation between BW and FEC, classical selection for FEC based on field measurements (Scheme 1BI) resulted in a total increase in response of 4.8% compared with when FEC was not included in the selection index (1AI). In case a QTL for FEC is available, the total response could be increased depending on the proportion of σ_A^2 explained. A QTL explaining a proportion of 0.2, 0.4, 0.6 and 0.8 of σ_A^2 of FEC (schemes 2AI–2FI) resulted in an increase of 2.5, 4.2, 5.4 and 7.0%, respectively, compared to the basic scheme (1AI). The increase in economic gain compared to the basic scheme when using a QTL explaining 0.2 and 0.4 of σ_A^2 of FEC, was less than for the classical selection (4.8%). Only when a QTL explaining 0.6 and 0.8 of the σ_A^2 of FEC would be available, would MAS result in a higher economic gain (0.6% and 3.2%) than selection based only on phenotypes.

When negative correlations between BW and FEC were used (scheme 1BII), traditional selection for FEC increased the economic gain by 5.5% compared to a selection index that did not include FEC (scheme 1AII). A QTL explaining a fraction of 0.2, 0.4, 0.6 and 0.8 of σ_A^2 of FEC (schemes

2CII-2FII) consequently increased the response with 3.7%, 7.2%, 9.3% and 12.7%, respectively. The response of a QTL explaining 0.2 of σ_A^2 of FEC was not higher than selection based on phenotypes (scheme 1BII) and, therefore, a QTL explaining at least 0.4 of σ_A^2 of FEC should be available for a MAS program which results in a higher gain than classical selection.

Effects of FEC on litter size, lambing interval and body weight

The effect of selection on reduction in FEC was dependent on how the FEC is included in the breeding goal and selection index. The magnitude of this effect depended on the correlation between FEC and BW (i.e., negative or positive), and the proportion of σ_A^2 of FEC explained by the QTL, which influenced the correlations between the FECQTL and the breeding goal traits. The effects of selection on FEC are shown in Figures 2 (schemes I) and 3 (schemes II). The response for each trait is expressed in US$ cents per ewe per year. Body weight accounted for the largest response in both schemes I and II, and most of the economic response was obtained because selection for BW resulted in a heavier animal. However, when selection was more focused on improving FEC, obviously the response in BW decreased, with the largest reduction in schemes I. Like the response for BW, the response for LS was in all schemes positive. Similar to the response of BW, selection for FEC resulted in a reduction of the increase in LS due to positive correlations between FEC and LS. In schemes II, the reduction in LS was larger than in scheme I. Also, the correlations between FEC, LS, BW and LI were slightly positive, which led to a negative response in LI. The response was almost equal in schemes I and II.

Figure 2. Selection responses in US dollars ($) for the breeding goal traits in schemes with a positive correlation between BW and FEC (Schemes I) in economic units x 100

Figure 3. Selection responses US dollars ($) for the breeding goal traits in schemes with a negative correlation between BW and FEC (Schemes II) in economic units x 100

Response of selection on FEC was negative in scheme 1AI where selection was based on field measurements and no emphasis was placed on selection for FEC. In scheme 1BI, more attention was paid to selection for FEC by including it in the index, which resulted in a slightly negative response. In schemes 2AI and 2BI where a QTL explaining a fraction of, respectively, 0.2 and 0.4 of $\sigma_A^{2,}$ of FEC was available, the response was more negative again. The reason for this was that the correlations between the different traits are dependent on the QTL fraction explained. The lower the fractions explained, the lower the correlations and the less the genetic progress made. In the case of a QTL explaining 0.2 and 0.4 of σ_A^2 of FEC, the progress was even lower than the progress achieved with classical selection. This implies that a positive response in a MAS program with positive correlations between BW and FEC can only be obtained if a QTL explaining at least 0.6 of σ_A^2 is available. The response for FEC if the correlations are negative (schemes II) were higher. In this case, selection for FEC resulted in a positive response for FEC in all selection indices. However, the response of MAS with a QTL explaining 0.2 of σ_A^2 of FEC was slightly lower than the response of classic selection. The responses for FEC can be increased

when a QTL explaining a fraction 0.4 or more of σ_A^2 of FEC would be available. Nevertheless, it should be kept in mind that obtaining a larger response for FEC will lead to a relative reduction in the other breeding goal traits although the total response is increased.

