Sheep Resources of Ethiopia

Genetic diversity and breeding strategy

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Dedicated to my brother

Dawit Gizaw GebreMichael

Abstract

Twenty percent of the world domestic animal breeds are classified as being "at risk" of extinction. Seventy percent of the mammalian breeds, for which no risk status data are available, are found in the developing world. This is a serious constraint to effective prioritization and planning of sustainable breed conservation measures, including sustainable breeding strategies. The objectives of this thesis were to develop improved approaches to characterization of sheep resources, and sustainable conservation-based sheep breeding strategies under smallholder traditional systems, taking Ethiopia as a case study. Analysis of microsatellite variation showed that geographic isolation is the primary cause of genetic differentiation among Ethiopian sheep breeds. However, there is a strong indication of adaptive divergence in morphological characters. Using a combination of microsatellite analysis and morphological divergence, we propose a classification of Ethiopian sheep into six breed groups and nine breeds. The objective of characterizing animal genetic resources is to facilitate decisions on prioritization in conservation of these resources. Our results show that a maximum-utility-strategy combining threat status, contributions to farmer livelihoods and to genetic diversity of livestock breeds should be adopted to prioritize them for conservation purposes. Such an approach balances the trade-offs between conserving breeds as insurance against future uncertainties and for current sustainable utilization. Selective breeding within indigenous livestock breeds is an option for conserving livestock breeds. Our results indicate that selective breeding can lead to significant genetic improvement under low-input systems and marginal environments. Assessment of farmers' selective breeding objectives showed that adaptive traits are more important than or as important as production traits, indicating that sustainable animal breeding strategies require a broad definition of breeding objectives that emphasize maintaining adaptation to local circumstances and biodiversity, in addition to profitability. It is concluded that the most rational and sustainable way to conserve livestock genetic resources is to improve their competitiveness through sustainable breed improvement programs (i.e. conservation through use). To this end, community- or village-based selective breeding schemes with full participation of farmers appear to be the best option to start with.

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CHAPTER 1

General Introduction

1. General introduction

Livestock contribute significantly to food production and economic output in all regions. The relative contribution of livestock to agricultural GDP is higher in the developed regions but the trend has been slightly downwards over the past 30 years, whereas in most developing regions there has been a rise in the importance of livestock (FAO, 2001). Country reports on farm animal genetic resources (FAO, 2007) illustrate that importance of farm animal genetic resources is very diverse, particularly for the poor under smallholder production systems in the developing world. Uses include subsistence consumption of livestock products, manure, traction, savings, risk management, capital accumulation and socio-cultural functions.

Ethiopia is an ideal case for studying livestock diversity in the context of developing regions. Ethiopia can be considered as a center of livestock diversity: it is a route of sheep migration from Asia into Africa, has large sheep population (CSA, 2006) and diverse traditional sheep breeds spread across diverse ecology, communities and production systems (Solomon et al., in press). At the national level, sheep/goat account for about 90% of the live animal/meat and 92% of skin and hide export trade value (FAO, 1994, 2004). At the farm level, sheep contribute as much as 22-63% to the net cash income derived from livestock production in the crop-livestock production system (Zelalem and Fletcher, 1993), and are a mainstay of the pastoral livelihoods in the lowland pastoral system.

Globally, sheep are the species with the highest number of recorded breeds, contributing 25% to the total mammalian breeds. Twenty percent of the world domestic animal breeds are classified as being “at risk”. No risk status data are available for 26.1% of the sheep breeds and 21.0% of domestic animal breeds (FAO/UNEP, 2000). Seventy percent of the mammalian breeds for which no risk status data are available are found in the developing world. Lack of such information, including for breeds in Ethiopia, is a serious constraint to effective prioritization and planning of breed conservation measures including sustainable breeding strategies.

1.1. Characterization of animal genetic resources

The term farm animal genetic resources (AGR) is used to include all animal populations, species, breeds and strains, particularly those of economic, scientific and cultural interest to mankind in terms of agricultural production for the present or the future (Rege and Lipner, 1992). Characterization of farm AGR is a prerequisite for designing conservation-based utilization programs. Characterization of farm animal species is primarily concerned in the classification and description of populations into management units termed as breeds in modern animal breeding nomenclature.

The first phase of characterization is surveying to identify populations based on morphological descriptors and describe their geographical distribution, uses, husbandry and production environments. Morphological or phenotypic characterization has been suggested and used to describe and classify wild species (e.g. Patterson et al. 1993; Tarkhnishvili et al., 2000; Brehem et al., 2001; Sanders et al., 2004) and breeds of farm animal species (e.g. Al–Rawi and Al-Athar, 2002; Nsoso et al., 2004).

However, outcomes of multivariate morphological surveys need to be verified by complementary genetic characterization (FAO, 2007). Genetic characterization has recently been the method of describing and classifying livestock breeds using measures of genetic distances between populations (Cavalli-Sforza and Edwards, 1967; Nei, 1972; Nei et al., 1983). Genetic characterization tools include biochemical (protein) polymorphisms and molecular polymorphisms. Biochemical markers lack the power to resolve differences between closely related populations because of low polymorphism of these markers (Meghen et al., 1994). Polymorphic molecular genetic markers include microsatellites, single nucleotide polymorphisms (SNPs), restriction fragment length polymorphisms (RFLPs), randomly amplified polymorphic DNA (RAPDs), mitochondrial DNA markers, Y-specific alleles and amplified fragment length polymorphisms (AFLPs). Currently, microsatellites have become markers of choice for diversity study (Ruane, 1999; Sunnucks, 2001) because of their codominant nature, ease of amplification and hypervariability. Microsatellites are also recommended markers by FAO for characterizing farm AGR (FAO, 2005).

Characterization of AGR in Ethiopia has largely been limited to description of production systems (e.g. Abebe, 1999, Solomon et al., 2005) and phenotypic description and classification of traditional breeds using multivariate morphological criteria (Workneh, 1992; Alemayehu, 1993; Sisay, 2002). On-farm and on-station performance and genetic evaluation (i.e. estimation of genetic parameters) of selected breeds is also considered as part of characterization effort (Rege and Lipner, 1992). Such activities have dominated national livestock programs in Ethiopia (Biniam, 1992; Abegaz and Duguma, 2000; Hassen et al., 2002; Solomon, 2002) and in most other African countries (see national reports in Rege and Lipner, 1992). Molecular genetic characterization of farm AGR has only recently received attention in Ethiopia (Tadelle, 2001; Tesfaye, 2004).

1.2. Conservation of animal genetic resources

Conservation of farm AGR has different paradigms in the developed and developing world. While breed conservation is seen as the protection of rare breeds in developed countries (e.g. Windig et al., 2004, 2007), conservation in the context of developing countries can be appropriately defined as the rational use and protection of existing local genotypes from genetic introgression (Rege and Lipner, 1992). Conservation of farm AGR thus incorporates preservation, maintenance, improvement and sustainable utilization (FAO, 1986). The primary focus of farm AGR conservation is on the conservation of breeds, including management for better utilization (breeding programs) and conserving those at risk, with the aim of minimizing the loss of diversity among breeds (Barker, 2001). However, conservation of within-breed variation is also a crucial component of diversity conservation.

The issue of farm AGR conservation has gained momentum in the last few decades and has become a major activity of regional (EAAP) and global bodies (FAO). Correspondingly, several studies addressing the theoretical and practical implementations of decision making in livestock conservation have recently been conducted. Two approaches on making conservation decision relating to issues of between-breed and within-breed diversity conservation (Weitzman, 1992 and Eding and Meuwissen, 2001) have dominated the literature on livestock conservation. The least studied approach is a comprehensive approach combining the criteria of contribution of breeds to genetic diversity conserved and to current farmer livelihood and society at large as suggested by Ruane (2000).

The state of farm animal genetic resources in Ethiopia including sheep resources have been reported as part of FAO global farm animal genetic resources survey (FAO, 2007). Regarding conservation efforts, purebred nucleus populations of few selected traditional sheep breeds are maintained in research centers, though these are not formally intended for conservation purposes. However, there is no comprehensive conservation program for the adapted indigenous sheep breeds of the country. There is also lack of research to support decision on conservation of sheep resources in Ethiopia.

1.3. Breeding strategies

Strategies for genetic improvement of livestock mainly involve the decision on the use of the variation between breeds (cross-breeding) and within a breed (pure-breeding). The strategy adopted in livestock genetic improvement in developing regions is mainly crossbreeding of the local breeds with exotic sires. Country reports on the state of farm animal genetic resources (FAO, 2007) and review of Kosgey et al. (2006) show that there are very few structured sheep pure-breeding programs in developing regions, particularly in Africa. Cross-breeding programs in developing regions have been criticized as incompatible with conservation of indigenous adapted breeds. However, still only 26% of African countries favor development of local breeds according to country reports on the state of the world's animal genetic resources (FAO, 2007).

There has been few attempts and successes in genetic improvement of sheep resources in Ethiopia. Crossbreeding is the primary breeding strategy adopted. On-station experimental results show that sheep crossbreeding increases body weight (Sisay et al., 1989; Demeke et al., 1995; Solomon, 2002). However, on-farm studies indicate that crossbreds are not superior to purebreds under low-input conditions (Ayalew, 2000; Hassen et al., 2002). Selective pure-breeding strategy is largely neglected. Selection projects in closed nucleus flocks of Black head Somali and Afar sheep remained unreported, while in Horro sheep no appreciable genetic progress was achieved (Abegaz and Duguma, 2000).

Improvement of local breeds through selective pure-breeding can be superimposed on and be an integral part of conservation programs (Henson, 1992; Woolliams et al., 1998). Design of selective breeding programs requires estimation of genetic parameters and selection responses, definition of breeding objective, and design of optimal breeding schemes. For sheep breeds in Ethiopia, estimates of genetic parameters are scant (Biniam, 1992; Abegaz et al., 2002, Hassen et al., 2003; Solomon and Joshi, 2004a, 2004b; Markos, 2006), and estimates of responses to selection are lacking. In developing nations an enabling farm animal genetic resource conservation policy could be successful by placing high priority on a community-based participatory approach and focusing on food security and poverty alleviation (Wollny, 2003). However, information on sheep breeding objectives targeting the needs and perceptions of farmers and design of community- or village-based breeding schemes is virtually absent.

1.4. Objectives and outline of the thesis

This thesis addresses two aspects of sustainable sheep breeding in Ethiopia. Part I of the thesis (Chapters 2-3) aims at improving characterization and conservation of sheep diversity in Ethiopia. Part II (Chapters 4-7) aims at generation of knowledge to develop sustainable conservation-based breeding strategies for sheep breeding under smallholder conditions.

Chapter 2 assesses the genetic and morphological diversity, and patterns and causes of population structuring in Ethiopian sheep populations using microsatellite DNA markers and morphological descriptors. This information is used in the classification of Ethiopian sheep into ‘genetic’ breeds. Chapter 3 presents an approach for setting conservation priorities combining genetic and non-genetic criteria. In Chapter 4, we present results of a selection experiment including estimates of genetic parameters and responses to selection. Chapter 5 addresses a problem of livestock breeding under village conditions, and investigates alternative selection criteria to improve live weight under village breeding programs. In Chapter 6, based on farmers’ preferences and basic information from chapters 4 and 5, a participatory approach to define breeding objectives and selection indexes for developing sustainable breeding strategies is presented. Based on breeding objectives defined in Chapter 6 and existing farmers' sheep breeding practices and breeding structure, design of optimal village breeding schemes under smallholder conditions is investigated in Chapter 7. The salient points of the thesis are discussed in general context in Chapter 8 and general conclusions drawn.

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CHAPTER 2

Population structure, genetic variation and morphological diversity in indigenous sheep of Ethiopia

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Abstract

We investigated genetic and morphological diversity and population structure of 14 traditional sheep populations originating from four ecological zones in Ethiopia (sub-alpine, wet highland, sub-humid lowland and arid lowland). All animals (n=672) were genotyped for 17 microsatellite markers and scored for 12 morphological characters. The sheep were initially classified as fat-tailed (11 populations), thin-tailed (1 population) and fat-rumped sheep (2 populations). This classification is thought to correspond to three consecutive events of sheep introductions from the Near-east into East Africa. For the 14 populations, allelic richness ranged from 5.87 to 7.51 and expected heterozygosity (H_E) from 0.66 to 0.75. Genetic differentiations (F_{ST} values) between all pairs of populations, except between sub-alpine populations, were significantly different from zero ($P<0.001$). Cluster analysis of morphological characters and dendrogram constructed from genetic distances were broadly consistent with the classification into fat-tailed, thin-tailed and fat-rumped sheep. Bayesian cluster analysis using microsatellite markers indicated that there has been further genetic differentiation after initial introduction of sheep into Ethiopia. Investigation of factors associated with genetic variation showed that an isolation-by-distance model, independently of other factors, could explain most of the observed genetic variation. We also obtained a strong indication of adaptive divergence in morphological characters, patterns of morphological variation being highly associated with ecology even when the effect of neutral genetic divergence (F_{ST}) was partialled out in partial Mantel tests. Using a combination of F_{ST} values, Bayesian clustering analysis and morphological divergence, we propose a classification of Ethiopian sheep into six breed groups and nine breeds.

Keywords: diversity, Ethiopia, microsatellite, morphology, sheep

1. Introduction

In wild animals, patterns of population genetic structure are usually explained by factors that disrupt gene-flow, such as isolation-by-distance (Wright, 1943), historical geological factors (Gübitz et al., 2000) or physical barriers (Nicholls and Austin, 2005; Trizio et al., 2005). In addition, ecological factors influence genetic diversity (Brehem et al., 2001; Via, 2002; Whiteley et al., 2004) through morphological adaptation to local conditions (Brown and Thorpe, 1991). Unlike populations in the wild, dispersal ability and hence gene flow among domestic animal populations is believed to be governed more by human intervention than by physical barriers. Differences in ancestral origins and migration events are important causative factors explaining genetic differences between current populations (Cañón et al., 2001; Alvarez et al., 2004; Rendo et al., 2004). Local management (Cañón et al., 2006) and cultural separation (Rege, 2002) can cause genetic isolation of populations leading to reduced effective population size and further divergence through drift.

African sheep are thought to be of Near Eastern origin (Epstein, 1954; Epstein, 1971; Ryder, 1984; Marshal, 2000). The earliest sheep in Africa were thin-tailed and hairy and introduced to East Africa through North Africa (Marshal, 2000). The second wave of sheep introduction to Africa constitutes fat-tailed sheep entering North Africa via the Isthmus of Suez straits and East Africa via straits of Bab-el-Mandeb (Ryder, 1984). Fat-rumped sheep entered East Africa much later (Epstein, 1954; Epstein, 1971; Ryder, 1984). Accordingly, African sheep have been traditionally described and classified based on their tail type (Epstein, 1971; Ryder, 1984). However, the relation between the traditional classification and genetic variation across currently recognized breeds is unknown.

Ethiopia is believed to be one of the major gateways for domestic sheep migration from Asia to Africa (Devendra and McLeroy, 1982). With 18 million sheep (CSA, 2005) and 14 traditional populations, there are highly diversified indigenous sheep populations in the country parallel to its diversity in ecology (Galal, 1983), ethnic communities and production systems. However, causes and patterns of genetic and morphological structuring of Ethiopian sheep have not been investigated.

Sheep types in Ethiopia are highly affiliated to specific ethnic communities. A number of traditional breeds are reared by and named after specific communities. A breed reared by a community may be isolated from other breeds because of isolation of communities due to cultural barriers. Some communities attach special cultural values to their sheep and exclude use of breeding stock from other populations, resulting in cultural barrier to gene flow.

Ethiopia is characterized by highly contrasting ecological zones (MOA, 1998) modified mainly by altitude ranging from 126 m below sea level to 4620 m above sea level. Observed ecological pattern of habitation of sheep populations in Ethiopia invokes the idea that ecological barriers through adaptive requirements (eg: wooly, short-legged sub-alpine breeds may not survive in arid lowlands), might have led to further genetic differentiation after initial introductions of sheep into the country. Furthermore, adaptive divergence in response to ecological variation has been indicated in patterning morphometric (Stroz, 2002) and color (Gübitz et al., 2000) variation. However, overlap between ecological variation and geographical distances between populations in the current study complicate assessment of the causes of genetic and morphological variation. One way of distinguishing between adaptive and non-adaptive causes of geographical variation in morphology is to compare relative levels of between-population divergence in quantitative traits and in neutral DNA markers (Stroz, 2002). Another approach is to include measures of neutral genetic divergence (F_{ST} values) as independent variable when testing for the association between observed patterns of morphological variation and causal hypotheses (Gübitz et al., 2000).

In this paper, we quantify genetic differences among traditional sheep populations in Ethiopia and evaluate factors associated with patterns of molecular genetic and morphological variation. We hypothesize that geographical isolation, ecological variation and community isolation are associated with the current population structure in Ethiopian sheep populations.

2. Materials and methods

2.1. Sampling strategy

The sampling structure is shown in Table 2.1 and sampling sites with ecological zones are shown in Fig. 2.1. We primarily targeted sheep populations traditionally recognized by ethnic and/or geographic nomenclatures. Major ecological zones and phenotypic distinctness were also considered in sampling. Fourteen populations representing the major ethnic communities, ecological zones and geographic regions were sampled. For each population, 48 animals from different villages and flocks (1-2 animals per flock) across different districts were sampled. Blood samples and morphological measurements (on full-mouth adult ewes only) were collected on the same set of animals.

2.2. Microsatellite analysis

2.2.1. Markers and genotyping

Forty-eight animals from each of 14 populations were genotyped for 17 microsatellite markers recommended by FAO (www.fao.org/dad-is): OARVH72, TGLA53, MCM42, OARFCB20, ILSTS005, ILSTS011, BM8125, ILSTS44, DYMS1, MAF209, MAF214, MCM527, OARFCB11, OARCB226, OARFCB304, OARJMP29, and

SRCRSP9. DNA was extracted from peripheral blood lymphocytes preserved in urea following standard procedures (Sambrook et al., 1989). PCR amplifications were carried out in 10-µl reaction volumes containing 40-80 ng of genomic DNA, 400 nM of each of the forward and reverse primers, 1x PCR buffer, 1.5-2.0 mM $MgCl_2$, 0.5 units of *Taq* polymerase, and 0.125 mM of dNTPS. PCR amplifications were performed on GeneAmp PCR system 9700 (Applied bios systems, Foster City, CA, USA) thermocycler. The cycling profile was: an initial denaturation cycle at 95 ^{0}C for 5 min followed by 35 cycles of 30 s at 95 ^{0} C, annealing for 35 cycles of 1 min at 48-65 ^{0}C, extension for 35 cycles of 1 min at 72 ^{0} C, and a final extension cycle at 72 ^{0}C for 10 min. PCR products were analyzed by capillary electrophoresis using ABI Prism genotyper and LIZ 500 internal size standard (Applied Biosystems). The data were collected and analyzed by GeneMapper^{TM} software using third order least-squares allele size calling method.

Table 2.1. Summary of sampled populations and their characteristics with respect to tail type, affinity to ethnic communities and distribution over ecological zones.

Population	Tail type	Zone [1]	Community	Nr[5]
Simien	Fat-tailed	I	Amhara	1
Sekota	Fat-tailed	I	Agaw/Tigray	2
Farta	Fat-tailed	I	Amhara	3
Tikur	Fat-tailed	I	Amhara	4
Wollo	Fat-tailed	I	Amhara	5
Menz	Fat-tailed	I	Amhara	6
Gumz	Thin-tailed	II	Gumz	7
Washera	Fat-tailed	III	Amhara/Agaw	8
Horro	Fat-tailed	III	Oromo	9
Adilo	Fat-tailed	III	WKH[2]	10
Arsi-Bale	Fat-tailed	III	Oromo	11
Bonga	Fat-tailed	III	Kaffa/Sheka	12
Afar[3]	Fat-rumped	IV	Afar	13
BHS[4]	Fat-rumped	IV	Somali	14

[1] See Fig. 2.1 for description of ecological zones.

[2] WKH: southern nations and nationalities

[3] Epstein (1971) described Afar sheep as fat-rumped.

[4] Black-head-Somali

[5] numbers refer to sampling locations given in Fig. 2.1.

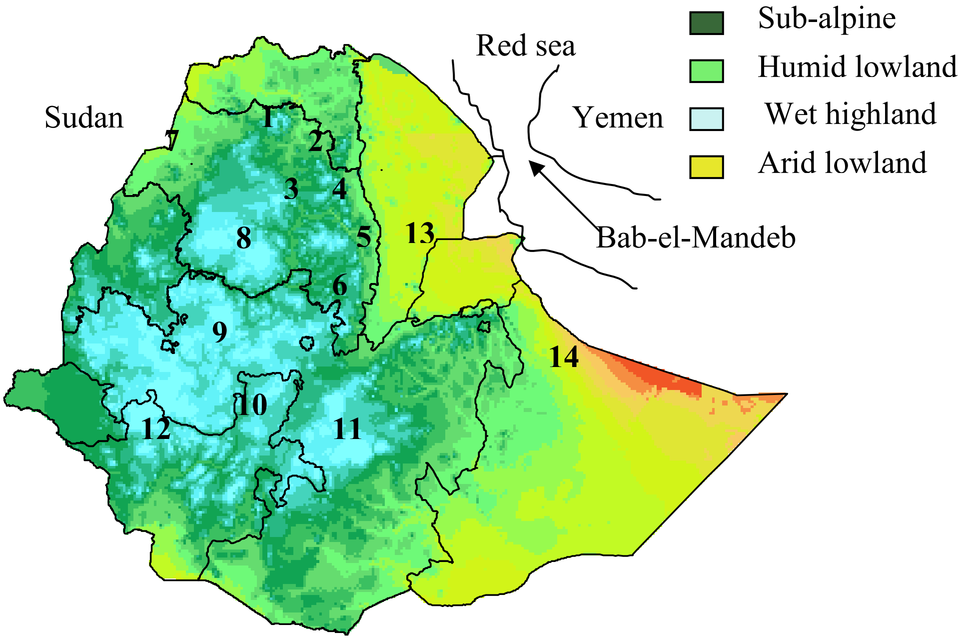

Fig. 2.1. Map of Ethiopia showing location of sampled populations and a sketch of the Red Sea area showing Bab-el-Mandeb, route of fat-tailed sheep introduction into Africa. See Table 2.1 for description of sampled populations indicated here by Arabic numbers.