Discussion

In the breeding objective, selection for a high BW could be of less relevance than selection for LS and LI in pastoralist communities. A number of studies show that most pastoralist households tend to increase their flock sizes because of the local prestige value of a large flock size (Kosgey 2004). The reason for selecting for a high BW was because of the inclusion of several other components, i.e., selection for a high growth rate, a high feed efficiency, a high birth weight or a superior mothering ability of the dam. All these components indicate a high adaptability and survival potential of the animals. However, LS could also be a good indicator of fitness and adaptability to the environment and, therefore, more emphasis could be on improvement of LS. Selection for LI seems to be useful because it reduces the generation interval and, consequently, increases the genetic gain. Disease resistance was also a trait of major importance, but resistance to a particular disease selected for might depend on the area and the prevalence of that disease. Any other trait of importance to the farmers should be determined in conjunction with the target farmers.

Prospects for developing genetic markers for FEC and their use in breeding programs

Currently, there are no genetic markers for FEC available that are suitable for direct use as selection criteria. However, prospects for the detection of QTL influencing gastrointestinal parasite resistance and the development of a genetic marker to identify genetically superior animals are optimistic (Beh and Maddox 1996). A constraint to the development of genetic markers is the genetic complexity of gastrointestinal parasite resistance. Supposedly, the trait is polygenic and influenced by the combined action of a number of genes at different loci that become activated in a particular sequence (Artis et al 1999). The effects of individual genes could vary from very large to extremely small. Another constraint to the identification of QTL is that results will vary depending on the nematode species, the challenging regime and the indicator trait measured (Dominik 2004).

A MAS program for gastrointestinal parasite resistance would be most beneficial if gastrointestinal parasite resistance was controlled by a major gene (Montgomery and Kinghorn 1997). Although it is not precisely known which genes are involved in resistance, some candidate genes have been suggested. Research has discovered a significant association between a QTL on the sheep chromosome 20 in the region of the Major Histocompatibility Complex (MHC) and parasite resistance (Schwaiger et al 1995; Buitkamp et al 1996). Another QTL associated with FEC was found at or around the interferon gamma locus (Coltman et al 2001). Proof of the presence of a QTL that associates with FEC has also been found on chromosomes 1, 3, 6 and 20 (Beh and Schewaiger et al 1995; Maddox 1996). However, the existence of these QTL has not yet been confirmed and the results of different studies are in many cases conflicting (Dominik 2004).

The main factor influencing the genetic progress that can be made in a MAS program is the fraction of the additive genetic variance explained by the QTL. The larger the QTL effect, the larger the genetic and economic response. Unfortunately, since a QTL for FEC is not yet available, one can only speculate about the fraction of the σ_A^2 explained by the QTL. A study by Schewaiger et al (1995) showed that MHC accounts for 33% of the σ_A^2 in FEC. However, MHC accounts for only 11% of the total phenotypic variation. Meszaros et al (1999) found more evidence for a QTL explaining 33% of the σ_A^2 and, therefore, having a large effect on FEC. Beh and Maddox (1996) suggested that considering the polygenic basis of parasite resistance, detection of markers explaining between 5 and 10% of the total variation in polygenic traits would be possible. The results of the foregoing studies imply that until now, only evidence of markers explaining a small to moderate fraction of the σ_A^2 has been found. The results of the computer simulations in the current study show that MAS programs only yield a higher total economic response compared to classic selection on FEC if a marker explaining at least a fraction 0.6 of the σ_A^2 in case of positive correlations between BW and FEC, and a proportion of 0.4 of the σ_A^2 in case of negative correlations between BW and FEC is available. Nonetheless, a positive economic response for FEC in a MAS program with positive correlations between FEC and BW (schemes I) is only obtained when a QTL explaining 0.6 of the σ_A^2 is available. In case of negative correlations between FEC and BW (schemes II), the response for FEC is in all cases positive. However, for a MAS program that results in a higher response for FEC than phenotypic selection, a QTL explaining 0.4 of the σ_A^2 is required. Consequently, MAS for FEC seems to be unrealistic at this moment.