Ecological zones:

I. Sub-alpine: Cool to very cold sub-moist/dry alpine mountains and plateaus, low vegetation, 3008 m a.s.l, 1102 mm rain, maximum 22.1 °C, minimum 7.6 °C.
II. Humid lowland: Hot sub-humid lowland plain, high vegetation, 637 m a.s.l, 894 mm rain, maximum 37.7 °C, minimum 20.1 °C.
III. Wet highland: Tepid to cool wet highlands, very high vegetation, 2091 m a.s.l, 1437 mm rain, maximum 24.8 °C, minimum 10.1 °C.
IV. Arid lowland: Hot arid lowland plain, very low vegetation, 894 m a.s.l, 404.5 mm rain, maximum 33.2 °C, minimum 17.4 °C.
Source: Based on MOA (1998).

2.2.2. Data analysis

2.2.2.1. HWE equilibrium and genetic diversity

Deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium across pairs of loci were evaluated using Genepop 3.3 (Raymond & Rousset, 1995). To assess within-population genetic diversity, observed heterozygosity (H_{o}), expected heterozygosity (H_{E}) and allelic richness per locus were calculated for each population.

2.2.2.2. Population genetic structure

Overall genetic differentiation among populations and between pairs of populations, F_{ST} values (Weir & Cockerham, 1984) were calculated using FSTAT version 2.9.3 (Goudet, 2001). Based on Nei et al. (1983) genetic distances (D_A) between populations, a dendrogram was constructed using neighbor-joining algorithm (Saitou and Nei, 1987) in DISPAN (Ota, 1993). Thousand bootstrap replicates were generated to evaluate the support of tree nodes.

Presence of real population genetic structure, regardless of sampled populations, was explored by Bayesian clustering analysis implemented in STRUCTURE (Pritchard et al., 2000). We ran five independent runs for each predefined number of populations (K = 2-14). The most probable number of populations (K) was inferred based on the highest computed log-likelihood of data, Pr(X/K). Individuals were assigned to inferred populations based on the highest probability of membership.

2.2.2.3. Hypotheses on population structuring

Tests of hypotheses on patterns of population structuring were carried out by Mantel tests (Manly, 1991) implemented in FSTAT 2.9.3 (Goudet, 2001). Pairwise geographical straight-line distances between populations were measured using digital map (Collis et al., 2001). Ecological zones I, II, III and IV (see Table 2.1) were scored as 0, 1, 2 and 3 respectively, and a matrix of pair-wise Euclidean distances in ecology between populations was constructed based on the scores. Following Gübitz et al. (2000), a pair-wise matrix expressing community isolation was constructed by assigning a value of zero if the populations in the pair were owned by the same community and a value of one if they belonged to different communities. Pair-wise and partial Mantel tests (simultaneous test of all independent variables) were run fitting F_{ST} values as dependent variable and matrices of geographical distances, ecology and community isolation as independent variables.

2.3. Morphological analysis

Twelve recommended (FAO, 1986) quantitative morphometric characters (body length, withers height, chest girth, substernal height, ear length, tail length, and tail width) and qualitative characters (fiber type, coat color, horn presence, tail type, and tail form) were recorded on each animal. Morphometric data were made size-free by using allometric transformation with body length taken as overall body size, as follows (Reist, 1985): $S = \exp(\ln Y - b(\ln X - \ln X_L))$, where S is the standardized measurement, Y the character length, b the slope of log Y against log X plot for each population, X the body length of the individual animal, and X_L the mean body length for the population. Qualitative characters were scored on a binary scale using dummy variables corresponding to each character state in each character. Dummy variables take values 0 or 1 to indicate the absence or presence of the characteristics described for the character state. Description of the characters and character states are provided in Table S2.1.

Hierarchical cluster analysis was conducted and dendrogram constructed based on Euclidean distances between populations using unweighted pair-group method to depict morphological clustering pattern of the 14 populations. In order to determine percentage assignment of individuals to the clusters, results of cluster analysis were evaluated by discriminant function analysis.

Mantel tests (Manly, 1991) were carried out to test the association of morphometric and color variation patterns with geographic distances, ecology and community affiliation of sheep types. For this analysis, two matrices of Euclidean distances using principal components (PC1 and PC2) of morphometric variables and original coat color variables were constructed.

3. Results

3.1. Microsatellite variation

3.1.1. Within-population genetic diversity

Five of the 238 locus-population combinations deviated significantly ($P < 0.05$) from Hardy-Weinberg equilibrium. Only one of the 1904 locus pairs across populations was in linkage disequilibrium ($P < 0.05$). Allelic richness varied from 5.87 in Bonga to 7.51 in Afar, with a mean of 6.79 across populations. Observed heterozygosity (H_o) ranged from 0.62±0.02 (Horro) to 0.72±0.02 (Wollo), and expected hetrozygosity (H_E) from 0.66±0.03 (Horro) to 0.75 ± 0.01 (Farta). Across populations, mean H_E was 0.71.

3.1.2. Population structure

Global F_{ST} value (0.046±0.004) indicated low but significant genetic differentiation among populations. F_{ST} values for all pairs of populations were also significantly different from zero (P<0.001), except between sub-alpine populations (Table S2.2). Simien was significantly differentiated from all other sub-alpine populations.

The largest Nei genetic distance (D_{A}) was between Simien and Bonga and the smallest distance was between Farta and Tikur (Table S2.2). Five distinct clusters (Fig. 2.2) can be discerned based on Nei genetic distances: (1) Menz, Sekota, Tikur, Farta, Wollo, and Simien; (2) Adilo, Arsi-Bale, Horro and Bonga; (3) Afar and BHS; (4) Gumz; and (5) Washera.

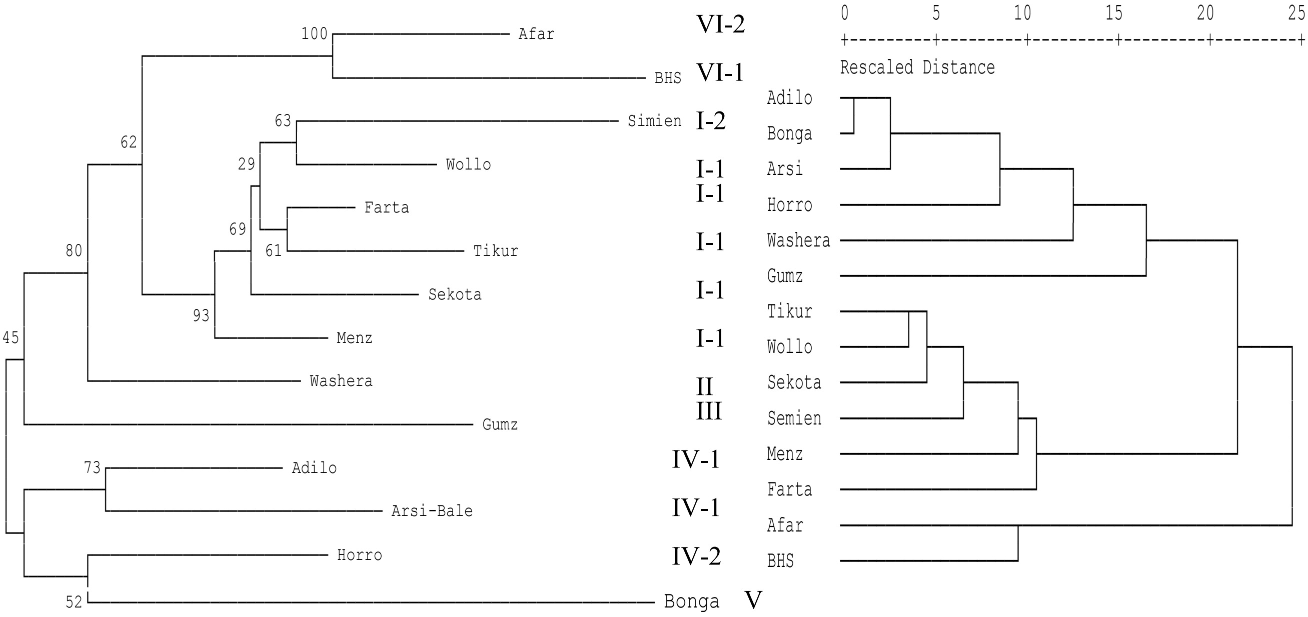

Fig. 2.2. Neighbor-joining dendrogram constructed from Nei's genetic distances (left), and UPGMA dendrogram constructed using between-population Euclidean distances derived from morphological variables (right). Roman numbers indicate breed groups, and within breed group Arabic numbers indicate breeds.

STRUCTURE analysis gave no definitive maximum likelihood values. There were small increases in Pr(*X*/*K*) values with increasing number of clusters (Fig. 2.3). However, beyond $K = 5$, almost all new inferred populations originated from divisions within sub-alpine populations, which clustered together at $K = 5$. The exceptions were that Horro was separated from Arsi and Adilo at $K = 8$ and BHS from Afar at $K = 14$. Therefore, we took the most probable number of inferred populations as five (Table 2.2).

Population structure at $K = 3$ nearly corresponded to the three putative precursor populations (fat tail, thin tail and fat rump). However, the fat-tailed populations Horro and Bonga clustered with thin-tailed Gumz sheep, while fat-tailed Arsi-Bale and Adilo sheep clustered with fat-rumped sheep. Washera sheep were jointly assigned to the three groups.

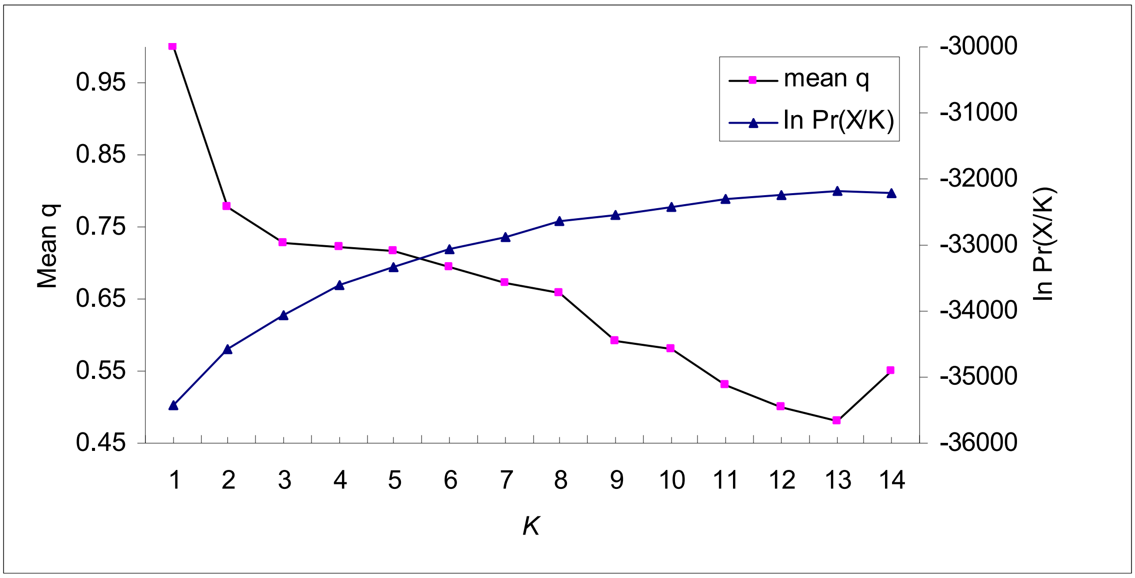

Fig. 2.3. Plot of data likelihoods [ln Pr(*X*/*K*)] and mean confidence assignment of all individuals to their most probable cluster (mean *q*, derived from proportion of an individual's genome that originated from population *K*) versus number of inferred populations (*K*). ln Pr(*X*/*K*) values are mean values of five independent runs each at 250 000 MCMC repetitions as suggested by Pritchard et al. (2000).

Table 2.2. Proportion of membership of each of the 14 predefined populations in each of the five inferred populations obtained from STRUCTURE analysis

	Inferred populations				
Predefined populations	1	2	3	4	5
Simien	0.043	0.027	0.079	**0.799**	0.053
Sekota	0.074	0.059	0.090	**0.569**	0.207
Farta	0.094	0.072	0.106	**0.582**	0.146
Tikur	0.052	0.065	0.143	**0.642**	0.099
Wollo	0.101	0.069	0.132	**0.574**	0.124
Menz	0.094	0.091	0.090	**0.507**	0.217
Gumz	0.073	0.038	**0.828**	0.031	0.030
Washera	**0.319**	0.054	**0.323**	**0.204**	0.099
Horro	**0.624**	0.143	0.116	0.048	0.068
Adilo	**0.669**	0.112	0.079	0.060	0.081
Arsi-Bale	**0.674**	0.051	0.097	0.059	0.119
Bonga	0.025	**0.892**	0.033	0.018	0.032
Afar	0.097	0.062	0.106	0.113	**0.621**
BHS	0.075	0.035	0.043	0.044	**0.803**

3.1.3. Hypotheses on population structuring

Pair-wise Mantel tests indicated significant relationships between F_{ST} and ecology (P = 0.0002), community (P = 0.0001) and geographical distances (P = 0.0001). The relationship between F_{ST} and geographical distances remained significant (P = 0.0005; R^2 = 53.7), even after the effects of ecology (P = 0.53) and community (P = 0.11) were accounted for in a partial Mantel test.

3.2 Morphological variation

Euclidean distances between the 14 populations are presented in Table S2.3. Cluster analysis grouped the 14 populations into five clusters (Fig. 2.2): 1) long fat tail with tapering end, short-hair, populations in wet highland zone (Horro, Adilo, Arsi-Bale and Bonga); 2) short fat tail, coarse-wool, populations in sub-alpine areas (Simien, Sekota, Farta, Tikur, Wollo, and Menz); 3) short fat tail, short-haired, populations in wet highland (Washera); 4) fat-rumped sheep, short-haired, populations in arid lowland (Afar and BHS); and 5) thin-tailed, short-haired, in sub-humid lowland (Gumz). Canonical discriminant function analysis (Table S2.4) confirmed the population grouping from cluster analysis.

Results of Mantel tests for morphological variables are given in Table 2.3. Ecology, independently of geographical distance, F_{ST} and community isolation, showed a significant association with quantitative traits and coat color. Geographical distance, F_{ST} and community isolation had no partial relationship with patterns of variation in morphology and coat color.

Table 2.3. Standardized regression coefficients with probabilities (in parentheses) after 10000 randomizations from Mantel tests for the association of morphometric and color variation patterns with causal hypotheses (ecology and affinities to communities), correcting (partial Mantel) or not correcting (pair-wise Mantel) for geographical distance (distance) and F_{ST}

		Distance	Ecology	Community	F_{ST}
Morphometry (PC1/2)	Pair-wise	0.000 (.986)	0.289 (.000)	0.116 (.606)	0.756 (.839)
	Partial	-0.001 (.267)	0.445 (.004)	-0.034 (.899)	-1.337 (.811)
Color	Pair-wise	0.001 (.098)	0.217 (.000)	0.239 (.840)	2.419 (.104)
	Partial	0.000 (.446)	0.201 (.002)	0.076 (.494)	-0.850 (.698)

4. Discussion

4.1. Genetic diversity

This study revealed the presence of high within-population genetic diversity in Ethiopian sheep populations. This is congruent with the high variability observed in phenotypic characters, particularly in coat color within the sub-alpine sheep populations. High within-population variability is characteristic of large traditional populations that have not been under strong selection (Lauvergne et al., 2000). Allelic richness and heterozygosity estimated in this study are comparable to values reported for domestic sheep populations (Rendo et al., 2004; Tapio et al., 2005; Calvo et al., 2006) and for wild sheep populations (Worley et al., 2004).

4.2. Population structure

Traditional populations are thought of as distinct types evolved as a result of geographical isolation and cultural separation of the communities keeping the animals (Rege, 2002). The current study showed significant but low genetic structuring (F_{ST} = 0.046) in the 14 traditional breeds. Lack of differentiation between most of the sub-alpine populations could be due to geographic proximity and similarities in ecology and communities who own them, which might have allowed gene flow. Large population size, and thus presumably large effective population size, might have reduced the effect of drift resulting in weaker genetic differentiation between the morphologically well differentiated and isolated BHS and Afar.

The history of introduction of sheep into Africa recognizes (Epstein, 1971) three waves of migration from Asia of precursor populations (fat-tailed, thin-tailed and fat-rumped sheep). Clusters derived from morphological characters and genetic distances (Fig. 2.2) indicate that this historical population structure has been broadly maintained in the current sheep populations in Ethiopia, except the fat-tailed sheep are divided into two separate clusters. Distance-based clusters may depend on the chosen distance measure and graphical representation (Pritchard et al., 2000). Bayesian clustering analysis (Pritchard and Wen, 2003) at K = 3 also returned results similar to distance-based methods. Furthermore, the result at K = 3 also indicated admixture between fat-tailed and thin-tailed sheep as the fat-tailed Horro and Bonga clustered with thin-tailed sheep. Horro and Bonga have tail shape intermediate between fat and thin tail. Sheep with intermediate tail are likely to be originally fat-tailed with admixture from thin-tailed sheep. This hypothesis is supported by the proximity of Ethiopia to Bab-el-Mandeb, i.e. the route of fat-tailed sheep introduction into Africa (Fig. 2.1). The proximity of Bab-el-Mandeb to Ethiopia may also explain the current predominance of fat-tailed sheep in the country. The only thin-tailed population in Ethiopia is confined to the western lowlands bordering The Sudan through which thin-tailed sheep were believed to be introduced into east Africa (Marshal, 2000).

We investigated the population structure further by varying K from 4 to 14. After K = 5, almost all new clusters resulted from splitting within the sub-alpine populations (except Simien). This is to be expected in populations showing high within-breed variation (as in sub-alpines), with allele frequencies varying across sampling locations or flocks (Pritchard et al., 2000). At K = 5, the analysis returned a very similar population structure (Table 2.2) to the distance-based genetic and morphological clusters. The results indicate that there has been further morphological and genetic differentiation within the fat-tailed group after initial introduction to Ethiopia. The sub-alpine fat-tailed populations (which have short fat tail and long coarse-wooled fleece) clustered together and separately from the wet highland fat-tailed populations (which have long fat tail and short hair coat). This could be the result of geographic isolation of populations, community breeding practices or interbreeding with other sheep types. Pyne (1964) suggested that some cattle morphotypes in Africa could be the result of interbreeding. Some of the traditional breeds in the current study (eg: Washera) showed high level of admixture.

4.3. Hypothesis on population structuring

Partial Mantel (Manly, 1991) tests showed that divergence among the current Ethiopian sheep populations in allele frequencies can be explained by isolation-by-distance model (Wright, 1943). Although the influence of ecological factors on patterns of genetic structuring has been hypothesized (Brehem et al., 2001; Via, 2002; Whiteley et al., 2004), there is no such indication in the current study. The observed strong association between ecology and F_{ST} and between community isolation and F_{ST} in pair-wise Mantel tests could merely be due to the confounding effect of geographical isolation.

Differences in body shapes among animals have been interpreted to mean that developmental homeostasis mechanisms generate variation in body shape corresponding to an optimal size for fitness (Brown et al., 1973). There is a strong indication of adaptive divergence in morphology in the current study (see Table 2.3). Discordant patterns of geographical divergence in body size and microsatellite markers have been implicated as evidence of adaptive divergence in morphology (Storz, 2002; Merila and Crnokrak, 2001). Coat color variation was found to be highly associated with ecological variation in this study. The character responds strongly to natural selection (Thorpe et al., 1996) and is primarily associated to climatic and vegetation differences (Thorpe and Brown, 1989; Brehem et al., 2001).

In conclusion, current population genetic structure in Ethiopian sheep is strongly associated to historical patterns of sheep migration, geographic isolation and interbreeding; while morphological diversity follow ecological patterns. Based on F_{ST} values, Bayesian clustering and morphological divergence, we propose a classification based on six breed groups and nine breeds (Table 2.4). The six groups are derived from the five clusters identified by Bayesian analysis. Washera is recognized as a separate breed because of its joint assignment to the different clusters. The nine breeds within the six breed groups are identified based on significance of genetic differentiation between populations (F_{ST} values; Table S2.2).

Table 2.4. Proposed classification of Ethiopian sheep in to major breed groups and breeds

Breed group	Breed	Population[2)]	Tail type/shape	Fiber type	B.W.[1)]
I. Short-fat-tailed	Simien	Simien	Fatty and short	fleece	26.9
	Short-fat-tailed	Sekota, Farta, Tikur, Wollo, Menz	Fatty and short	fleece	25.4
II. Washera	Washera	Washera	Fatty and short	hair	32.8
III. Thin-tailed sheep	Gumz	Gumz	Thin and long	hair	31.0
IV. Long-fat-tailed	Horro	Horro	Fatty and long	hair	35.4
	Arsi	Arsi-Bale, Adilo	Fatty and long	hair	28.6
V. Bonga	Bonga	Bonga	Fatty and long	hair	34.2
VI. Fat-rumped sheep	Afar	Afar	Fat rump/fat tail	hair	31.0
	BHS	BHS	Fat rump/tiny tail	hair	27.9

1) average adult body weight for a given breed in kg.
2) see also Table 2.1

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Table S2.1. Summary of variable definition for morphological characters

Character	Variable	Description
	Continuous variables	
Withers height	Withers height	Height from ground to withers, cm
Chest girth	Chest girth	Circumference of the chest, cm
Body length	Body length	Distance between shoulder and pin bone
Substernal height	Substernal	Height from ground to sternum, cm
Ear length	Ear length	Length of ear, cm
Tail length	Tail length	Length of tail, cm
Tail width	Tail width	Width of tail at the widest point, cm
	*Dummy variables***	
Fiber type	1*	Animal has short-haired coat
	2	Animal has long coarse-wool coat
Coat color	1	Plain black
	2	Plain white
	3	Plain brown
	4	Plain beige
	5	Black with white patches
	6	Brown with white patches
	7	Brown with black belly (*Tazma*)
	8	Black with brown on belly and head (*Woyni*)
	9	Black body and white patch on head (*Boqa*)
	10	White body and black head
	11	Brown body and white head
	12	White body and brown head
Horn presence	1	Animal has horn
	2*	Animal has no horn
Tail form	1	Triangular, straight long tapering end
	2	Triangular, coiled/twisted long tapering end
	3	Cylindrical, short, straight
	4	Cylindrical, short, twisted
	5	Cylindrical, short, turned-up
	6	Tubular, long, straight
	7	Bi-lobbed, turned-up
	8*	Rudimentary, tiny appendage
Tail type	1	Animal is fat-tailed
	2	Animal is thin-tailed
	3*	Animal is fat-rumped

* Reference categories excluded from analysis.

** Dummy variables took values 0 or 1 to indicate the absence or presence of the characteristics described for the character state (dummy variable).

Table S2.2. Pair-wise F_{ST} (above diagonal) and Nei's genetic distances, D_{A} (below diagonal) between the 14 populations

Population	Simien	Sekota	Farta	Tikur	Wollo	Menz	Gumz	Washera	Horro	Adilo	Arsi	Bonga	Afar	BHS
Simien		0.0312	0.0195	0.0294	0.0271	0.0275	0.0703	0.0449	0.0847	0.0713	0.0916	0.1074	0.0558	0.0848
Sekota	0.0791		0.0072$^{\mathrm{NS}}$	0.0158	0.0136	0.0078	0.0541	0.0223	0.0587	0.0481	0.0656	0.0740	0.0277	0.0476
Farta	0.0654	0.0394		0.0001$^{\mathrm{NS}}$	0.0048$^{\mathrm{NS}}$	0.0035$^{\mathrm{NS}}$	0.039	0.0183	0.0422	0.0322	0.0503	0.0607	0.0279	0.0481
Tikur	0.0838	0.0556	0.0368		0.0112	0.0005$^{\mathrm{NS}}$	0.0378	0.0251	0.0456	0.0302	0.0505	0.0654	0.0292	0.0540
Wollo	0.0694	0.0538	0.0425	0.0595		0.0089	0.0393	0.0231	0.0480	0.0351	0.0520	0.0590	0.0381	0.0522
Menz	0.0807	0.0511	0.0377	0.0486	0.0507		0.0503	0.0229	0.0467	0.0351	0.0592	0.0680	0.0265	0.0537
Gumz	0.1647	0.1346	0.1170	0.1279	0.1109	0.1292		0.0357	0.0482	0.0496	0.0587	0.0585	0.0494	0.0741
Washera	0.1082	0.0843	0.0736	0.0931	0.0689	0.0692	0.1115		0.0317	0.0287	0.0457	0.0623	0.0436	0.0626
Horro	0.1645	0.1183	0.0994	0.1220	0.1101	0.0958	0.1235	0.0828		0.0287	0.0573	0.0660	0.0561	0.0874
Adilo	0.1551	0.1124	0.0949	0.1133	0.0915	0.0983	0.1241	0.0859	0.0711		0.0246	0.0597	0.0414	0.0706
Arsi	0.1593	0.1161	0.1078	0.1336	0.1065	0.1147	0.1317	0.1075	0.1044	0.0681		0.0979	0.0430	0.0542
Bonga	0.2235	0.1716	0.1531	0.1614	0.1489	0.1506	0.1509	0.1449	0.1220	0.1239	0.1729		0.0748	0.1069
Afar	0.1375	0.0830	0.0884	0.1086	0.0988	0.0749	0.1389	0.1062	0.1151	0.1145	0.1133	0.1623		0.0222
BHS	0.1628	0.1064	0.1117	0.1344	0.1155	0.1011	0.1619	0.1232	0.1447	0.1290	0.1163	0.1864	0.0747	

Except those marked NS, all F_{ST} values were significantly different from zero at 0.1% level of significance based on 91 000 permutations.

Table S2.3. Squared Euclidean distances between populations derived from morphological characters

Population	Simien	Sekota	Farta	Tikur	Wollo	Menz	Gumz	Washera	Horro	Adilo	Arsi	Bonga	Afar
Sekota	2.82												
Farta	4.38	3.01											
Tikur	3.37	2.77	3.69										
Wollo	2.73	2.27	3.70	2.17									
Menz	4.43	3.13	4.16	3.75	2.95								
Gumz	6.83	6.23	8.09	8.31	7.29	6.96							
Washera	3.19	3.95	4.90	5.81	4.49	6.71	6.14						
Horro	7.15	6.12	7.41	8.39	8.68	9.86	5.59	4.68					
Adilo	5.65	4.58	5.47	5.92	5.93	6.52	5.06	3.64	3.31				
Arsi	5.58	6.02	7.22	7.64	7.26	6.97	4.48	5.40	4.65	1.53			
Bonga	4.85	4.50	5.95	6.72	6.97	7.57	4.78	3.55	2.32	1.49	2.47		
Afar	8.67	6.32	8.75	8.61	9.19	8.64	6.86	7.46	7.88	7.87	9.13	6.36	
BHS	7.03	5.62	7.76	7.33	7.71	7.89	4.98	5.84	6.07	5.74	7.01	4.56	3.69

Table S2.4. Group membership (%), predicted by canonical discriminant functions derived from morphological variables, of five clusters predefined by cluster analysis

	Predicted Group Membership (%)					
Population	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Total
Cluster 1	100.0	0.0	0.0	0.0	0.0	128
Cluster 2	0.5	94.0	5.4	0.0	0.0	184
Cluster 3	7.7	11.5	80.8	0.0	0.0	26
Cluster 4	0.0	0.0	7.9	86.8	5.3	38
Cluster 5	2.8	0.0	8.3	0.0	88.9	36

CHAPTER 3

Conservation priorities for Ethiopian sheep breeds combining threat status, breed merits and contributions to genetic diversity

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Abstract

Prioritizing livestock breeds for conservation needs to incorporate both genetic and non-genetic aspects important for the survival of the breeds. Here, we apply a maximum-utility-strategy to prioritize 14 traditional Ethiopian sheep breeds based on their threat status, contributions to farmer livelihoods (current breed merits) and to genetic diversity. Contributions of the breeds to genetic diversity were quantified using Eding's marker-estimated kinship approach. Non-genetic aspects included threats (e.g. low population size, low preferences by farmers) and current merits (economic, ecological and cultural merits). Threat analysis identified eight of the 14 breeds as threatened. Analysis of current merits showed that sub-alpine and arid-lowland breeds contribute most to farmer livelihoods in comparison to other breeds. The highest contribution to the genetic diversity conserved was from the Simien breed. Simien showed high between-breed (low between-breed kinship = 0.04) as well as high within-breed diversity (low within-breed kinship = 0.09 and high H_E = 0.73 and allelic richness = 6.83). We combined the results on threat status, current breed merits and contributions to genetic diversity to produce a ranking of the 14 breeds for conservation purposes. Our results balance the trade-offs between conserving breeds as insurance against future uncertainties and for current sustainable utilization. The ranking of breeds provides a basis for conservation strategies for Ethiopian sheep and contributes to a regional or global conservation plan.

Keywords: conservation, sheep, diversity, threat status, breed merit

1. Introduction

The primary objective of livestock conservation for developing countries is conservation for sustainable use (Simon, 1999; Ruane, 2000). Conservation is not only about endangered breeds but also about those that are not being utilized efficiently (Barker, 2001). Conservation aims of farm animal genetic resources range from avoiding extinction, maintaining genetic diversity and/or the cultural, ecological or socio-economic values of breeds, to provide the right conditions for their evolution within an evolving production system (Gandini et al., 2004).

Because of resource limitations, priorities on which population/breed to conserve need to be set. Commonly, contribution of a breed to total genetic diversity has been analyzed using phylogenetic methods based on genetic distances between breeds (Thaon d'Arnoldi et al., 1998; Cañón et al., 2001; Reist-Marti et al., 2003; Simianer et al., 2003) using Weitzman's (1992) approach. However, Caballero and Toro (2002) showed that conservation decisions based on genetic distances can be misleading when applied to subpopulations of a metapopulation, as it ignores the within-population variability component. Within-population variability constitutes a crucial part of the metapopulation variability and is highly relevant for conservation strategies because of its impact on adaptive and economic traits. An approach based on marker-estimated average kinship between and within populations has recently been suggested (Eding and Meuwissen, 2001; Caballero and Toro, 2002).

Both approaches described above ignore non-genetic factors such as the cultural, economic and ecological values or merits of the breeds. However, the human socio-political context needs to be fully understood for conservation priorities to have any impact on human livelihoods (Rege and Gibson, 2003). Ruane (2000) proposed a framework that incorporates both genetic diversity and non-genetic criteria for prioritizing breeds at the national level. However, applications of this framework are lacking and conservation priorities have largely been based solely on contributions of breeds to genetic diversity.

Twelve percent of sheep breeds known worldwide have already become extinct in the last 100 years (Hall and Ruane, 1993). Sheep resources of Ethiopia are not well studied and there is practically no rational conservation-based improvement plan in the country. With 18 million sheep (CSA, 2005) and 14 traditionally recognized breeds (Solomon et al., 2007), Ethiopia possesses highly diversified and adapted indigenous sheep populations parallel to its highly diverse agro-ecology, ethnic communities and production systems (Galal, 1983). However, changes in production systems, in response to socio-economic factors, have led to the use of exotic germplasm, endangering the survival of the adapted indigenous breeds. Besides, population sizes and flock structures of some populations are currently not commensurate with optimal genetic resource management levels.

In this paper, we assess the threat status, contributions to farmer livelihoods (current breed merits) and to genetic diversity of 14 traditionally recognised Ethiopian sheep breeds. We rank the 14 sheep breeds for conservation purposes adapting the conceptual frameworks of Ruane (2000) and Simianer et al. (2003). Our results can be used in defining conservation priorities at the national level and can contribute to a regional or global conservation plan.

2. Materials and methods

2.1. Breeds and genotyping

Fourteen Ethiopian sheep populations are traditionally recognized as sheep breeds. Microsatellite DNA-based analysis revealed that some breeds could not be separated at the genetic level, resulting in six genetically distinct breed groups (Solomon et al., 2007). In Table 3.1 breeds and breed groups are listed together with some basic statistics. We ran two preliminary analyses using the six breed groups or the 14 traditional breeds. Ranking of breeds (based on their contribution to genetic diversity) obtained from the two analyses were similar.

Table 3.1. Traditional breeds, breed groups, ecology, expected heterozygosity (H_E), and allelic richness

Traditional breeds	Breed groups	Ecology	H_E	Allelic richness
Farta[1]	Short-fat-tailed	Sub-alpine	0.746	7.116
Menz[1]	Short-fat-tailed	Sub-alpine	0.723	6.711
Sekota[1]	Short-fat-tailed	Sub-alpine	0.726	7.102
Simien[2]	Short-fat-tailed	Sub-alpine	0.728	6.830
Tikur[1]	Short-fat-tailed	Sub-alpine	0.738	6.455
Wollo[1]	Short-fat-tailed	Sub-alpine	0.729	7.193
Afar[1]	Fat-rumped	Arid lowland	0.743	7.508
BHS[2]	Fat-rumped	Arid lowland	0.682	6.597
Adilo[1]	Long-fat-tailed	Wet highland	0.696	6.399
Arsi-Bale[1]	Long-fat-tailed	Wet highland	0.676	6.589
Horro[2]	Long-fat-tailed	Wet highland	0.658	6.205
Bonga	Bonga	Wet highland	0.669	5.869
Gumz	Thin-tailed	Sub-humid lowland	0.728	7.133
Washera	Washera	Wet highland	0.719	7.404

[1, 2] Within breed groups, traditional breeds with different superscripts are genetically distinct using microsatellite markers (Solomon et al., 2007).

BHS: Black-head-Somali.

The results reported here are from the analysis of the 14 traditional breeds. This analysis was chosen since data collected on non-genetic criteria (indicators of threat status and breed merits) used in priority setting were specific to the 14 traditional breeds, which differ for most of the criteria.

Forty-eight animals from each of the 14 breeds were genotyped at 17 recommended (FAO, 2005) microsatellite loci: *MAF214, MAF209, ILSTS011, MCM527, OARFCB11, DYMS1, BM8125, OARCB226, ILSTS44, OARVH72, MCM42, ILSTS005, TGLA53, OARFCB20, OARFCB304, OARJMP29,* and *SRCRSP9*. DNA was extracted from peripheral blood lymphocytes preserved in urea following standard procedures (Sambrouk et al., 1989). PCR amplifications were carried out and the PCR products were analyzed by capillary electrophoresis using ABI Prism genotyper and LIZ 500 internal size standard (Applied Biosystems). The data were collected and analyzed using the GeneMapper^{TM} software with the third order least-squares allele size calling method.

2.2. Non-genetic criteria

2.2.1. Threat status

Threat status was assessed using five indicators adapted from the FAO (1995) recommended list: (1) population size extracted from CSA (2005) based on the geographic distribution of breeds, (2) average number of rams per flock based on 12 - 28 flocks per breed, (3) indiscriminate crossbreeding, (4) maintenance of pure stock, and (5) farmers' opinion towards their breed. For the fifth indicator, key informant farmers scored their breeds from 1 (poor) to 4 (excellent) using growth, meat quality, fertility, prolificacy and market value as separate criteria. The scores presented here are averages over all the traits. We assumed that breeds have a higher likelihood of being replaced when farmers assign a low value/score to their breed. In order to rank breeds on threat status, relative extinction probabilities were estimated adapting the approach of Reist-Marti et al. (2003). To calculate extinction probabilities, values between 0 (no effect on threat) and 0.3 (high effect on threat) for threat indicators 1-3 or between 0 and 0.1 for indicators 4-5 were assigned: (1) if population size > 100,000 = 0.0, <100,000 = 0.3; (2) if average number of rams per flock ≥ 1 = 0.0, 0.5 - 0.9 = 0.1, 0.25 - 0.49 = 0.2, 0 - 0.24 = 0.3; (3) if level of indiscriminate crossbreeding is very high = 0.3, high = 0.2, low = 0.1, none = 0.0; (4) pure stock maintained = 0.0, partially maintained = 0.05, not maintained = 0.1; (5) farmers opinion score 2 - 2.9 = 0.1, 3 - 4 = 0.0. Three times higher weight was attached to indicators 1-3 because of their larger impact on the survival of breeds. Extinction probability (z) for each breed was computed as the sum of the values. Breeds with very low extinction probability (≤ 0.2) were considered relatively safe or not threatened.

2.2.2. Breed merit

Breed merits include economic or production, ecological and socio-cultural values of breeds (Barker, 2001). Ranking of breeds on their merits was based on the conceptual framework of Ruane (2000). The 14 breeds were scored for their current economic, ecological and socio-cultural merits by one of us (Solomon Gizaw) based on discussion with farmers and development experts, field observations and literature review. Average breed merit (*W*) for each breed was subsequently calculated by averaging the scores over all merits (economic, ecological and cultural merits).

Economic merits of breeds were scored based on their relative contributions to farm livelihoods and domestic and export market shares, which were assumed to reflect special traits such as quality of product. Breeds with relatively high importance to the farm economy (where cropping is unreliable and sheep production is a primary or sole enterprise) and contributing to domestic or export market were considered of 'very high' economic merit (score = 0.4). Those highly important to farm economy but not contributing to the national or export markets were rated as 'highly' important (score = 0.3). Breeds relatively less important to farm economy (located in high agricultural potential and cash crop area) but contributing to either the national or export market were of 'medium' merit (score = 0.2). The rest were scored as 0.1.

Ecological values reflect adaptive characters of the breeds. A high (0.3) or medium score (0.2) was assigned to breeds that inhabit marginal environments (arid, mountainous or degraded landscapes) to which the adapted sheep population could contribute to the human and environmental welfare. Breeds in stable ecologies were given a 'low' score (0.1).

Cultural values were defined by the degree of traditional association of a community to a particular sheep breed and contribution of the breed to socio-cultural functions and rituals. Accordingly scores from 0.4 (very high) to 0.1 (low) were given.

2.3. Genetic criteria

Contribution of the breeds to genetic diversity was analyzed using Eding and Meuwissen (2001) approach. Eding diversity is based on f_{ij}, the coefficient of marker-estimated kinship between individuals i and j. A high kinship implies low genetic differentiation and diversity. f_{ij} at each locus was calculated as:

$$f_{ij} = \frac{S_{ij} - s}{1 - s},$$

where S_{ij} is similarity between i and j based on alleles being alike in state and s is the probability of the two alleles being alike-in-state but not identical by descent.

Estimation of f_{ij} and s can be done because f_{ij} is constant over loci but not over combinations of individuals, while s differs between loci but is constant over populations. We used Weighted Log-Linear Model (Eding and Meuwissen, 2003) to estimate kinship coefficients where each similarity score per locus was weighted by the expected variance of the similarity score which results in more informative markers having larger influence on the solutions of both f and s. The final f_{ij} was the average over the 17 loci typed. Within- and between-breed kinships were computed by averaging the corresponding values for all the within or between population pairs of individuals.

The total diversity of the set of breeds was estimated by determining optimal contributions. Optimal contributions of breeds are derived in such a way that the average kinship in the core set is minimal, and thus the genetic diversity maximal. This results in a core set C_{cor}, which is a mixture of populations such that “genetic overlap” is minimised, and the complete genetic diversity represented (Eding et al., 2002). Negative contributions to the core set can occur, but have no practical relevance. We followed Eding et al. (2002) and fixed the most negative contribution to 0 and resolved the optimal contributions for the remaining breeds. This was repeated until all breeds had a contribution greater than or equal to 0.

A safe set of breeds was formed of populations with an estimated extinction probability of 0.2 or less, following Eding et al. (2002). Gain in diversity (additional diversity) from conserving an extra breed in addition to the safe set (Safe set + 1) was calculated, following the European Cattle Genetic Diversity Consortium approach (2006), as

$$[V\,(\text{Safe}+1)/V\,(\text{Safe})] - 1,$$

where V is diversity conserved.

2.4. Conservation priorities

In this study, we assumed as conservation objective sustainable contributions of breeds to current farm livelihoods and insurance against uncertain future. We used a simplified approach to rank breeds on their total utility by adapting the conceptual framework of Simianer et al. (2003). Total utility of breed i (U_i) was estimated as:

$$U_i = 2(z_i * D_i) + W_i,$$

z_i is extinction probability, D_i is partial contribution of breed i to Eding core set (Eding et al., 2003). D_i is Weitzman’s (1992) marginal diversity in Simianer et al. (2003). Marginal diversities have to be known only to proportionality (Bennewitz et al., 2007) for the purpose of ranking breeds and correlation between partial contributions and marginal diversities is very high, $r = 0.9 – 0.98$ (Reist-Marti et al., 2003; Bennewitz et al., 2007). W_i is current merit of breed *i*. The 'conservation potential' ($z_i * D_i$) is the possible increase in expected diversity if an endangered breed *i* was made completely safe. Conservation potential has been used to rank breeds when the objective is to conserve diversity per se (Simianer et al., 2003; Bennewitz et al., 2006).

3. Results

3.1. Threat status and breed merits

Results on indicators of threat status and breed merits are presented in Table 3.2. Relative extinction probabilities, calculated using indicators of threat status, indicate that Arsi-Bale, BHS, Afar, Horro, Washera and Sekota could be considered relatively safe (designated Safe set) with extinction probabilities of 0.2 or less. Economic merit of arid lowland breeds, most of sub-alpine breeds, Horro, Arsi, and Washera is very high. Sub-alpine breeds and lowland breeds (BHS, Afar and Gumz) have relatively very high ecological values.