Effects of MAS on the long-term

In the current study, only the difference between selection for FEC based on phenotype and selection based on QTL has been evaluated. However, it might be possible to include both phenotype and genotype information for FEC in the selection index. This possibly increases the total genetic progress made in the breeding program for FEC. Gibson (1994) concluded that selection based on genotype resulted in the largest selection response in the short-term, while phenotypic selection resulted in the largest response in the long-term. This might be due to fixation of the major gene within a few generations in a MAS program while conventional programs make more use of the polygenes with only a small effect (Meeuwissen and van Arendonk 1992). When a major gene for FEC is discovered, the strategy for including the marker in a selection program should, therefore, be optimized. By combining phenotypic and genetic information in the selection index, the response to selection might be increased and genetic variability maintained.

Possible constraints of selection for FEC

One of the main drivers to breed sheep for gastro-intestinal parasite resistance is the increasing problem of resistance of internal parasites to anthelminthics. However, there is a possibility that a parasite that is able to adapt to anthelminthics is also able to adapt to a resistant host (Le Jambre 1993). If this is indeed the case remains unclear and experimental results are conflicting. Indigenous breeds (e.g., the Red Maasai sheep of East Africa) that have co-evolved with parasites for long periods of time are found to be more resistant than breeds from other environments where no large infection pressure exists (Baker et al 1999). This might imply that

breeding for host resistance to parasites is sustainable in the long term. According to Beh and Maddox (1996), a consequence of modern husbandry is that the host-parasite balance has been pushed in favour of the parasite because a highly susceptible animal has been allowed to survive in a population with a high stocking rate, which maximizes infection rate. In combination with parasite control strategies, this has increased the genetic variation in the host's resistance to parasites. Selection for this trait while reducing genetic variation will only restore the natural host-parasite balance and apply no adaptive pressure on the parasite. According to Woolaston and Baker (1996), in case parasites do adapt to their hosts, a possible solution to this problem is to breed for resilience instead of resistance. Resilience is the ability of the host to maintain a relatively un-depressed production level under parasite challenge and applies little selective pressure on the parasite.

A potential negative effect of breeding for parasite resistance is the possibility that breeding for resistance to one disease might increase susceptibility to another disease or even to another parasite (Sonstegard and Gasberre 2001). This might be caused by the fact that immune responses are divided in two broad categories, i.e., Th1 and Th2 responses (Finkelman et al 1997). Selective breeding for a particular disease might stimulate the host to prefer one type of immune response to the other, leaving the host susceptible to diseases normally mediated by the other type of response (Stear et al. 2001). However, it has often been observed that sick animals are more prone to disease infection than healthy ones. This suggests a positive instead of a negative correlation between different diseases. Unfortunately, the immune response to nematodes is not yet fully understood and there is insufficient proof to determine whether resistance to one disease confers susceptibility to another (Douch et al 1996). More research is needed in this field to understand the immune response and to find proof for the hypothesis that resistance to one disease confers susceptibility to another.