Table 3.2. Indicators of threat status (population size, average number of rams per flock, degree of indiscriminate crossbreeding, maintenance of pure stocks *ex situ,* and farmers' opinion) and current breed merits for Ethiopian sheep breeds

	Indicators for threat status[1]					Breed merits		
Breed	Population ('000)	Number of rams	Cross-breeding	Pure stock	Farmer assessment[2]	Economic merit	Cultural value	Ecological value
Farta	555.6	0.27	+++	-	3.50	+++	++	+++
Menz	971.4	1.45	++++	++++	2.80	++++	++++	++++
Sekota	732.3	1.00	-	-	3.17	+	++	++++
Simien	347.6	0.25	-	-	3.33	+++	+++	++++
Tikur	525.3	1.00	+	-	2.17	+++	+++	++++
Wollo	1395.9	1.20	++++	-	2.50	++++	+++	+++
Afar	681.9		-	+	3.17	++++	++++	++++
BHS	906.2	8.47	-	++++	2.83	++++	++++	++++
Adilo	407.7	0.09	-	-	3.50	++	++	+
ArsiBale	6345.1	1.07	-	-	3.50	++++	+++	+
Horro	3409.3	0.34	-	++++	3.60	++++	+++	+
Bonga	517.5	0.07	-	-	3.83	+++	+	+
Gumz	50.9	0.70	++++	-	2.50	+	++	++++
Washera	1227.7		-	-	4.00	++++	+++	+

[1] The following scale is used: - None, + Low, ++ Medium, +++ High, ++++ Very high.

[2] Farmers scored their breeds on a scale of 1 (poor) to 4 (excellent) using growth, meat quality, fertility, prolificacy and market value as separate criteria. Values given are scores averaged over traits.

3.2. Contributions to genetic diversity

Coefficients of kinship are presented in Table S3.1. Within-breed coefficients of kinship varied from 0.09 in Simien sheep to 0.18 in Bonga and BHS. Higher within-breed kinship coefficients corresponded to lower within-breed genetic diversity (expected heterozygosity and allelic richness, Table 3.1). Between breeds, BHS and Afar are the most related breeds with a kinship coefficient of 0.121, while Simien and Bonga are the most distant ($f = 0.0$).

Plotting coefficients of kinship (Fig. 3.1) revealed a pattern of population structure. Breeds within the major breed groups (Table 3.1) showed closer kinship with breeds in the group than with breeds outside of the group (Fig. 3.1).

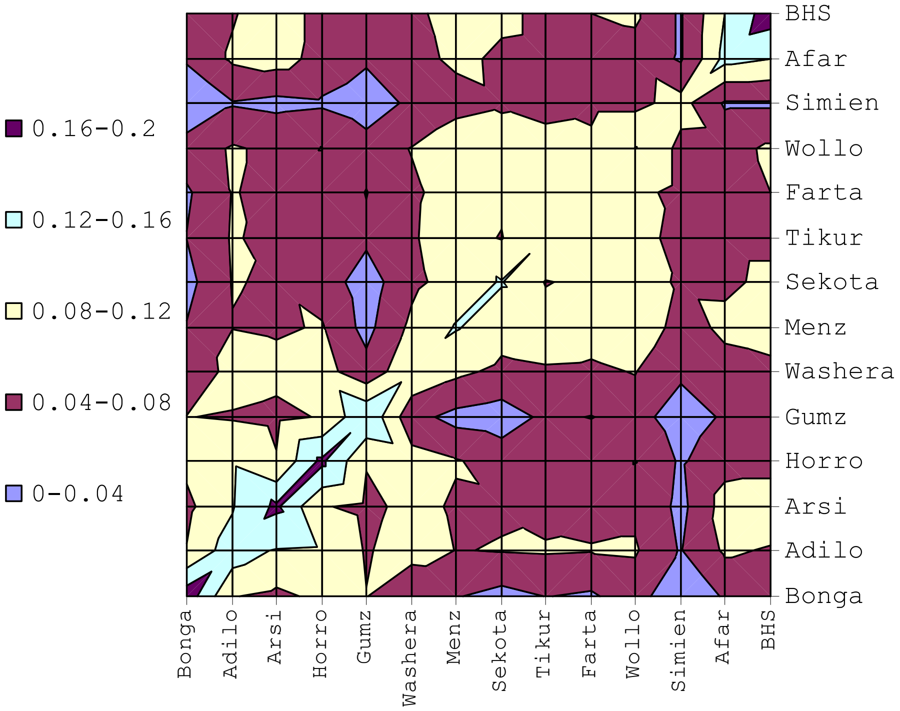

Fig. 3.1. Contour plot of within- and between-breed kinships. Kinships are estimated based on microsatellite markers following Eding and Meuwissen (2001). Low kinship implies high genetic diversity. Populations within the same breed group (Table 3.1) clustered together within the same range of kinship coefficients.

Contribution of breeds to the core set from the full set of breeds is presented in Table 3.3. Simien constituted nearly half of the core set (46.92%), followed by Bonga, Afar, Gumz and Washera. The estimated loss of diversity from maintaining only the Safe set was 2.37% (Table 3.3). The additional gain in diversity from adding one non-safe breed to the safe set ranged from 1.37% (Simien) to 0.0% (Adilo). Simien, Bonga and Gumz were the largest contributors.

Table 3.3. Eding (2002) total diversity[†] conserved from the full set of breeds and contribution of each breed to the core set C_{cor} ; contribution of a non-safe breed to the diversity in Safe+1 set (C_{s+i}), diversity conserved from the Safe set of breeds (††) or the Safe set plus one additional non-safe breed $V(S+i)$ with the corresponding percentage gain in additional diversity from the extra non-safe breed (Gain %)

		Full set	Safe set + 1		
Breed (i)	Threat status	C_{cor}	C_{s+i}	$V(S+i)$	Gain %
		0.9286 [†]		0.9066 [††]	-2.37[‡]
Farta	Non-safe	0.0000	0.4280	0.9106	0.44
Menz	Non-safe	0.0000	0.1143	0.9078	0.13
Sekota	Safe	0.0000			
Simien	Non-safe	0.4355	0.5289	0.9190	1.37
Tikur	Non-safe	0.0000	0.2357	0.9107	0.45
Wollo	Non-safe	0.0000	0.2149	0.9092	0.29
Afar	Safe	0.1291			
BHS	Safe	0.0000			
Adilo	Non-safe	0.0000	0.0000	0.9051	0.00
Arsi-Bale	Safe	0.0000			
Horro	Safe	0.0000			
Bonga	Non-safe	0.1774	0.2444	0.9146	0.88
Gumz	Non-safe	0.1170	0.3333	0.9147	0.89
Washera	Safe	0.0696			

[†] Eding total genetic diversity in the core set calculated as 1-f_{cs} , where f_{cs} is the average kinship in the core set.

[††] Diversity conserved from the Safe set of breeds

[‡] Gain relative to the full set

3.3. Conservation priorities

Ranking of the 14 breeds based on their total utility combining their threat status, current merits and contributions to genetic diversity is presented in Table 3.4. The highest five priority breeds were Simien, Gumz, Afar, Menz and BHS in ranking order.

Table 3.4. Relative conservation priorities for Ethiopian sheep breeds based on contributions to Eding core set diversity, extinction probability and overall breed merits

Breed	Contribution to diversity[1]	Extinction probability[2]	Average breed merit[3]	Total utility [4]	Conservation priority
Farta	0.0000	0.50	0.27	0.27	10
Menz	0.0000	0.40	0.40	**0.40**	4
Sekota	0.0000	0.10	0.23	0.23	13
Simien	0.4355	0.30	0.33	**0.60**	1
Tikur	0.0000	0.30	0.33	0.33	8
Wollo	0.0000	0.50	0.33	0.33	7
Afar	0.1291	0.05	0.40	**0.41**	3
BHS	0.0000	0.10	0.40	**0.40**	5
Adilo	0.0000	0.40	0.17	0.17	14
ArsiBale	0.0000	0.10	0.27	0.27	12
Horro	0.0000	0.20	0.27	0.27	11
Bonga	0.1774	0.40	0.20	**0.34**	6
Gumz	0.1170	0.90	0.23	**0.44**	2
Washera	0.0696	0.10	0.27	0.28	9

[1] Contribution to Eding core set diversity was taken from C_{cor} in Table 3.3.

[2] Extinction probabilities were calculated based on indicators of threat status (Table 3.2) as described in text.

[3] Average breed merits were calculated as average of economic, ecological and socio-cultural merits (Table 3.2) as described in text.

[4] Total utility of a breed was calculated as the sum of twice its 'conservation potential' (product of extinction probability and marginal diversity) and its average merit.

4. Discussion

In this study we ranked 14 traditional sheep breeds of Ethiopia for conservation purposes. Earlier studies, except Ruane (2000) and Reist-Marti et al. (2006), have prioritized breeds based solely on their contributions to genetic diversity (*e.g.* Cañón et al., 2001; Mateus et al., 2004; Tapio et al., 2006). Here, we applied a maximum-utility-strategy (Bennewitz et al., 2007) by combining threat status, current breed merits and contributions to genetic diversity. The results show that the relative conservation priorities for Ethiopian sheep breeds change when they are ranked based on their contributions to genetic diversity alone or on their total utility.

Eding's core set approach (2003) gives highest priority to conservation of breeds with lowest average kinship between individuals within (highest within-breed diversity) and across breeds (highest between-breed diversity). In the current study, the highest contribution to Eding's core set of breeds was made by Simien sheep. Simien is well differentiated from other breeds and has high within-breed diversity (lowest within-breed kinship, high heterozygosity and high allelic richness). Similar results have been reported for Portuguese cattle (Mateus et al., 2004).

Maximum genetic diversity is conserved by maintaining individuals or breeds with minimum genetic relationships. An earlier study on degree of genetic differentiation, relationships and population genetic structure based on Nei (1983) genetic distances and F-statistics among the 14 populations studied here revealed that Ethiopian sheep could be classified into six breed groups and nine breeds (Solomon et al., 2007). The current analysis based on kinship coefficients (Fig. 3.1) and the earlier study on the genetic structure of the same populations (Solomon et al., 2007) indicate that some of the traditional breeds within the six breed groups (Table 3.1) cannot be genetically distinguished. The core set method is robust in such a situation as it excludes individuals/breeds that have high kinship values with other individuals/breeds in the set (Eding and Meuwissen, 2003). This is illustrated in our results; the five breeds that contributed to the core set represent each of five breed groups, with the rest of the breeds within each group having zero contribution. The sixth group (Horro/Adilo/Arsi) did not contribute to the core set. They have high kinship with other breeds in the core set (Bonga, Gumz and Washera). They also have higher within-breed kinship coefficients (0.14 – 0.17) compared to breeds contributing to the core set. These findings support the idea that Eding's approach disfavours inbred populations or those with low within-breed diversity.

When breeds are ranked based on their total utility (Table 3.4), two of the five breeds that constitute Eding's core set based on their contributions to genetic diversity (Table 3.3) are excluded from the five highest ranking breeds. The two excluded breeds (Bonga and Washera) have lower total utility value because of either lower extinction probabilities or lower average breed merits. On the other hand, the two breeds (Menz and BHS) that replace Bonga and Washera have higher average breed merit values although they do not contribute to the total genetic diversity conserved. Conservation of the five breeds with highest total utility would still conserve 73.4% of the genetic diversity in Ethiopian sheep. The reduction in the total genetic diversity conserved when considering current breed merits in this study is higher than reported for African cattle breeds (Reist-Marti et al., 2006), where only 0.5% of the diversity conserved (disregarding breeds with special merits) would be lost when breeds with special merits were favoured for conservation. Inclusion of the sixth highest ranking breed (Bonga) would conserve most of the genetic diversity (92.5%). These six breeds are also economically, ecologically and culturally the most important breeds in Ethiopia.

Ruane (2000) suggests that the primary criterion for conservation priorities should be the degree of endangerment (maximum-risk-strategy). The six breeds with highest total utility value in this study exclude some of the eight non-safe breeds (Table 3.3). This is because some of the excluded non-safe breeds (*e.g.* Wollo and Farta) are genetically overlapping, as discussed above, with the high ranking Simien breed. Breeds with a high probability of extinction will not necessarily have highest priority for conservation, as their contribution to diversity will depend on whether there are other closely related breeds (Barker, 2001).

Consideration of current breed merits and threat status, besides to neutral genetic diversity, enabled us to balance the trade-offs between conserving diversity as insurance against future uncertainties and current sustainable utilization. There has been very limited research (Simianer et al., 2003; Reist-Marti et al., 2006) on optimally combining measures of neutral diversity and breed merits in order to rank breeds on their total utility. The simplified approach adopted in this study with an arbitrary twofold weight on neutral diversity provided a working ranking of the breeds studied. A conceptual framework for a maximum utility through a weighted summation of measures of neutral diversity and breed merits suggested by Simianer et al. (2003) merits consideration. However, currently there is no obvious way of obtaining weights such as relative economic values of neutral diversity (Bennewitz et al., 2007).

The ranking of breeds provided here could be used to define conservation priorities for Ethiopian sheep and could contribute to a regional or global conservation plan. Recommended conservation measures could include supporting genetic improvement programs to increase market competitiveness of indigenous breeds of lower productivity and stratification of production zones to avoid indiscriminate crossbreeding (*e.g.* sub-alpine breeds). For breeds threatened by erosion of within-breed variation (*e.g.* Bonga), within-breed genetic management (such as circular mating scheme and restocking of breeding rams) aiming at reduction of inbreeding rates could be recommended.

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Table S3.1. Marker-based within- and between-breed coefficients of kinship estimated using weighted log-linear model [Eding and Meuwissen 2003]

	Farta	Menz	Sekota	Simien	Tikur	Wollo	Afar	BHS	Adilo	Arsi	Horro	Bonga	Gumz	Washera
Farta	0.0951													
Menz	0.0939	0.1229												
Sekota	0.0905	0.0938	0.1226											
Simien	0.0712	0.0673	0.0760	0.0929										
Tikur	0.0841	0.1004	0.0775	0.0671	0.1184									
Wollo	0.0886	0.1040	0.0938	0.0702	0.0956	0.0815								
Afar	0.0676	0.0865	0.0775	0.0345	0.0738	0.0692	0.1337							
BHS	0.0800	0.0914	0.0858	0.0349	0.0734	0.0815	0.1210	0.1823						
Adilo	0.0815	0.0789	0.0814	0.0370	0.0833	0.0830	0.0857	0.0765	0.1413					
Arsi	0.0737	0.0753	0.0771	0.0303	0.0712	0.0734	0.0965	0.1050	0.1165	0.1671				
Horro	0.0758	0.0828	0.0643	0.0353	0.0758	0.0803	0.0652	0.0641	0.1154	0.0831	0.1681			
Bonga	0.0348	0.0427	0.0265	0.0000	0.0409	0.0594	0.0465	0.0469	0.0819	0.0720	0.0884	0.1816		
Gumz	0.0387	0.0273	0.0181	0.0194	0.0480	0.0544	0.0450	0.0608	0.0764	0.0709	0.0825	0.0809	0.1551	
Washera	0.0741	0.0882	0.0722	0.0472	0.0756	0.0815	0.0675	0.0732	0.0980	0.0911	0.0966	0.0408	0.0537	0.1106

CHAPTER 4

Estimates of genetic parameters and genetic trends for live weight and fleece traits in Menz sheep

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Abstract

Menz sheep are indigenous to the highlands of Ethiopia, and highly valued for their meat and wool production. The area is characterised as a low input sheep-barley production system. In 1998, a selection experiment was set up to evaluate the response of Menz sheep to selection for yearling live weight (WT12) and greasy fleece weight (GFW) combined in an economic index. In this paper, we report the results of this breeding program obtained between 1998 and 2003. Average annual expected responses for WT12 and GFW were 1.506 kg and 0.043 kg in the selected flock and 0.392 kg and –0.008 kg in the control flock. Annual genetic trends in the selected flock, estimated by regressing BLUP estimated breeding values on year of birth, were 0.495±0.053 kg for WT12, 0.012±0.002 kg for GFW, and Birr 5.53±0.55 for the aggregate breeding value (1 Birr = 0.11 Euro). Corresponding values for the control flock were 0.276±0.065 kg, 0.003±0.002 kg and Birr 2.93±0.69. Correlated responses in birth weight (WT0), weaning weight (WT3), six-month weight (WT6) and staple length (STPL) in the selected flock were 0.038±0.005 kg, 0.271±0.03 kg, 0.388±0.039 kg and 0.011±0.017 cm, respectively. Heritabilities, estimated by fitting a multitrait individual animal model were 0.464±0.014, 0.477±0.016, 0.514±0.017, 0.559±0.019, 0.393±0.016 and 0.339±0.014 for WT0, WT3, WT6, WT12, GFW and STPL, respectively. Phenotypic and genetic correlations between all traits were positive, except for STPL and WT12. Estimates of genetic parameters and observed genetic trends confirm that selective breeding can lead to significant genetic improvement in Menz sheep.

Key words: genetic trends, genetic parameters, live weight, fleece, Menz sheep

1. Introduction

Menz sheep, numbering about 1.5 million, are indigenous to the highlands of Ethiopia. The breed is fat tailed, medium-sized (30-35 kg), predominantly black, brown or white in plain and patchy coat colour pattern, and raised for its meat and coarse wool (Mason, 1969). Menz sheep are in high demand during festivals owing to their delectable meat and are an important source of cash income for smallholder farmers from the sale of live sheep. The coarse wool is widely used for weaving traditional blanket (*Zitet* or *Banna*) and carpet, and is a second source of farm income, especially for women.

Although the breed is highly adapted to the harsh environment of the area, profitability from Menz sheep farming is limited by biological and socio-economic factors. Market weight of yearling Menz sheep is inferior to other local breeds (Awgichew et al., 1989). Overall reproductive efficiency is also low owing to absence of twinning and a relatively high pre-weaning mortality rate (Mukasa-Mugerwa and Lahlou-Kassi, 1995).

For the last three decades, the predominant genetic improvement strategy for this breed has been crossbreeding by importing various exotic sires (Corriedale, Rhomney, Hampshire and Awassi). However, the effort produced no positive impact at village level. Under village conditions superiority of crossbred lambs at birth was lost in subsequent weighing periods (Hassen et al., 2002) as the small Menz dams could not support their growth. There were also organizational and technical difficulties in disseminating genetic gains and maintaining desired levels of exotic inheritance at village level. As a result, Menz sheep crossbreeding program has failed. A similar result has been reported for a goat crossbreeding program in the country (Workneh, 2000).

Crossbreeding programs have so massively prevailed in the tropics that very few within breed selection experiments have been conducted (Kosgey et al., 2004). Commonly cited obstacle to the design and implementation of conservation-based selective breeding programs in the tropics is the lack of estimates of genetic parameters to predict genetic gains. As a result, there are few publications on successful selective breeding programs conducted in a tropical context.

There exists high within breed additive genetic variability in Menz sheep for traits of production (Zelealem, 1987) and endoparasite resistance (Rege et al., 1996). However, available genetic parameter estimates are either limited to six and nine month weights (Toe et al., 2000), or to estimates for pre-weaning traits from combined data of Menz and other breeds (Hassen et al., 2003). Some of these estimates were obtained from less efficient sire models (Solomon and Joshi, 2004ab,). Yet, it is known that in order to design more optimal breeding programs, breed-specific genetic and phenotypic parameters are needed.

In 1998, a selective breeding program for Menz sheep was set up. The overall objective of the program was to increase productivity of Menz sheep while maintaining its vital adaptability to the harsh environment and low-input system of Menz highland. The specific traits in the breeding objective were yearling live weight and yearling greasy fleece weight. The basis for selection of the traits and construction of the selection index was literature estimates of genetic parameters for other breeds. In this paper, we report the results of this breeding program obtained between 1998 and 2003. We also present estimates of genetic parameters for economically important traits.

2. Materials and methods

2.1 Location, flock structure and management

The selection project was undertaken at Debre Birhan Agricultural Research Centre. The centre is located in the central highlands of Ethiopia. The Menz sheep area is located at 39-40^{0}E longitude and 10-11^{0}N latitude and is characterized as a sheep-barley production system at altitude range of 2500 - 3200 m. Temperatures vary from 5 to 18^{0}C and frost is common from October to November. Average annual rainfall is 980 mm with bimodal distribution during March-April and June-September.

The foundation flock was established in 1998 through purchase of 300 yearling lambs from Menz area. The pedigree of the animals was unknown. After stratification based on live weight and fleece colour, the animals were allotted at random to selection (200 animals) and control (100 animals) flocks. Each flock was divided into five single-sire mating groups with ram to ewe mating ratio of 1:40 and 1:20 in the selection and control flocks, respectively. Mating started in January 1998 using unselected rams. Rams used for the second mating season in 1999 were also unselected since lambs born from the 1998 mating had not yet attained mating age. The first crop from selected rams/ewe lambs was thus produced in 2000. In the 2002 mating, the selection and control flocks were merged (after culling the inferior ewes based on their EBVs) into a single flock and selection continued. The reason for merging was that it was lately known that response to selection could be estimated from the yearly genetic trend without the need to compare with a control flock and it was also decided to establish an elite nucleus flock of larger size.

Both the selected and control flocks were managed as a single flock. All animals were maintained on grazing natural pasture throughout the year except during mating when concentrates are supplemented. Mating season was from November to December each year. Within selected and control flocks, mating groups were maintained as distinct groups and replacement rams and ewes born in one group were allotted to another group in an orderly circular pattern to avoid mating of related animals. Lambs were weaned at three months of age and male and female lambs were herded in separate flocks from six months of age onwards. Replacement rams and ewes were mated at one year of age. Rams were used for one mating season only while ewes were used until they were culled (usually after 4-5 yrs). Each year five rams for each of the selection and control flocks were used. In 2002, seven rams were used.

2.2 Breeding goal, evaluation of animals and selection

The breeding objective was to improve sale weight and fleece production while maintaining adaptation to the environment. The selection criteria were yearling live weight and greasy fleece weight. BLUP breeding values (EBV) were estimated fitting a multivariate individual animal model. Literature estimates of genetic parameters were used during the initial stage of the project but in later years parameters were estimated from the data set itself. The candidate animals were evaluated based on their aggregate genotype calculated from the selection index $I = (10.2)g_{WT12} + (38.4)g_{GFW,}$ where g_{WT12} and g_{GFW} are EBV for yearling live weight and greasy fleece weight, and the economic weights are in Birr (1 Birr = 0.11 Euro). Ram replacements for the selection flock were those with the highest aggregate breeding values (except for the 2001 crop when selection was made on own performance only), while for the control flock those with average values were used. There was no intentional selection on ewe lambs as most of the available ewe lambs were used as replacement.

2.3 Traits recorded

Data collected over a period of six years (1998-2003) were used for this analysis. Records on 1440 lambs born of 58 sires and 479 dams were analysed. Live weight traits were recorded at birth (WT0), three months (WT3), six months (WT6), and 12 months (WT12) of age. Lambs were weighed on the day of birth. Other live weights were measured in the morning following overnight fast within ±10 days of the intended age of weighing. Greasy fleece weight (GFW) and staple length (STPL) were measured at one year of age. The data structure and means and standard deviations are presented in Table 4.1.

Table 4.1. Characteristics of the data structure

	WT0 (kg)	WT3 (kg)	WT6 (kg)	WT12 (kg)	GFW(kg)	STPL (cm)
No. records	1440	1203	986	877	877	877
No. animals	1787	1514	1260	1138	1138	1138
Sires [a]	58	58	58	56	56	56
Dams [a]	479	413	353	323	323	323
MGD [b]	142	117	89	65	65	65
MGS [b]	38	37	36	31	31	31
Mean 1998 [c]	2.07±0.45	7.93±1.55	9.74±1.90	15.76±2.67	0.53± 0.15	7.05± 1.24
Mean 2003 [c]	2.31±0.45	8.03±1.64	10.72±2.20	16.69±2.80	0.34± 0.15	6.28± 1.43

[a] Sires and dams with progeny record

[b] Maternal grand dams and maternal grand sires with grand progeny records

[c] Means ± standard deviations in 1998 and 2003 in the selected flock.

2.4 Genetic analysis

2.4.1 Estimation of genetic parameters

(Co)variance components for traits were estimated with a multivariate individual animal model. The data were analyzed employing average information REML, using ASREML (Gilmour et al., 2002). The following model was fitted to the data:

$$\boldsymbol{Y}_i = \boldsymbol{X}_i b_i + \boldsymbol{Z}_i \mathrm{a}_i + e_{i,} \qquad (1)$$

where $\boldsymbol{Y}_i$ is vector of observations for trait $_i$, b_i denotes a vector of fixed effects for trait $_i$ (sex and year as class variables and age of the dam as covariate), a_i is a vector of random animal effects for trait $_i$, e_i is vector of random residual effects for trait $_i$, and $\boldsymbol{X}_i$ and $\boldsymbol{Z}_i$ are incidence matrices relating records for trait $_i$ to fixed and random animal effects, respectively. Heritabilities were calculated as σ^2_a/σ^2_p using the estimated variance components. Maternal effects were ignored.

2.4.2 Estimation of response to selection

2.4.2.1. Phenotypic contrasts

Annual phenotypic changes were measured as the difference between average performance of the selected and control flocks. Within year least squares analyses were carried out fitting fixed effects of flock (selected or control) and sex of the lamb as class variables and age of the dam at measurement as covariate. Since both selection and control flocks were managed as a single flock, any difference between the flocks could be assumed to be attributed to genetic differences.

2.4.2.2. Genetic changes

Expected responses were calculated as deviations of average EBV of selected sires from the average EBV of their male cohort. The ratio of observed responses (here taken as deviations of average EBV of male crop/progeny from the parental male population) to expected responses should be ½ when no selection in ewes is practised. Similarly, expected responses were calculated for replacement ewe lambs to check for any unintentional selection.

Genetic trends were evaluated for index component traits (WT12 and GFW), the aggregate breeding value and correlated traits. BLUP estimates of breeding values were estimated fitting a multivariate individual animal model as described above in Eq. (1). The aggregate genotype of each animal was calculated using the selection index *I*. The yearly mean estimated breeding values (EBV) for lambs born in each year were then calculated. Deviations of yearly mean EBV from the base levels were taken as estimates of genetic progress in each year and used to plot responses. The base animals with unknown pedigree were assumed to have EBV of zero. Genetic trends (average yearly increases in EBV) were estimated by regressing yearly mean EBV on year of birth.

3. Results

3.1 Estimates of genetic parameters

Table 4.2 presents variance components and heritability estimates for live weight and fleece traits. Heritability estimates for live weight traits were all high and close to 0.50. There was an increasing trend for heritability estimates with age, with a maximum heritability of 0.55±0.019 for WT12. Heritabilities of GFW and STPL were 0.39±0.016 and 0.33±0.014, respectively.

Phenotypic correlation estimates among live weight and fleece traits are given in Table 4.3. All of the phenotypic correlations were positive. Correlations among live weight traits ranged from 0.49±0.02 between WT0 and WT12 to 0.81±0.02 between WT6 and WT12. GFW was moderately correlated with STPL. Phenotypic correlations between live weight traits and GFW were between 0.34±0.02 and 0.44±0.02. Correlation of STPL with live weight traits ranged from 0.18±0.03 to 0.24±0.03.

Genetic correlations among most pairs of traits were higher than the corresponding phenotypic correlations (Table 4.3). Live weights measured at successive ages were highly correlated, ranging from 0.61±0.10 to 0.98±0.02. Correlations between live weight and fleece traits were between - 0.002±0.18 and 0.49±0.11.

Table 4.2. Variance components and heritability estimates for live weight and fleece traits

	WT0	WT3	WT6	WT12	GFW	STPL
σ^2_p	0.211	4.007	6.054	8.692	0.028	2.148
σ^2_e	0.113	2.097	2.942	3.828	0.017	1.418
σ^2_g	0.098	1.910	3.112	4.864	0.011	0.730
h^2	0.464 ± 0.014	0.477 ± 0.016	0.514± 0.017	0.559± 0.019	0.393 ± 0.016	0.339±0.014

σ^2_p: Phenotypic variance; σ^2_e: Residual variance; σ^2_g: Additive genetic variance; h^2: direct heritability. WT0 - WT12: weights at age 0, 3 months, 6 months and 12 months respectively. GFW: greesy fleece weight; STPL: staple length.

Table 4.3. Phenotypic (above diagonal) and genetic (below diagonal) correlations among live weight and fleece traits

	WT0	WT3	WT6	WT12	GFW	STPL
WT0 [a]		0.51 ±0.02	0.52 ±0.02	0.49±0.02	0.34 ±0.02	0.18±0.03
WT3	0.67±0.07		0.82±0.01	0.69 ±0.01	0.38 ±0.02	0.22 ±0.02
WT6	0.69±0.06	0.98±0.02		0.81 ±0.02	0.44± 0.02	0.24 ±0.03
WT12	0.61±0.10	0.94±0.08	0.97±0.08		0.42 ±0.0225	0.23 ±0.03
GFW	0.43±0.11	0.49±0.11	0.49±0.11	0.46±0.14		0.50 ±0.02
STPL	0.14±0.13	0.18±0.15	0.10±0.17	- 0.002±0.18	0.65±0.09	

[a] For legend see Table 4.2.

3.2. Responses to selection

3.2.1. Phenotypic contrasts between selected and control flocks

Phenotypic means of selected and control flocks obtained from within year least-squares analysis for WT12 and GFW are given in Table 4.4. WT12 increased in both flocks until 2001 and dropped in 2002. Yearly deviations of the selected flock from the control in WT12 were positive starting 2000 when the first crop from selected rams was born. Within year comparison of the flocks showed that the phenotypic means were significantly ($P<0.05$) different only in 2002. Similarly, phenotypic differences in GFW between the flocks were significant only in 2002. Least squares means for WT0, WT3 and WT6 (data not shown) also increased over the selection period.

Table 4.4. Least-squares means (±se) of yearling live weight and greasy fleece weight for selected and control flocks and significance of within-year differences between the flocks

Trait	Year	Selected flock		Control flock		*P* value[a]
		N	Mean	N	Mean	
WT12 (kg)	1998	111	15.85±0.25	54	15.37±0.33	0.237
	1999	47	14.40±0.21	13	15.21±0.51	0.271
	2000	77	19.05±0.31	38	18.75±0.54	0.552
	2001	128	20.97±0.28	60	20.84±0.35	0.788
	2002	129	16.71±0.25	62	15.32±0.32	0.001
GFW (kg)	1998	111	0.53±0.01	53	0.55±0.02	0.330
	1999	47	0.42±0.02	14	0.37±0.04	0.261
	2000	77	0.49±0.02	38	0.51±0.03	0.748
	2001	127	0.49±0.01	60	0.49±0.03	0.969
	2002	129	0.43±0.01	63	0.37±0.02	0.009

[a] Significance of differences between selected and control flocks.

3.2.2. Genetic changes

Number of rams selected, expected responses and observed responses for the aggregate genotype, WT12 and GFW are presented in Table 4.5. Intensity of selection in the selected flock ranged from 1.458 to 1.918 over the years. Expected responses (or selection differentials) were higher in the selection flock than the control. However, in the control flock too, a considerable amount of unintended selection was applied, since the selection differentials were not close to zero as might be expected.

Table 4.5. Number of rams selected, expected responses (EBV) and observed responses (EBV) for aggregate genotype (AG), WT12 and GFW in selected and control flocks

Crop [a]	Flock	Rams		Expected response [b]			Observed response [c]		
		Candidates	Selected	AG	WT12	GFW	AG	WT12	GFW
2000	Selected	51	5	19.66	1.529	0.025	12.35	0.705	0.018
	Control	21	5	7.83	0.708	- 0.021	7.33	0.592	- 0.001
2001	Selected	27	5	15.48	0.386	0.034	10.64	0.047	- 0.001
	Control	8	5	-1.23	-0.026	0.033	-5.21	- 0.305	0.026
2002	Selected	34	5	23.11	1.869	0.081	9.56	0.630	0.021
	Control	22	5	4.00	0.495	- 0.036	-3.36	- 0.315	0.035
2003	Selected	102	7	23.81	2.240	0.033	18.58	1.299	0.029

[a] Year progeny are born.

[b] Deviations of EBV of selected and control sires from their male cohorts

[c] Deviations of EBV of male crop/progeny from the parental male population.

The observed response (here taken as deviations of average EBV of male crop/progeny from the parental male population) in the aggregate genotype ranged from 41.4% to 78.0% of the selection differentials in males in the selected flock. The corresponding ranges for WT12 and GFW were 12.2% to 57.9% and - 2.1% to 87.9%, respectively. The proportion of ewe lambs selected every year was on average very high (0.81). However, the selection differentials were very low ranging from Birr - 1.75 to 5.22 for the aggregate breeding value, - 0.17 to 0.46 kg for WT12 and 0 to 0.016 kg for GFW.

Fig. 4.1 shows yearly mean estimated breeding values (EBV) for WT12 for selected and control flocks. There was an overall increasing level of EBV over time for WT12 with a few fluctuations. EBV increased from 1.068 kg in 1998 (when there was no selection) to 3.072 kg in 2003. The genetic trend obtained by fitting linear regression of yearly mean EBV on year of birth was significantly different from zero ($P<0.001$; Table 4.6), amounting to 0.49 kg/yr or 3.1% of the 1998 phenotypic mean.

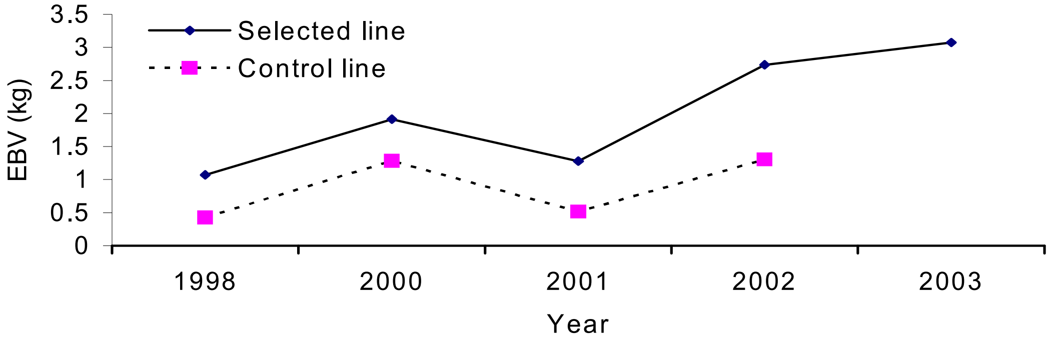

Fig. 4.1. Yearly mean EBV for WT12 in selected and control flocks

Contrary to expectation, there was also an increase in the control flock in EBV of WT12 from 0.428 kg in 1998 to 1.303 kg in 2002. The trend (0.276±0.065 kg) was also significant ($P<0.05$), with average yearly genetic response of 55.7% of that of the selected flock (Table 4.6). Response measured as phenotypic deviation of the selected flock from the control is shown in Fig. 4.2. A deviation of 1.39 kg was achieved in 2002.

Table 4.6. Genetic trends measured as regression of yearly mean EBV on year of birth for live weights, fleece traits and aggregate genotype for selected and control flocks

Trait	b ±s.e	
	Selected flock	Control flock
Direct responses		
WT12 (kg)	0.495±0.053***	0.276±0.065*
GFW (kg)	0.012±0.002***	0.003±0.002 ^{NS}
Aggregate genotype (Birr†)	5.53±0.55***	2.93±0.69*
Correlated responses		
WT0 (kg)	0.038±0.005***	0.017±0.007 ^{NS}
WT3 (kg)	0.271±0.03***	0.114±0.038*
WT6 (kg)	0.388±.039***	0.204±0.039**
STPL (cm)	0.011±0.017 ^{NS}	- 0.004±0.001 ^{NS}

* $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS: non-significant; † 1 Birr = Euro 0.11.

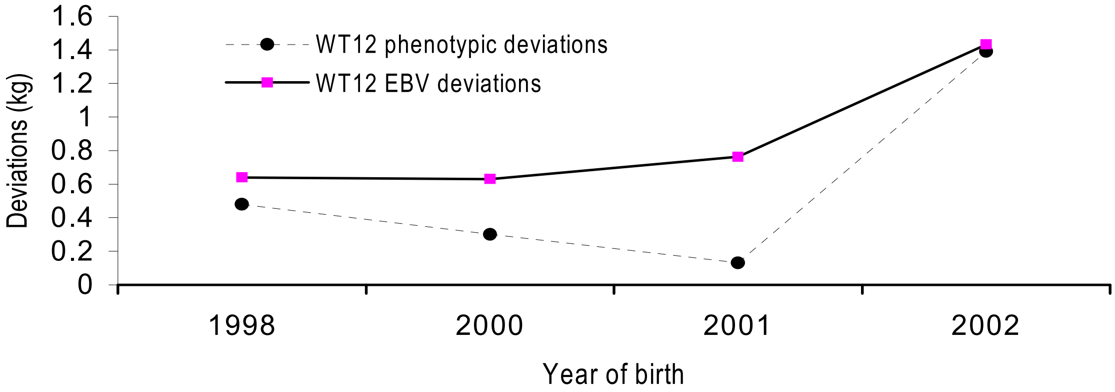

Fig. 4.2. Deviation of selected flock from control flock in phenotypic means and EBV of WT12.

GFW showed a slight increase from 0.009 kg in 1998 to 0.069 kg in 2003 (Fig. 4.3). The average annual genetic response (genetic trend) was also positive and significant ($P<0.001$; Table 4.6). Genetic change in the control flock was not significantly different from zero (Table 4.6).

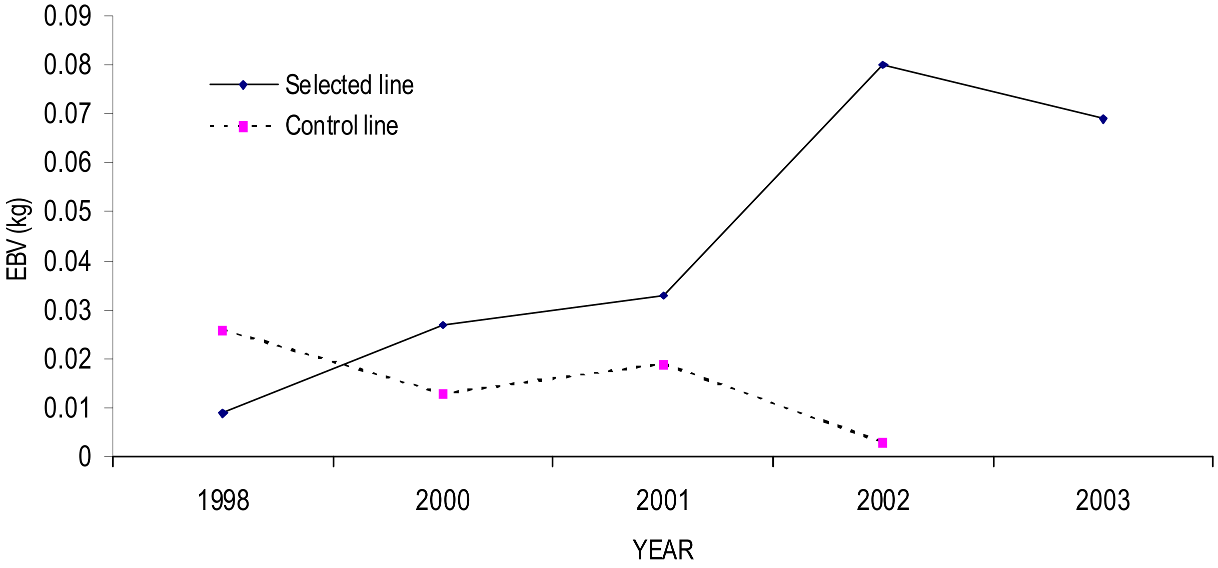

Fig. 4.3. Yearly mean EBV for GFW in the selected and control flocks.

The mean aggregate genotype increased from Birr 11.2 in 1998 to 33.9 in 2003 in the selected flock. The linear trends for the aggregate genotype represented average economic gains to selection of Birr 5.5±0.5 and Birr 2.9±0.7 per year per lamb in the selected and control flocks, respectively.

The mean EBV attained after four years of selection (2003) for the correlated traits WT0, WT3 and WT6 were 0.203, 1.728 and 2.443 kg respectively. Except for WT0, correlated responses in the control flock were also significant ($P<0.05$), but less so than in the selected flock (Table 4.6). The correlated responses in STPL were close to zero in both flocks ($P>0.001$; Table 4.6).

4. Discussion

4.1. Estimates of genetic parameters

The current heritability estimates for WT0 and WT3 are somewhat higher than previous estimates for pure-bred Menz sheep estimated using sire model (Solomon and Joshi, 2004a) and for a mixture of genotypes including Menz sheep using direct-maternal animal model (Hassen et al., 2003). These previous studies utilised field records from sheep multiplication ranches which are more likely to have higher residual variance. Synman and Olivier (1999) found higher heritability estimates for body weight traits from data collected at experimental stations than from performance testing schemes. Heritabillity estimates for WT0 and WT3 in this study are within the range, but closer to the upper limit, of other estimates for tropical sheep obtained from individual animal models (Al-Shorepy, 2001; Abegaz et al., 2002), direct-maternal models (Al-Shorepy, 2001; Neser et al., 2001) or sire models (Abegaz et al., 2002).

The relatively higher estimates in this study could be due to, among other factors, the fact that maternal genetic effects were ignored in the model. The effect of data structure on the reliability of parameter estimates from maternal models has been well emphasized (Willham, 1972; Olivier et al., 1998). The data size and structure for this analysis was considered insufficient to fit maternal effects considering the small number of maternal grand dams with progeny and own records and the few progeny per grand dam.

Heritability estimates for WT6 and WT12 are rarely reported in literature. Toe et al. (2000) estimated heritabilities of 0.16±0.15 from direct-maternal animal model and 0.22±0.17 from sire model for WT6 in Menz ram lambs. The present estimates for WT6 and WT12 are closer to those obtained previously with a sire model (Solomon and Joshi, 2004a). In general, heritability estimates for live weight traits and the trend for the estimates to increase with age in this study are in agreement with the weighted mean estimates for European, Australian and USA breeds (Fogarty, 1995) and average of published estimates in the last decade (Safari et al., 2005).

Heritability estimates for greasy fleece weight and staple length are not available for sheep breeds in the tropics. The present estimates of 0.39 and 0.33 are lower than estimates for GFW and STPL at one year of age for some temperate breeds (Lee et al., 2000; Hanford et al., 2002). A similar estimate to the current one is reported for Suffolk, Polypay and Targhee breeds from across-flock analysis (Notter, 1998). The Phenotypic and genetic correlations for live weight and fleece traits are also within the range of estimates in the literature (Fogarty, 1995; Safari et al., 2005; Solomon and Joshi, 2004a).

4.2. Response to selection

Phenotypic performance levels achieved over the years clearly indicate that there has been improvement in the flock, including in the control flock, although at a lower level. A deviation of 1.4 kg in phenotypic mean of the selected flock from the control in 2002 is indicative of change in performance levels as a result of genetic selection. This phenotypic deviation was similar to the deviation in EBV of the selected flock from the control in 2001 (Fig 4.2). It was, however, lower than the genetic level (2.7 kg) in EBV in 2002 in the selected flock (Fig. 4.1). This is to be expected since in the control flock rams with average EBV were selected, which resulted in reduced magnitude of the phenotypic deviation.

There was fluctuation in the yearly phenotypic means, which is a reflection of variation in the environment or management over the years. The fluctuation was not related to genetic trends in breeding values. Most likely there was a high management input and\or favorable environment in 2000 and 2001.