Profitability and application of marker-assisted selection in a community-based breeding program

The advantages of using MAS for FEC are that it is no longer required to withhold animals from parasite vaccinations or treatments and that the collection of individual DNA samples is relatively simple compared to the collection of individual faecal samples. The DNA samples can be collected anywhere and at any moment. Collection should be done at the appropriate time (i.e., at 5 and 12 months of age) and samples should be labeled with the animals' registration numbers, and time and place of collection. It would be possible to simply use animal hair or wool from which DNA can be obtained as a sample. This makes the collection of DNA easy to apply and the breeding organization's staff could be responsible for this. However, like faecal samples, DNA samples will also have to be processed in a laboratory. The processing of DNA samples requires knowledge on the use of the appropriate techniques of DNA analysis and, consequently, only trained staff should be responsible for this. Where it is possible to make use of the services and facilities of a research institute's, government's or university's laboratory, it is recommended to do so. After the samples have been processed, feedback and information on how to interpret and use the results should be given to the breeding organization. The veterinarian or animal scientist that is part of the organization's staff should be responsible for applying the results in the community, and for the training and education of the farmers. Where no official laboratory is willing to co-operate, possibilities of the establishment of a community-

owned laboratory should be considered. However, this will be expensive and the required knowledge of the staff members will be lacking. In case a number of communities are co-operating, a laboratory shared by these communities might be an option. A number of organizations, possibly with the support of a donor, might have the financial means to build a laboratory and to hire skilled staff.

Marker-assisted selection is expensive to perform and, therefore, it is necessary to make an economic cost-benefit analysis before it can be used in practice. Whether the benefits of MAS are higher than the costs depends on the production system. First, the parasite infection rate should be large enough so that production efficiency can be increased substantially using MAS. For populations at low-grazing density, MAS might not be that much profitable (Sonstegard and Gasberre 2001). However, the costs of treatment, production losses and the labour intensity, and costs of collecting faecal samples of populations at high-grazing density might be higher than the application of a MAS program. Genetic improvement is not the only factor of importance to decrease damage caused by parasites. The main part of the solution to this problem will result from appropriate management and veterinary strategies.

Marker-assisted selection for increased fecundity

A MAS program for FEC might be successful, which implies that MAS could then also be used for other traits. A MAS program is most efficient in early generations of selection and for traits that can be measured only after selection has taken place and/ or for traits with a low heritability, as is the case with the traits relating to fertility (Davis and DeNise 1998). Candidates are selected at 12 months of age but LS and LI can both only be measured after selection at 24 months of age. Besides, heritabilities are low (0.07 and 0.10, respectively). A marker for fecundity in sheep has already been found; the Booroola fecundity gene has been mapped at chromosome 6. For each expressed copy of the gene, the average number of lambs per litter is increased and ovulation rate is improved (Montgomery and Kinghorn 1997). In the breeding program evaluated, only limited progress was made in LS and LI. This was mainly due to positive correlations between LS and FEC, and to the low heritability of LS. By selecting for Booroola fecundity gene in a MAS program, LS might be increased as well as LI due to increased ovulation rate.

Conclusion

Classic selection for FEC resulted in an increased selection response as compared to no inclusion of FEC in the selection index and, therefore, classical selection seems to be feasible. However, a detailed analysis of the costs of measuring FEC in the field is necessary to determine if this is indeed true. A MAS program with positive correlations between BW and FEC resulted only in a higher total selection response than classical selection when a QTL explaining 0.6 of the σ_A^2 of FEC was used. A MAS breeding program with negative correlations between BW and FEC required a QTL explaining between 0.3 and 0.4 of σ_A^2 of FEC. Currently, there are no genetic markers for parasite resistance available and if genetic markers become available in the future, they will probably only explain up to 0.33 of σ_A^2 of FEC. In case of positive correlations between BW and FEC, this proportion of σ_A^2 of FEC will be too low to make a MAS program profitable. A proportion of 0.33 of σ_A^2 of FEC might just be sufficient to make a MAS program with

negative correlations between BW and FEC profitable, if the costs of a MAS program are lower than or equal to the cost of a classical selection program. It should also be kept in mind that increased emphasis on selection for FEC will reduce the relative responses to the breeding goal traits BW, LS and LI. Consequently, the goal of selection for FEC should be to reach sufficient levels of gastrointestinal parasite resistance as well as sufficient improvement of LS and BW.

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