Our results show that there has been a significant genetic improvement in WT12 and GFW and indicate that long term selection, particularly for WT12, will be effective in Menz sheep. This is in agreement with the heritability estimates for WT12 and GFW obtained in the current and in a previous study (Solomon and Joshi, 2004a) for Menz sheep. The genetic trend in GFW was less consistent; this could be due to the low genetic correlation between GFW and WT12 obtained in this study and reported by Safari et al. (2005), which is much lower than initially assumed when designing the breeding program. The genetic trend in WT12 achieved in this study (0.495 kg/yr) is within the range of available estimates for tropical breeds of 1.02 kg for Barki (Mansour et al., 1997) and 0.059 kg for South African Dohne Merino (Klerk and Heydenrych, 1990).

Although the genetic trends achieved in both WT12 and GFW were positive and significant, there were fluctuations in yearly mean estimated breeding values, particularly in 2001. The decline in mean EBV in 2001 was evidently due to selection of inferior rams as indicated by the low selection differential. This low selection differential in turn traces back to selection of the sires for this crop on their phenotypes rather than their EBV. There were also some unexpected results. The higher than expected genetic trend for WT12 in the control flock could be explained by the selection of control sires with average EBV. This was reflected in the higher selection differential in the control flock, which was not close to zero as might be expected under random selection. In 1998 also, there was improvement in the average EBV although no intended selection of rams was practiced as the rams used were from the base population with unknown pedigree.

The favorable responses in correlated traits (WT0, WT3 and WT6) corroborate the estimated high genetic correlation of these traits with WT12 obtained in this and a previous study (Solomon and Joshi, 2004a) for Menz sheep. Increased birth weight is known to improve lamb survival and increased six-month weight is also relevant to Menz sheep producers' marketing objective as young animals are sold to fulfill unexpected cash needs. Similarly, the low genetic response in STPL is consistent with its relatively low genetic correlation with WT12 and GFW. The genetic gain in WT0 (0.038±0.005) for Menz sheep is comparable with available literature values for tropical breeds of sheep: 0.02 kg for Egyptian Barki (Mansour et al., 1997) and 0.005 kg for South African Dohne Merino (Klerk and Heydenrych, 1990). Reported trends for weaning weight in tropical sheep include 0.092 kg for Rahmani and 0.020 kg for Ossimi (Shaat et al., 2004) and 0.25 kg for Barki (Mansour et al., 1997). Klerk and Heydenrich (1990) reported 0.059 kg annual genetic response for weight at six months.

A substantial improvement in economic terms has been attained in the nucleus flock. Economic gain of Birr 5.53/year per animal on average has been realized.

However, the economic values used to weigh the index traits seem to be underestimated compared to Kosgey et al. (2004) estimation for tropical African sheep ($1.02 for yearling weight). Besides, prices used in deriving the economic values were for a breeding objective targeting local markets, but prospective export market for Menz sheep is expected. The economic gains are thus likely to be higher than realized in this study. Formulation of separate breeding objectives may need to be considered for the subsistence low-input production on one hand, and the (yet to emerge) commercial production and marketing systems on the other hand.

Efficiency of the selection practiced can be considered as high. The observed responses in both trait units and economic units were close to the expected responses. The realised response is roughly half of the selection differential in males. This is to be expected as selection in the females was low which resulted in average annual selection differentials close to zero (0.15 kg for WT12, 0.005 kg for GFW and Birr 1.79 for aggregate breeding value). It could thus be argued that the realized response could have been higher if simultaneous selection on females had been practiced.

The selection program has so far been confined to the nucleus flock at the research center. Schemes to disseminate genetic gain achieved in the nucleus need to be devised. This requires consideration of maintaining genetic diversity in the base population by retaining the desirable merits of the breed regarding traits conferring better adaptation. Observation on fertility and survival rates in this study showed no declining trend in these traits as a consequence of selection. The average inbreeding level was also kept to a minimum (0.00076). Nevertheless, the longer-term consequences of selection need to be investigated, as increased rate of genetic gain is associated with increased inbreeding level, particularly in small populations. Selection methods that maximise selection response at predefined low inbreeding rate, developed by Meuwissen and Sonesson (1998), need to be adopted. Furthermore, inclusion of adaptive traits in Menz sheep breeding objective need to be considered. For instance, there seems to be substantial within-breed variation in resistance to endoparasites in this breed (Rege et al., 1996) and there may be opportunity for improvement of resistance through selection.

5. Conclusion

Estimates of genetic parameters from this study suggest that there exists substantial additive genetic variability in the population. The observed genetic trends confirm that selective breeding can lead to significant genetic improvement in Menz sheep. The high genetic correlation between WT6 and WT12 indicates that breeding rams could be selected at an earlier age of six months.

The low genetic correlation between traits in the selection index (WT12 and GFW), the less consistent genetic trend in GFW and the low selection differential on the female side indicates that the program could be further improved. The availability of more reliable phenotypic and genetic parameter estimates from this study would enable the formulation of a more accurate selection index than the one currently used in the breeding program. The outputs of this study could also be utilized to evaluate alternative improvement and dissemination schemes for Menz sheep and other sheep breeds in the country. Finally, the cost of testing breeding animals and investment need to be appraised to predict the net economic benefit of the program.

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CHAPTER 5

Selection on linear size traits to improve live weight in Menz sheep under nucleus and village breeding programs

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Abstract

Ease of measurement of linear size traits is of particular significance in livestock breeding, particularly under village breeding programs where measuring live weight is difficult. In this study, we estimated genetic parameters and realized responses for live weight (LW) and linear size traits using data from an ongoing Menz sheep nucleus selection program. Using the estimated genetic parameters and simulating a nucleus breeding program and a village-based breeding program for Menz sheep, we compared predicted responses from indirect selection on linear size traits and direct selection on LW. Heritability estimates were 0.46, 0.36, 0.27, 0.31, 0.08, 0.48 and 0.23 for LW, wither height, body length, chest girth, pelvic width, tail length and tail circumference, respectively. Genetic correlations of LW with linear size traits ranged from 0.40 for tail length to 0.98 for chest girth. Realized responses in LW resulting from selection for LW and fleece weight in the ongoing Menz sheep selection program ranged from 0.27 to 0.86 kg per generation. Based on estimated genetic parameters, we chose chest girth, wither height and body length for the simulation study. Predicted responses in LW from indirect selection on chest girth, wither height and body length were 94.8% (nucleus program) and 92.6% (village program) of the responses to direct selection. Our results strongly indicate that genetic improvement in LW through indirect selection on linear size traits is possible both under nucleus and village-based breeding programs. Implications of results of simulated selection programs on the ongoing Menz sheep improvement program are discussed.

Keywords: indirect selection, live weight, linear size traits, sheep, breeding programs

1. Introduction

A closed nucleus selection program to improve yearling live weight and fleece weight in Menz sheep of Ethiopia has been going on since 1998. This program was initiated as a pilot scheme to initially address selected production traits, though livestock breeding objectives in subsistence production systems and marginal environments such as Menz area include both production and adaptive traits. The program also attempts to disseminate genetic gains in the nucleus flock to village flocks, which can be hindered by the difficulties of measuring live weight under village conditions. Linear size traits such as chest girth and body length have been proposed as indirect selection criteria for genetic improvement of meat production in cattle (Kahi and Hirooka, 2005; Maiwasha et al., 2002) and for prediction of live weight in sheep (Mohammed and Amin, 1997) and carcass traits in cattle (Afolayan et al., 2002). Besides, linear size measurements have been suggested as more objective measures of body conformation of animals (Janssens and Vandepitte, 2004; Janssens et al., 2004).

Linear measurements are not affected by plane of nutrition (Bailey et al., 1985) and measurement errors associated with gut fill (Kamalzadeh et al., 1998). They are also more stable throughout the animal's production cycle than live weight. Linear size traits have been found to be moderately heritable and to have a strong positive relationship with live weight in cattle (Afolayan et al., 2007). However, the use of linear size traits as indirect selection criteria in Menz sheep improvement is currently hindered by lack of relevant genetic parameter estimates.

In this study, we first estimate genetic parameters for and realized selection responses in live weight and linear size traits using data from an ongoing Menz sheep nucleus selection program. Subsequently, the estimated genetic parameters are used to compare predicted responses in live weight to indirect selection on linear size traits and to direct selection on live weight for a nucleus breeding program and a village-based breeding program for Menz sheep using deterministic simulations. Implications of results of simulated selection programs on the ongoing Menz sheep improvement program are discussed.

2. Materials and methods

2.1. Genetic parameters and realized responses

Data collected from 1998 to 2003 in a Menz sheep closed nucleus selection program at Debre Birhan Agricultural Research Centre, Ethiopia, were used in the current study to estimate genetic parameters and realized selection responses. The selection program was set up in 1998 with a flock of 300 yearling ewes. Candidate animals were evaluated based on their BLUP estimated breeding values (EBV) for yearling live weight and greasy fleece weight. Details on breeding objective, selection criteria, flock structure and mating design were previously reported (Solomon et al., 2007).

Genetic parameters were estimated for live weight (LW), chest girth (CG), wither height (WH), body length (BL), pelvic width (PW), tail length (TL), and tail circumference (TC). All traits were measured at yearling age (12 months). Means and coefficients of variation for the traits are presented in Table 5.1. All available pedigree information over six generations was used to estimate genetic parameters. The data structure for all traits was as follows: 1138 animals with pedigree relationships, 877 animas with records, born of 323 dams and 56 sires.

Table 5.1. Means, coefficients of variation (CV), variance components and heritability estimates (h^2) with standard errors in parentheses for live weight and linear size traits

Trait	Mean	CV (%)	σ^2_p	σ^2_a	h^2
Live weight	17.44	6.81	7.77	3.58	0.460 (0.021)
Chest girth	62.18	8.44	21.44	6.73	0.314 (0.013)
Wither height	54.07	9.88	15.10	5.44	0.361 (0.015)
Body length	47.91	10.43	15.38	4.13	0.269 (0.012)
Pelvic width	15.02	16.12	4.51	0.34	0.076 (0.004)
Tail length	18.41	21.63	10.83	5.18	0.479 (0.019)
Tail circumference	13.47	23.08	7.03	1.64	0.234 (0.010)

σ^2_p: phenotypic variance; σ^2_a: additive genetic variance.

(Co)variance components were estimated employing a multitrait individual animal model with AIREML as implemented in ASREML (Gilmour et al., 2002). The following model was fitted to the data for a trait *i*:

$$\boldsymbol{Y}_i = \boldsymbol{X}_i b_i + \boldsymbol{Z}_i \alpha_i + e_i \qquad (1)$$

where $\boldsymbol{Y}_i$ is vector of observations for trait *i*, b_i denotes vector of fixed effects for trait *i* [sex, line (selected or control line) and year as class variables and age of the dam as covariate], α_i is vector of random animal effects for trait *i*, e_i is vector of random residual effects for trait *i*, and $\boldsymbol{X}_i$ and $\boldsymbol{Z}_i$ are incidence matrices relating records to fixed and random animal effects, respectively. Inclusion of LW in the multitrait analysis accounted for effect of selection on this trait on parameter estimates. Heritabilities, genetic and phenotypic correlations and phenotypic variances estimated for LW, CG, WH and BL were used to predict responses in the simulation study (see below).

Realized responses were computed for LW, CG, WH and BL. BLUP estimates of breeding values (EBV) were obtained by fitting multitrait individual animal model as described above in Eq. (1), but excluding the fixed effect of line. Average EBV of lambs in each year starting 2000, when the first lamb crop from selected sires was born, were taken as estimates of yearly cumulative selection responses. In order to compare realized responses with predicted responses (which were computed on per generation basis), average realized responses per generation were computed by dividing yearly cumulative responses by average generation interval.

2.2. Predicted responses

2.2.1. Simulated breeding programs

Two breeding structures were considered: a closed nucleus breeding program and an alternative one-tier village-based breeding program. The nucleus program consists of a closed flock at government ranches or research centers where genetic improvement takes place. The nucleus flock provides improved seed-stock to village flocks, but there is no migration from village flocks into the nucleus flock.

A village program was simulated based on existing village breeding practices and opportunities in Menz area. Village breeding programs are breeding activities carried out by communities of smallholder farmers, often at subsistence level (Sölkner et al., 1998) and are also characterized by small flock-size (reducing the possibility of within-flock selection) uncontrolled mating and absence of performance and pedigree recording. Commercial flocks in Menz area are structured into villages (*gots*) within a kebele (smallest administrative unit). Flocks in a village share common grazing and watering points, and are separated from flocks of other villages. A group of flocks in a village could thus be considered as a contemporary group. Replacement animals are selected across flocks within villages. Selected rams are used communally in the village. Ewes are not used communally. Consequently, farmers whose ewe lambs are not selected would need to arrange transfer of selected ewe lambs from other farmers.

2.2.2. Population structures

Based on existing situations in Menz sheep production and breeding, a population was simulated for a nucleus (500 ewes) and a village breeding program (200 ewes = 20 flocks per village × 10 ewes per flock) described above. The following assumptions were made for both programs: ram:ewe mating ratio = 1:40, lambing rate = 0.9, twinning rate = 0.0, yearling survival = 76.5%, ram replacement = 100%, and ewe replacement = 10%. Based on these assumptions, 172 males and 172 females in nucleus centre and 69 males and 69 females in village breeding unit were available at yearling age. Among these, the top ranking 7.3% of the males and 29.1% of the females in both programs were selected to produce the next generation. Selection under nucleus program is based on BLUP EBV (see below) which includes information on half-sibs. Applying the above assumptions to a single mating between a ram and 40 ewes, 27 yearling half-sibs were available to each candidate ram or ewe in each generation of selection under nucleus program.

2.2.3. Selection schemes

The breeding objective assumed in this study was improvement of yearling LW as the objective was to investigate efficiency of indirect selection to improve live weight. Six alternative selection schemes to improve LW were compared in terms of genetic responses and rate of inbreeding under nucleus and village breeding programs. The schemes were: 1) direct selection for LW, 2) indirect selection on CG, 3) indirect selection on WH, 4) indirect selection on BL, 5) indirect selection on CG, WH and BL, and 6) direct selection for LW and indirect selection on CG, WH and BL. Linear size traits included in the selection indices were chosen among the six linear size traits studied because of their high genetic correlation with LW (see Results section). Records for all traits were simulated for each animal.

Selection responses per generation (ΔG) and rates of inbreeding per generation (ΔF) were predicted by deterministic simulation of the six selection schemes using the program Sel*A*ction (Rutten et al., 2002). Selection in the nucleus centre was based on animal model BLUP breeding values combining the selection candidate's own phenotype and information on its relatives (EBV of the sire and dam, mean EBV of the dams of its half-sibs, and observations on its half-sibs). Selection under village conditions was on the candidate's own phenotype only. Selection was carried out until Bulmer equilibrium genetic parameters were reached and selection response was predicted for the Bulmer equilibrium situation, which may take 4–5 generations of selection under discrete generation. Sel*A*ction accounts for reduction in variance due to selection (Bulmer, 1971) and corrects selection intensities for finite population size and for the correlation between index values of family members (Meuwissen, 1991). The program assumes a hierarchical mating structure and random mating of selected animals. Prediction of the rate of inbreeding was based on the long-term genetic contribution theory (Bijma et al., 2001).

3. Results

3.1. Genetic parameters

Heritability estimates ranged from 0.08 for pelvic width to 0.48 for tail length (Table 5.1). Genetic correlations among linear size traits varied between 0.28 and 0.96. Genetic correlations between live weight and linear size traits ranged from 0.40 for tail length to 0.98 for chest girth (Table 5.2). Phenotypic correlation of live weight with linear size traits ranged from 0.39 for tail length to 0.77 for chest girth.

Table 5.2. Genetic (above diagonal) and phenotypic (below diagonal) correlations (with standard errors in brackets[†]) among linear size traits and live weight

Traits	LW	CG	WH	BL	PW	TL	TC
LW		0.98(0.08)	0.89(0.05)	0.97(0.04)	0.98[†]	0.40(0.10)	0.71[†]
CG	0.77(0.01)		0.87(0.12)	0.94(0.19)	0.95[†]	0.41(0.16)	0.62[†]
WH	0.70(0.01)	0.65(0.02)		0.96(0.08)	0.86[†]	0.55(0.12)	0.64[†]
BL	0.69(0.02)	0.54(0.02)	0.63(0.02)		0.94[†]	0.54(0.13)	0.72[†]
PW	0.45(0.02)	0.50(0.02)	0.33(0.03)	0.27(0.03)		0.28[†]	0.70[†]
TL	0.39(0.02)	0.35(0.03)	0.34(0.03)	0.29(0.03)	0.18(0.03)		0.54[†]
TC	0.56(0.02)	0.55(0.02)	0.44(0.02)	0.38(0.03)	0.38(0.03)	0.36(0.02)	

[†] Standard errors could not be estimated for these genetic correlations.

3.2. Realized responses

Realized cumulative responses in live weight, chest girth, wither height and body length are plotted in Fig. 5.1. The first lamb crop from selected sires was born in 2000. A cumulative response of 1.52 kg was achieved for live weight after five years of selection in 2003. Response per generation in live weight was between 0.27 and 0.86 kg. Cumulative responses of 1.59 to 1.99 cm were realized in chest girth, wither height and body length.

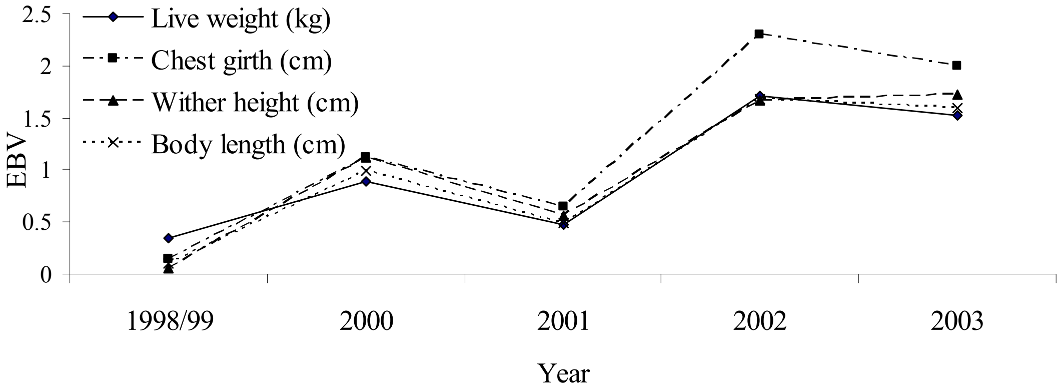

Fig. 5.1. Realized cumulative responses (EBV) in live weight and linear size traits to selection on live weight in Menz sheep.

3.3. Predicted responses

Predicted response in live weight to direct selection on live weight was 1.55 kg under nucleus breeding program and 1.35 kg under village program (Table 5.3). Response in live weight to indirect selection on either chest girth, wither height or body length as percent of response to direct selection ranged from 83.6 to 88.4% under nucleus and from 79.3 to 84.4% under village program. The response in live weight to selection on a multitrait selection criteria including chest girth, wither height and body length was 94.8% under nucleus and 92.6% under village program. When live weight was included in the multitrait selection criteria, the response increased to 100.6% in nucleus and 100% in village program.

Predicted responses in linear size traits ranged from 1.18 to 2.08 cm per generation. Direct responses in linear traits as percentage of responses to indirect selection on LW were above 100% for WH and below 100% for CG and BL. This could be due to the higher heritability of WH (Table 5.1). Rate of inbreeding per generation was 1.74 in direct and 1.93% in indirect selection schemes under nucleus program. Under village program, rates of inbreeding were 2.79 in direct and 2.78% in indirect selection schemes.

Table 5.3. Predicted responses per generation (ΔG) in live weight (kg) and linear size traits (cm) using different selection indices under nucleus and village breeding programs

Breeding program/ selection scheme	Traits in index	Predicted responses [†]				Inbreeding[††] rate (%)
		LW	CG	WH	BL	
Nucleus program						
Direct selection	LW	1.55	2.08	1.70	1.62	1.74
Indirect selection	CG	88.4	91.8	88.2	87.7	2.16
	WH	83.6	83.2	105.6	93.2	2.06
	BL	84.5	83.2	93.5	89.5	2.28
	CG, WH, BL	94.8	95.7	102.4	98.1	1.93
Direct and indirect	LW, CG, WH, BL	100.6	100.5	102.9	101.9	1.73
Village program						
Direct selection	LW	1.35	1.80	1.48	1.41	2.79
Indirect selection	CG	84.4	87.8	83.8	83.7	2.75
	WH	80.7	81.1	102.7	90.1	2.68
	BL	79.3	81.1	102.7	90.1	2.68
	CG, WH, BL	92.6	93.9	102.0	96.5	2.78
Direct and indirect	LW, CG, WH, BL	100.0	100.6	103.4	102.1	2.79

Selection method: BLUP in nucleus program and on own phenotype in village program.

[†] Responses to direct selection are in trait units, and responses to indirect selection are expressed as percent of responses to direct selection. [††] Rate of inbreeding is increases of inbreeding per generation, calculated as $[(F_{t+1}-F_t)/(1-F_t)]*100$.

4. Discussion

In this study, we compared efficiency of indirect selection on linear size traits with direct selection on live weight to improve live weight under simulated closed nucleus breeding and village-based breeding programs. Simulation studies have often used literature estimates of genetic parameters to predict selection responses (e.g. Kuhlers and Kennedy, 1992; Kosgey, 2004). In the current simulations, we used genetic parameters estimated in this study for a Menz sheep population in which results of the simulation study are intended to be applied. Genetic parameter estimates for linear size traits in sheep are lacking in the literature, as it is clear from extensive reviews of genetic parameter estimates for sheep by Safari et al. (2005) and Fogarty (1995). Heritability estimates for CG, WH and BL in the present study are within the range of estimates available for sheep (Janssens and Vandepitte, 2004) and cattle (Maiwasha et al., 2002; Afolayan et al., 2007). Pelvic width was the least heritable trait in the current study. Loin width, a measure closely related to pelvic width, was also found least heritable of body dimension traits studied by Janssens and Vandepitte (2004).

Genetic correlations of LW with CG, WH and BL were high in this study (0.89–0.98), and moderate to high in other studies in sheep (0.58–0.93; Janssens and Vandepitte, 2004) and in cattle (0.58–0.78; Afolayan et al., 2007). These moderate to high genetic correlations indicate that CG, WH and BL can be used as indirect selection criteria to improve LW in sheep. However, linear traits are less heritable than LW. Heritability estimates for LW in Menz sheep in the current and earlier studies (Solomon and Joshi, 2004; Solomon et al., 2007) were higher than estimates for CG, WH and BL in this study. Janssens and Vandepitte (2004) also found higher heritability estimates for weight compared to estimates for linear measurement traits.

Our predictions of responses to simulated selections indicate that 94.8 (nucleus program) and 92.6% (village program) of the genetic gain in LW from direct selection could be achieved through indirect selection on CG, WH and BL. These levels of genetic gain could be achieved without much loss (nucleus program) or with no loss (village program) of genetic diversity within village or nucleus flocks, as can be seen from the highly comparable inbreeding rates under direct and indirect selection schemes (Table 5.3). A simpler indirect selection could be based on CG alone with expected responses of 88.4% of direct selection, provided measures are taken to minimize the increased inbreeding rate under this scheme. Results on responses in LW to indirect selection on linear size traits in sheep are not available in the literature. In general, indirect selection schemes have been found fairly efficient as compared to direct selection to improve mature weight in cattle (Kahi and Hirooka, 2005), lean growth rate in pig (Chen et al., 2003), and meat production in poultry (Zerehdaran et al., 2005).

Besides their use as indirect selection criteria to improve LW, linear size traits are important traits by themselves since they are positively correlated with subjectively scored body conformation characteristics of sheep (Janssens and Vandepitte, 2004). Body conformation highly influences market value of meat sheep in traditional markets where prices are bargained on whole sheep rather than on price per kilogram live weight basis. Body conformation also accounts for more than 20% of price per kilogram of live cattle (Afolayan et al., 2007). Heritability estimates for linear size traits in the current study indicate that moderate response is expected in all linear size traits studied, except pelvic width. Selection for size traits is also expected to result in improved body conformation since they are highly correlated as discussed above.

The ongoing Menz sheep nucleus selection program appears to be moderately efficient, with realized responses per generation in LW of 55.6% of the predicted responses being achieved in some years, although there are fluctuations in responses due to variation in selection intensities over the years (Solomon et al., 2007). However, the high rates of inbreeding in the current simulation study indicate that there is a long-term risk of losing within-breed diversity and reduced responses under the current selection scheme. Different approaches point towards acceptable levels of inbreeding rates of around 0.5 and 1% per generation (Van Arendonk and Bijma, 2003). The predicted high inbreeding rates in the current study could be due to selection on BLUP EBV, which increases rates of inbreeding (Bijma et al., 2001). The high intensity of ram selection and the small ram to ewe mating ratio in the ongoing program (Solomon et al., 2007), which was also simulated in this study, also contributes to increases in inbreeding rates. Further, it was assumed that the nucleus flock in the ongoing program remains closed, and this also has implication in the rate of inbreeding in the nucleus flock. Kosgey (2004) showed that rate of inbreeding is higher in closed than open nucleus schemes where ewes are allowed to migrate from the base commercial flock into the nucleus. Schemes to increase genetic gain while restricting rates of inbreeding, such as a dynamic selection tool introduced by Meuwissen (1997), should be used to avoid too high levels of inbreeding rates (Van Arendonk and Bijma, 2003).

This study provided spin-off results which can be used to compare efficiency of nucleus and village breeding programs in terms of responses to indirect selection for LW. The two programs differed in the population structures and selection methods simulated (BLUP in nucleus and phenotypic selection in village). Compared to village program, 17.6% more genetic gain in LW was achieved through indirect selection on linear size traits in the nucleus program. This is in agreement with earlier findings that responses are higher in nucleus programs (Kosgey, 2004) and that BLUP selection yields more response (Kuhlers and Kennedy, 1992; Quinton et al., 1992). Lower inbreeding is expected with phenotypic selection compared to BLUP selection (Kuhlers and Kennedy, 1992; Quinton et al., 1992). However, in the current study, inbreeding was higher in village breeding with phenotypic selection compared to nucleus program with BLUP selection. This is due to the small population size in the village program resulting from fragmentation of the population into villages with small flock sizes. This could lead to loss of diversity within village flocks, particularly since village flocks are closed. However, diversity could be maintained at population level if rams are exchanged between neighboring villages. General guidelines for implementing village breeding programs under conditions of developing countries are given in Sölkner et al. (1998).

Farmers breeding objectives may not only include live weight. The ongoing nucleus program could be refined by including other relevant production and adaptive traits such as resistance to disease and feed conversion efficiency. Regarding village program, optimal village breeding scheme balancing genetic progress and acceptable level of inbreeding needs to be devised as alternative to centralized nucleus programs.

5. Conclusion

The estimated genetic parameters for linear size traits strongly indicate that genetic improvement in live weight through indirect selection on linear size traits is possible both under nucleus and village-based breeding programs. The predicted high efficiencies of the simulated indirect selection schemes have an important implication in sheep breeding, particularly in developing tropical regions and under village breeding programs where measuring live weight is difficult. Our results also indicate that concurrent genetic improvement in linear body size/conformation is expected under the indirect selection scheme.

The rates of inbreeding in both nucleus and village programs were high. Flock structure may need to be changed in the ongoing Menz sheep nucleus breeding program and/or the nucleus flock needs to be opened to allow migration of ewes from the base population to reduce the rate of inbreeding in the nucleus.

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CHAPTER 6

Participatory definition of breeding objectives and selection indexes for sheep breeding in traditional systems

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Abstract

A farmer participatory approach was used to define breeding objectives and selection indexes for short-fat-tailed sheep in sheep-barley systems and Black Head Somali sheep in pastoral systems in Ethiopia. Breeding-objective traits were identified based on producers' preferences for traits collected during interviews. The desired gains in the various traits were calculated based on the producers' preferences for traits and were used to derive relative weights of traits in the breeding objective using selection-index method. This study recognized subsistence producers (producing yearlings) and subsistence+ producers (producing and finishing yearlings) within sheep-barley and pastoral systems. Producers' preferences for traits showed that adaptive traits are more important (pastoral system) or as important (sheep-barley system) as production traits. Subsistence producers gave more weight to adaptive traits than did the more market-oriented subsistence+ producers. A low correlation (0.31) was found between selection indexes constructed for subsistence and subsistence+ producers in the sheep-barley system. This demonstrates that breeding objectives need to be tailored to the specific needs of the different groups of farmers. The results of our study can be used to design sheep breeding programs in Ethiopia. We present an approach to incorporate producers' preferred breeding objectives into conventional selection tools.

Keywords: breeding objective; selection index; sheep-farming; farmer participatory approach

1. Introduction

Sustainable animal breeding strategies require a broad definition of breeding objectives that emphasize maintaining adaptation and biodiversity in addition to profitability (Olesen et al., 2000; Neilson et al., 2005, 2006). Sölkner et al. (1998) and Kosgey et al. (2004) argued that when defining animal breeding objectives, particularly for subsistence farmers in marginal situations, the needs and interests of the target group should be incorporated. This involves incorporating both tangible and intangible benefits of livestock keeping.

Defining breeding objectives involves identifying breeding-objective traits, deriving their relative importance, and constructing the aggregate genotype that can subsequently be translated into a selection index. It is important to involve the stakeholders in the process of defining breeding objectives. Most studies on participatory definition of breeding objectives have been limited to identifying breeding-objective traits (*e.g.*, Jaitner et al., 2001; Tano et al., 2002; Wurzinger et al., 2006; Ndumu et al., 2008). These "traits" are usually defined in general composite terms such as "adaptation", "growth", or "reproduction". Too little emphasis has been placed on using information from participatory studies to derive relative weights and selection indexes for such traits.

Here, we used subsistence sheep-farming in Ethiopia as a case study for developing participatory breeding objectives and selection indexes. In Ethiopia, sheep are produced in two main types of systems: 1) sheep-barley systems in sub-alpine areas, and 2) pastoral systems in arid lowlands (Solomon et al., in press). Sheep production in these systems is characterized by subsistence-level management, a wide range of production objectives and marketing strategies, and marginal production environments. Breeding-objectives are defined by the farmers' and pastoralists' preferences for different traits. We present an approach for weighting traits in the breeding objective based on farmers' preferences.

2. Materials and Methods

2.1. Definition of production systems

Two short-fat-tailed traditional sheep breeds, Menz and Wollo, representing the sub-alpine sheep-barley production system, and the Black-head-Somali breed, representing the arid lowland pastoral production system in Ethiopia were surveyed. For a detailed description of breeds, see Solomon et al. (2007a). One hundred and sixty-one farmers from sheep-barley systems and 101 pastoralists were interviewed individually.

A semi-quantitative method (proportional piling) was used to determine the priorities of farmers and pastoralists. Each person was asked to allocate 20 pebbles to seven functions of sheep, as summarized in Table 6.1. The functions were presented using drawings, as described in more detail below. Respondents were also interviewed about their finishing and marketing strategies using the descriptions presented in Table 6.2. These results were used to allocate farmers to one of two groups within each production system:

1. Subsistence lamb producers (S): produce unfinished yearlings for sale to consumers or finishers
2. Subsistence lamb+ producers (S^+): produce unfinished and finished yearlings and culled rams

2.2. Identification of breeding objective traits

Six categories of traits that influence the important functions of sheep (Table 6.1) were identified (Table 6.3): adaptation, growth/weight, *qumena* (farmers' general physical description of an animal in relation to its market value, which includes size, conformation, tail, horn, color), reproduction, fleece, and milk. We defined a trait category as a 'characteristic' consisting of one or more biological component traits. Defining such broad trait categories facilitated discussions with farmers since farmers describe animal performance using such expressions. In addition, individual biological traits could be too detailed and their numbers too large to be used in discussions with farmers.

The six trait categories were described to producers using drawings of six hypothetical types of sheep. Generally, each sheep type encompassed one of the trait categories, but trade-offs between the different trait categories were also described verbally and with the aid of drawings. For example, the adapted sheep type was shown in the drawing as smaller in size than a less adapted but fast-growing sheep type. The trait categories were rated by producers using 20 pebbles. Wilcoxon Signed Rank test was used to evaluate similarities between the ratings of the six trait categories. Trait categories that did not differ significantly in rating were assigned the same ranking (Table 6.3).

The trait categories used during the interviews with the farmers were too broad to be used directly in the selection indexes. Therefore, each trait category was translated into component traits. Component traits for which estimates of genetic parameters were available were chosen for this study. The component traits identified for each trait category were:

1. *Adaptation*: fecal worm egg count (FEC)
2. *Growth/weight*: yearling weight (YW), mature weight (MW), and daily gain during finishing (ADG; S^+ producers only)
3. *Qumena*: chest girth (CG)
4. *Reproduction*: number of lambs weaned (NLW)

5. *Fleece*: greasy fleece weight (GFW; sheep-barley system only)
6. *Milk*: daily milk yield (MY; pastoral system only)

2.3. Desired-gain selection indexes

2.3.1. Derivation of relative weights

We used a desired-gain selection index method to derive relative weights for breeding-objective traits that result in gains desired by producers. Producers' desired gains were established based on their preferences for trait categories (Table 6.3). Two desired selection indexes were constructed for each of S and S^+ producers in sheep-barley and pastoral systems. For the first index, desired gains for component traits that were ranked first were set equivalent to maximum gains achievable. For the second index, gains were maximized for component traits that ranked first and second. Weights for component traits in the breeding objective were set to zero if their respective trait categories ranked below first in the case of first index and below second in the case of second index. The genetic response observed for these traits is the correlated response that results from selecting for the traits included in the breeding objective.

The maximum gain for each trait was the gain achieved from single trait selection on that trait only, i.e. with only this trait in both the aggregate genotype and the selection index. For the sheep-barley system, the first index (first-ranked traits only) maximized gain for YW for S, and YW and ADG for S^+ producers. The second index (first- and second-ranked traits) maximized gain for YW, CG, and FEC for S, and YW, ADG, CG, and NLW for S^+ producers. In the pastoral system, the first index maximized gain for FEC for S and S^+ producers. The second index maximized gain for FEC, CG, NLW, and MY for S, and FEC and NLW for S^+ producers.

Relative weights for traits were derived by iterating on arbitrarily assigned starting weights until the desired genetic gains were approached using the program Sel*A*ction (Rutten et al., 2002). Four sets of relative weights were derived for each production system. These correspond to the desired gains by S and S^+ producers and two alternative indexes for each of S and S^+ producers, as described above.

2.3.2. Population structure for calculating responses

Genetic gains were predicted by deterministic simulation of a nucleus breeding scheme using the Sel*A*ction program (Rutten et al., 2002). A nucleus population with 500 ewes mated to 12 rams in each generation was simulated. The ewe population was assumed to produce for five years based on sheep flock structure in traditional systems (Abebe, 1999). All breeding males were replaced each mating season. The proportion of rams selected for breeding was 0.075 (12 out of 160 available yearling males). The proportion of ewes selected for breeding was 0.30 (48 out of 160 yearling females) from the youngest females to replace culled ewes, while all available ewes from the older age groups were selected for breeding.

All candidates for selection had records for all traits studied, except for NLW, MY, and MW, which were recorded on the dams of the selection candidates only. Genetic and phenotypic parameters used in the simulation are shown in Appendix 6.1. The same parameters were used in all systems in order to enable direct comparison of the indexes for different systems.

2.3.3. Correlation between selection indexes

To evaluate the similarity of indexes, correlations among the different indexes ($r_{jj'}$) were estimated using the following equation:

$$r_{\mathrm{jj'}} = \mathbf{b}'_{\mathrm{j}}\mathbf{P}\mathbf{b}_{\mathrm{j'}} \Big/ \left[\left(\mathbf{b}'_{\mathrm{j}}\mathbf{P}\mathbf{b}_{\mathrm{j}} \right) \left(\mathbf{b}'_{\mathrm{j'}}\mathbf{P}\mathbf{b}_{\mathrm{j'}} \right) \right]^{1/2}$$

where $\mathbf{b}_{\mathrm{j}}$ is a vector of selection index weights for the j^{th} index, and **P** is the variance-covariance matrix among selection index traits.

Selection index weights ($\mathbf{b}_{\mathrm{j}}$) for the j^{th} index was calculated as

$\mathbf{b}_{\mathrm{j}} = \mathbf{P}^{-1}\mathbf{G}\boldsymbol{w}$,

where **P** is as described above, **G** is the variance-covariance matrix among selection index traits and breeding objective traits, and $\boldsymbol{w}$ is a vector of relative weights for traits identified using the desired gain selection index method.

3. Results

3.1. Farmers' and pastoralists' preferences

Farmers' and pastoralists' ratings of the relative importance of different functions of sheep are presented in Table 6.1. Regular cash income and financing/insurance benefits derived from sheep production were identified as the most important functions of sheep in both sheep-barley and pastoral production systems. Manure production is an important function in sheep-barley systems, but less so in pastoral systems. This reflects the greater contribution of sheep production to crop production in sheep-barley systems. Sheep production contributes more to the diet of pastoralists (in the form of milk) than to the diet of farmers in sheep-barley system. Fleece is not produced in pastoral systems.

Table 6.1. Sheep producers' ratings of the relative importance of functions of sheep in sheep-barley and pastoral production systems

Function of sheep	Sheep-barley system	Pastoral system
Regular cash income	6.12	4.84
Financing/insurance benefits [†]	7.28	7.26
Socio-cultural importance	1.25	3.51
Meat (home consumption)	1.82	1.68
Fleece (home use and sale)	1.33	0.00
Manure (home use)	1.96	0.34
Milk (home consumption)	0.04	2.46

[†] For sheep-barley systems, this includes insurance against crop failure.

Results of the survey on production and marketing strategies (Table 6.2) showed that most farmers and pastoralists sell unfinished yearlings. Most farmers and pastoralists finished culled rams rather than yearlings. Table 6.2 also presents the relative rankings of different classes of sheep in terms of their contribution to the farm economy.

Table 6.2. Survey of sheep producers' production and marketing strategies

	Sheep-barley system	Pastoral system
Percentage of farmers		
Selling unfinished yearlings	77.8	66.1
Finishing yearlings	22.8	31.4
Finishing culled rams	77.2	68.6
Most sold class of sheep (rank) [†]		
Surplus yearling males	1.9 (1)	2.8 (2)
Surplus yearling females	3.5 (3)	3.7 (3)
Fattened males	2.4 (2)	1.4 (1)
Culled ewes	3.2 (3)	3.9 (3)
Culled rams	3.8 (4)	3.1 (2)

[†] The scale used was 1 = most important to 5 = least important class of sheep. Equivalent ranks (in parentheses) were assigned to average rankings that did not differ significantly based on Friedmans test ($P > 0.05$).

Table 6.3 shows producers' preferences for trait categories they would like to be improved. Trait categories that ranked first and second based on Wilcoxon Signed Rank test were considered to be the most desired trait categories in subsequent analysis. In sheep-barley systems, the most desired trait categories, in order of importance, were growth/weight, adaptation, and *qumena* for S producers, and growth/weight, *qumena*, and reproduction for S^+ producers. In pastoral systems, adaptation was the first-ranked trait category both for S and S^+ producers. The other most desired trait categories were reproduction, milk, and *qumena* for S, and reproduction for S^+ producers.

Table 6.3. Sheep producers' mean ratings and rankings (in parentheses) of sheep trait categories they would most like to be improved

	Sheep-barley system			Pastoral system		
Trait category	Overall	S	S^+	Overall	S	S^+
Adaptation[†]	4.1 (2) [‡]	4.7 (2)	3.7 (3)	7.4 (1)	9.0 (1)	7.1 (1)
Growth/weight	5.7 (1)	5.9 (1)	5.5 (1)	3.1 (3)	1.9 (3)	3.5 (3)
Qumena[††]	4.7 (2)	4.6 (2)	4.8 (2)	2.7 (4)	2.7 (2)	2.6 (4)
Reproduction	4.3 (2)	3.7 (3)	4.7 (2)	4.8 (2)	3.4 (2)	5.2 (2)
Fleece	1.1 (3)	1.1 (4)	1.1 (4)	0.0 (6)	0.0 (4)	0.0 (6)
Milk	0.1 (4)	0.0 (5)	0.1 (5)	1.9 (5)	3.0 (2)	1.6 (5)

S farmers/pastoralists produce yearlings and S^+ farmers/pastoralists produce and finish yearlings and culled rams; [†]Adaptation represented tolerance to disease, drought, and cold in sheep-barley systems, and tolerance to drought, disease, and heat, and ability to trek long distances in pastoral systems; [††]*Qumena* refers to physical characteristics such as size, conformation, color, horn, and tail, which influence market value in traditional markets; [‡] Equivalent ranks (in parentheses) were assigned to ratings that did not differ significantly based on Wilcoxon signed rank tests ($P > 0.05$).

3.2. Selection indexes

Table 6.4 displays the genetic gains that resulted from selection on different breeding objectives in the sheep-barley system. The single-trait response represents the genetic gain that can be obtained when this trait alone is included in the breeding objective and selection index. The single-trait response depends on the genetic parameters used and the amount of information collected on selection candidates. Genetic parameters and amounts of information collected were the same for all systems; therefore, the single-trait responses were equal for all production systems. The single trait responses were used as starting points for deriving the desired-gain indexes.

The first-ranked breeding objective for S^+ producers included YW and ADG. The relative weights for both traits were derived using the desired-gain approach in which the gains in YW and ADG were maximized while keeping all other traits in the breeding objective constant. The relative gains in YW and ADG were set equal to 0.64 and 0.016 kg, respectively. The responses in the seven breeding-objective traits resulting from selection on the first-ranked breeding objective are presented in Table 6.4. The responses in YW and ADG were 98.4% and 81.2% of the single-trait responses, respectively. This reduction in response was caused by including desired gains of all traits in the breeding objective. Including the second-ranked traits NLW and CG in the breeding objective lead to a 3.2% reduction in genetic gain of YW, a 15.4% reduction in genetic gain of ADG, and a 46.7% increase in the genetic gain of NLW. Gain in CG could not be increased as desired because of its high genetic correlation with YW. Including only the second-ranked traits had a small effect on the relative weights in the breeding objective and the responses resulting from the index. The rankings of animals based on both indexes were very similar, as reflected by the high correlation coefficient (0.95; Table 6.4).

For S producers, the selection index constructed from first-ranked trait (YW) resulted in a favorable response in YW and all other traits except FEC (Table 6.4). The index constructed from first and second-ranked traits resulted in a much larger response in FEC but a 50% reduction in the response of YW. The correlation between the two indexes was low, 0.31. The correlation between S and S$^+$ indexes for first and second-ranked traits was 0.32.

Results for the pastoral system are presented in Table 6.5. For both S and S$^+$ producers, including the second-ranked traits had little effect on the responses obtained when only first-ranked traits were included. The correlations between the indexes were high (r = 0.98 - 0.99) for both S and S$^+$ producers, and the correlation between S and S+ indexes was 0.98 (data not shown).

Table 6.4. Genetic gains attained from single trait selection and from selection indexes constructed using first-ranked and first- and second-ranked traits in sheep-barley systems

	Breeding-objective traits ‡							
Selection index	YW	MW	ADG	CG	NLW	GFW	FEC	$r_{jj'}$
Single traits†	0.64	0.35	0.016	0.79	0.056	0.034	-13.8	
S producers								
First-ranked traits ††	0.64	0.50	0.012	0.85	0.009	0.017	-3.8	0.31
First- and second-ranked traits	0.32	0.21	0.009	0.43	0.009	0.010	-13.7	
S$^+$ producers								
First-ranked traits	0.63	0.51	0.013	0.84	0.030	0.017	-4.2	0.95
First- and second-ranked traits	0.61	0.49	0.011	0.81	0.044	0.014	-3.1	

S farmers produce yearlings, and S$^+$ farmers produce and finish yearlings and culled rams; $r_{jj'}$ represents the correlation between indexes; † the single-trait response represents the genetic gain that can be obtained when only this trait is included in the breeding objective and selection index; †† these are traits translated from trait categories ranked first and second by farmers (Table 6.3). For subsistence sub-systems, the first-ranked trait is YW, and second-ranked traits are FEC and CG. In Subsistence+, first-ranked traits are YW and ADG, and second-ranked traits are NLW and CG; ‡ FEC, fecal worm egg count; YW, yearling weight; MW, mature weight; ADG, daily gain during finishing; CG, chest girth; NLW, number of lambs weaned; GFW, greasy fleece weight.

Table 6.5. Genetic gains attained from indexes constructed using first-ranked and first- and second-ranked traits in pastoral systems.

	Breeding-objective traits							
Selection index	YW	MW	ADG	CG	NLW	MY	FEC	$r_{jj'}$
S producers								
First-ranked traits †	0.13	0.05	0.006	0.18	0.00	0.00	-13.85	0.98
First- and second-ranked traits †	0.26	0.15	0.008	0.36	0.003	0.001	-13.82	
S^+ producers								
First-ranked traits	0.13	0.05	0.006	0.18	0.00	0.00	-13.85	0.99
First- and second-ranked traits	0.14	0.06	0.006	0.18	0.002	0.00	-13.81	

S pastoralists produce yearlings, and S^+ pastoralists produce and finish yearlings and culled rams; $r_{jj'}$ represents the correlation between indexes; † these are traits translated from trait categories ranked first and second by pastoralists (Table 6.3). In Subsistence sub-systems, the first-tanked trait is FEC and the second-ranked traits are NLW, CG, and MY. In Subsistence+, the first-ranked trait is FEC and second-ranked trait is NLW. See Table 6.4 for description of traits.

In both production systems, the relative weights of the traits in the breeding objective were positive except for FEC. FEC was weighted negatively because for this trait a reduction in egg count is desirable. Conversely, the relative weights for traits with a minimum or no desired gain were zero. The relative weights of traits derived from the different indexes are presented in Appendix 6.2.

4. Discussion

In this study, we presented a farmer/pastoralist participatory approach for defining breeding objectives for Ethiopian sheep. Participatory approaches for evaluating the relative importance of traits in selection are rarely applied in animal breeding, whereas they are frequently used in plant breeding (see review by Sölkner et al., 2007). Understanding the target production system and involving the farmers when defining breeding objectives is essential for designing sustainable breeding strategies. This is particularly the case in traditional livestock management systems in which farmers and pastoralists have complex production and marketing objectives and strategies. Our participatory approach provides an opportunity to address these objectives and strategies. In this study, we have shown how data gained during interviews with the farmers can be used to develop breeding objectives, including relative weights for the traits in the breeding objective.

The sheep production objectives identified in this study are similar to those identified in previous studies in developing countries (Jaitner et al., 2001; Van Dorland et al., 2003; Wurzinger et al., 2006). In our study, regular cash income, financing, and insurance are the main reasons for keeping sheep in sheep-barley and pastoral systems. Bosman et al. (1997) and Kosgey et al. (2004) also reported that the intangible benefits from financing and insurance are important reasons for raising sheep. Ayalew et al. (2003) found that these intangible benefits account for a larger portion of the total net benefit under traditional than improved management systems. However, in our study, S farmers and S^+ farmers with improved management rated intangible benefits of sheep comparably (data not shown). This suggests that intangible benefits are equally important for both groups of farmers.

Livestock production systems in developing regions are broadly recognized as mixed crop-livestock or pastoral systems (Van Dorland et al., 2003; Kosgey, 2004; Solomon et al., in press). However, Sölkner et al. (1998) argued that differences in production strategies and breeding objectives between groups of farmers within a traditional management system are often much greater than commonly understood. In our study, we recognized two groups of producers (S and S^+) that can be described as sub-systems within the mixed sheep-barley and pastoral systems (Tables 6.2 and 6.3). Although the S and S^+ producers were identified based on production and marketing strategies (production and sale of yearlings vs. finishing), they also differed in the weights they attached to adaptive, reproduction, milk, and weight gain traits. This underscores the idea that differences in production systems in which a breed is used needs to be considered when defining the breeding objectives (Phocas et al., 1998; Hirooka and Groen, 1999; Vargas and van Arendonk, 2004; Barwick and Henzel, 2005; Wolfová et al., 2005).

Little attention has been paid to defining the relevant breeding objectives for sheep in Ethiopia, or for traditional systems and marginal areas in general (Sölkner et al., 1998). Our finding that adaptive traits are as important as production traits in subsistence farming in marginal areas agrees with findings by Tano et al. (2002). Our results also indicate that less market-oriented subsistence farmers and pastoralists prefer more adapted animals over productive animals as compared to more market-oriented producers who practice finishing. Adaptive traits such as resistance to disease have rarely been considered in conventional expert-derived breeding objectives for marginal areas (e.g., Gicheha et. al., 2007). However, sustainable livestock production requires a trade-off between increased productivity and adaptation (Olesen et al., 2000; Neilson et al., 2005, 2006). In this study, a sacrifice of 25.0-58.0% in genetic gain of production traits in subsistence sheep-barley systems was required in order to obtain the desired changes in disease resistance (FEC).

This study incorporated producers' preferred breeding objectives into breeding programs. Few studies about incorporating farmers' preferences into breeding objectives have been published (Tozer and Stokes, 2002). The first step in our procedure was to translate the broad trait categories used by farmers to describe performance of their animals into traits that could be measured and included in the selection index. This translation process is inherently limited. For instance, in our study, two important trait categories (adaptation and *qumena*, see Table 6.3) could not be fully translated into traits due to the lack of genetic parameters that were needed for subsequent analysis. Adaptation was restricted to resistance to disease (FEC). Resistance to disease is an important adaptive trait in Africa (Wurzinger et al., 2006); however, adaptation also includes tolerance to drought and cold in the frosty sub-alpine environment, and also tolerance to heat and the capacity for long trekking in the arid lowlands. Similarly, *qumena* (general appearance) was represented by one of its component traits (chest girth), which has estimates of genetic parameters (Solomon et al., 2008), and is favorably correlated with conformation traits (Janssens and Vandepitte, 2004). Translating farmers' perceptions into index traits can be difficult because of the absence of measurable, defined traits to represent their perceptions. It is not yet clear how components of adaptation, such as tolerance to cold and capacity for long trekking, can be measured. It is also not clear how other qualitative components of *qumena*, such as color, could be incorporated into aggregate genotypes or whether they should be selected for independent of quantitative traits. However, our general method for translating producers' preferences can be used for a larger number of traits.

The desired-gain selection-index method has been suggested as a means for implementing multi-trait selection in the absence of economic values (Yamada et al., 1975; see reviews by Galal, 1986 and Sölkner et al., 2007), as well as for deriving relative weights (Suzuki et al., 2005). In this paper, we presented a method for translating farmers' preferred changes in trait categories into relative weights for traits in the breeding objective. Our approach results in implied relative economic weights that can be compared to economic values derived from profit equations. This comparison yields insights into the values that farmers attach to intangible benefits. Such comparisons also help us to better understand that farmers' preference ratings of traits are also based on economic rationale and thus reflect implicit economic values of traits.

5. Conclusion

We defined breeding objectives and selection indexes that can be used for sheep breeding programs in different production systems in Ethiopia. We used a participatory approach to collect information on farmer preferences. The approach presented in this paper can be adapted to other situations and populations.

Definitions of sheep breeding objectives in Ethiopia should include adaptive traits because they are as important as (sheep-barley system) or more important than (pastoral system) production traits. *Qumena* (overall appearance) is also an important economic trait that influences the value of the animal, particularly in traditional markets.

We derived breeding objectives and selection indexes for different systems, groups of producers or sub-systems (S and S^+ producers), and for different numbers of traits. In general, we found close agreement between indexes for different (sub)systems, with the exception of indexes constructed for S and S^+ producers in sheep-barley production systems. The exception was caused by including FEC, which was negatively correlated to other traits, in the breeding objective. Our results demonstrate that a single index and hence a single breeding program might not satisfactorily meet the objectives of different systems and producers.

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Appendix 6.1. Phenotypic standard deviations (σ_p), heritabilities along diagonal, and genetic (above diagonal) and phenotypic (below diagonal) correlations used in simulated selection

Traits	σ_p	YW	MW	ADG	CG	NLW	GFW	FEC	MY
YW	2.79	0.46	0.93	0.62	0.98	0.29	0.46	-0.24	0.08
MW	2.91	0.74	0.30	0.78	0.80	0.33	0.22	-0.12	0.16
ADG	0.11	0.44	0.34	0.25	0.50	0.10	0.30	0.00	0.07
CG	4.63	0.77	0.74	0.40	0.31	0.06	0.50	-0.24	0.06
NLW	0.90	0.10	0.09	0.09	0.10	0.07	0.00	0.00	0.38
GFW	0.17	0.42	0.37	0.25	0.60	-0.12	0.39	-0.15	
FEC	90.44	-0.03	-0.08	-0.05	-0.03	0.00	-0.02	0.27	0.00
MY	0.21	0.08	0.09	0.07	0.06	0.38		0.00	0.15

Sources of genetic parameter estimates: Mavrogenis et al. (2000); Rege et al., (2002); Solomon (2002); Snowder and Van Vleck (2003); Safari and Fogarty (2003); Hamman et al. (2004); Safari et al. (2005); Sawalha et al. (2005); Solomon et al. (2007b); Solomon et al. (2008).

Appendix 6.2. Relative weights of traits derived using desired-gains selection-indexes, maximizing gains for first and first- and second-ranked traits

	Breeding-objective traits						
Selection index	YW	MW	ADG	CG	NLW	GFW [†]	FEC
Sheep-barley system							
S producers							
First-ranked traits	90.9	0.0	0.0	0.0	0.0	0.0	0.0
First- and second-ranked traits	18.7	0.0	0.0	24.8	0.0	0.0	-12.1
S^+ producers							
First-ranked traits	86.5	0.0	519.8	0.0	0.0	0.0	0.0
First second-ranked traits	5.4	0.0	50.0	40.2	248.0	0.0	0.0
Pastoral system							
S producers							
First-ranked traits	0.0	0.0	0.0	0.0	0.0	0.0	-34.7
First- and second-ranked traits	0.0	0.0	0.0	84.6	55.5	357.5	-34.7
S^+ producers							
First-ranked traits	0.0	0.0	0.0	0.0	0.0	0.0	-34.7
First- and second-ranked traits	0.0	0.0	0.0	0.0	360.0	0.0	-34.7

[†] Milk yield, in case of pastoral system.

CHAPTER 7

Optimal village breeding schemes under smallholder sheep farming systems

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Abstract

Despite challenges in the implementation of livestock genetic improvement programs in developing regions, including centralized nucleus breeding schemes, these programs can contribute to the improvement of the livelihood of smallholder farmers. In this paper, we present a community- or village-based breeding scheme in which breeding activities are carried out by communities of smallholder farmers. We evaluated genetic responses and the rate of inbreeding from alternative village sheep breeding schemes that were based on a survey of existing flock structure and breeding management in a sheep-barley system in Ethiopia. This survey showed that individual flock sizes were small, and that the majority of farmers practiced mixed grazing and uncontrolled mating of their flocks in communal grazing lands within villages. Here we evaluated within-village schemes (selection across flocks within a village) and across-village schemes (selection across villages) at different intensities of ram selection (i.e. proportions of rams selected, P). Our results showed that under within-village schemes, intensity of selection could not be increased (i.e. P could not be decreased below 0.149) when the rate of inbreeding was constrained to an acceptable level of 0.01, resulting in low genetic gain. The most optimal scheme was found to be across-village selection with at least three villages cooperating and P = 0.05. Our results also indicated that genetic gain from village breeding schemes with mass selection and BLUP selection are comparable. Village breeding schemes can make a significant contribution to the genetic improvement of livestock in Ethiopia and other developing countries.

Keywords: village breeding scheme, smallholder farmers, genetic gain, inbreeding rate, sheep

1. Introduction

Country reports on the state of farm animal genetic resources (FAO, 2007) and the review by Kosgey et al. (2006) show that there are very few structured sheep breeding programs in developing regions, particularly in Africa. Lack of effective, sustainable breeding programs for local breeds is one reason that such breeds lose their competitive advantage, especially where production systems or external conditions are subject to change (Hiemstra et al., 2007). Although smallholder farmers have informal breeding goals and strategies, there is a lack of breeding programs relevant for low-input systems. Formalizing genetic improvement for these conditions is a challenging task (FAO, 2007).

Livestock production in developing regions is generally characterized by small flock-size, communally shared grazing, uncontrolled mating, and the absence of pedigree and performance recording. These characteristics limit the implementation of effective genetic improvement programs. To overcome these problems, nucleus breeding schemes have been suggested, in which genetic improvement is centrally organized in a population maintained in research institutes or government farms (Galal, 1986; Terill, 1986; Kosgey, 2004). Implementation of nucleus breeding schemes in low-input environments has proven to be difficult because it requires long-term commitment of sponsors and involvement of farmers (Kosgey et al., 2006). An alternative to centrally organized nucleus schemes is community- or village-based selection schemes, which are breeding activities carried out by communities of smallholder farmers (Sölkner et al., 1998). Village breeding programs help overcome the problems of genotype-environment interaction, avoid the genetic lag between nucleus and village populations, and are appropriate for *in situ* conservation of indigenous animal genetic resources. Village programs also help bridge the gaps between the skills of the breeders (nucleus centers or breeding companies) and the farmers, and ensure property rights of farmers for improved genetic materials.

Only a few studies in the literature have assessed the optimal design of village breeding schemes under smallholder conditions and their consequences on genetic diversity (Rönnegård, 2003; Kosgey, 2004). Optimizing breeding schemes requires consideration of both short-term (high rate of genetic gain) and long-term (maintenance of genetic variance and avoidance of inbreeding depression) effects of selection decisions (Bijma et al., 2001; Fimland, 2007).

Here we report the results of a survey to determine the current sheep breeding structure and management in villages where sheep are kept under the sheep-barley system in Ethiopia. We used the results of this survey to design alternative village breeding schemes and evaluate these schemes in terms of genetic gain and maintenance of within-breed genetic diversity.

2. Materials and methods

2.1. Description of breeding management and structures

We conducted a survey of the sheep flock structures and breeding management practices in the sheep-barley and pastoral production systems in Ethiopia. The breeds surveyed in the sheep-barley system were short-fat-tailed sheep (Menz and Wollo; Solomon et al., 2007), and black-head-Somali sheep (BHS) in the pastoral system. A sample of 161 farmers in the sheep-barley system and 101 pastoralists in the pastoral system were individually interviewed regarding their flock structure, flock management, pedigree identification and selection and mating practices using the descriptions provided in Tables 7.1-7.4. A detailed description of the survey procedure is given in Solomon et al. (submitted).

2.2. Evaluation of selection schemes

2.2.1. Population structure

In this study, design and evaluation of selection schemes was illustrated using parameters for the short-fat-tailed sheep population in the sheep-barley system in Ethiopia. A similar scheme can be designed for BHS sheep in the pastoral system, for which basic information on flock structure and breeding management are also presented in this study. A population with discrete generations was simulated based on the existing population structure in the sheep-barley system presented in Table 7.1. In this system, males are used for breeding once at one year of age and culled as yearlings or castrated for finishing; generations in the male population were considered discrete. In practice, breeding ewes are maintained for more than one year. In our study, we ignored the selection of females. Algorithms to predict the rate of inbreeding in populations under selection are only available for discrete generations (Rutten et al., 2002), and therefore, we assumed that only one-year old ewes were used and that no selection was practiced in ewes.

A flock of 200 ewes per village was used, corresponding to the average number of flocks in a village (20) and average number of ewes in a flock (10). The number of male selection candidates in each mating season was calculated using the following parameters derived from the literature on short-fat-tailed sheep (Abebe, 1999; Solomon, 2000): lambing frequency = 1.5 times per year (i.e. three lambings in two years), conception rate = 0.90, twinning rate = 1.03, survival 0-3 months of age = 0.80, survival 3-12 months of age = 0.90, and sex-ratio of 50%. Based on these parameters, 100 male selection candidates are available each generation from 200 ewes. Each generation (year), 200 female candidates were available, i.e. no selection was practiced among females.

2.2.2. Selection schemes

In this study we compared two types of breeding schemes: within-village and across-village schemes. In the within-village schemes, evaluation and selection of replacement animals was carried out across individual flocks (flocks owned by individual farmers) within the village. Under the across-village schemes, selection was across neighbouring villages, with all the flocks in the villages participating in the scheme considered as one large population. For each scheme, five different proportions of rams were selected. Mating within a village was assumed to be syndicate mating, i.e. flocks in a village share a common male pool. A constant number of ewes per village (200) was assumed for all schemes. Under across-village schemes, an exchange of rams among cooperating villages was assumed.

All breeding males were assumed to be replaced each generation. Selection of replacement rams was according to the intensity of selection under the different schemes. No selection was assumed for replacement females in this study.

Within-village selection schemes:

Random selection: no selection, i.e. proportion of rams selected (P) = 1.0.
Scheme-30%: the base scheme, as it corresponds to the existing flock structure (ram:ewe mating ratio of 1:6.9; see Table 7.1), $P = 0.3$.
Scheme-20%: $P = 0.2$.
Scheme-10%: $P = 0.1$.
Scheme-5%: $P = 0.05$.

Across-village selection schemes:

We evaluated across-village selection schemes in which the number of cooperating villages within one scheme ranged from two to five. Each across-village selection scheme was evaluated for the four proportions of selection of rams, i.e. $P = 0.3$, 0.2, 0.1 and 0.05.

2.2.3. Prediction of genetic gain and inbreeding rate

Genetic gains and rates of inbreeding were predicted by deterministic simulation of selection schemes using SelAction (Rutten et al., 2002). SelAction accounts for a reduction in variance due to selection (Bulmer, 1971) and corrects selection intensities for finite population size and for the correlation between index values of family members (Meuwissen, 1991). Prediction of the rate of inbreeding was based on the long-term genetic contribution theory (Bijma et al., 2001).

Phenotypic information on traits was collected for males only. We compared schemes under mass selection (i.e. where selection is entirely based on the phenotype of selection candidates) and BLUP selection (where information on relatives is also used for calculating the breeding values of selection candidates).

Traits and relative weights of traits included in the selection indexes were based on the breeding objectives of farmers in the sheep-barley system. Details on the identification of breeding-objective traits and derivation of relative weights for the traits were previously reported (Solomon et al., submitted). The traits in the breeding objective were yearling live weight (YW), greasy fleece weight (GFW), number of lambs weaned per year per ewe joined (NLW), chest girth (CG), and fecal egg count (FEC). NLW was included as a correlated trait under mass selection since selection on own performance for this trait is not possible as the candidates were selected at a younger age (12 months). The aggregate genotype was defined as:

$$H = 90.9g_{YW} + 0.0g_{GFW} + 0.0g_{NLW} + 24.8g_{CG} - 12.1g_{FEC}$$

where g is the genetic value for trait i, and the figures attached are the corresponding relative weights.

Responses to selection were calculated both for individual breeding-objective traits and the aggregate genotype. Aggregate responses were calculated both as total economic response and as a proportion of the genetic standard deviation of the aggregate genotype (H/σ_H), where H is total economic response and σ_H is genetic standard deviation of the aggregate genotype. The maximum aggregate responses and the minimum attainable P when rate of inbreeding was constrained to an acceptable level of 0.01 was calculated using linear interpolation.

3. Results

3.1. Breeding management

The flock structures identified by the survey are presented in Table 7.1. Total flock size ranged from 13.6 to 68.6 in sheep-barley systems and from 15.6 to 81.4 in pastoral systems. Breeding ewes constituted 59.5% of the flock in sheep-barley systems and 50.4% in pastoral systems, and mating ratios (ram:ewe) were 1:6.9 and 1:3.2 in the sheep-barley and pastoral systems, respectively.

Flock grazing management practices and the degree of flock mobility are shown in Table 7.2. Nearly 70% of the pastoralists in the pastoral system and 60% of farmers in the sheep-barley system graze their sheep mixed with sheep from other farmers/pastoralists within the same village. However, 66.5% of the farmers keep their flocks on their own crop aftermath during non-cropping seasons. Most of the surveyed pastoralists (70.3%) are mainly sedentary, with 10.9% nomadic and 18.8% transhumant.

Table 7.1. Flock structure in sub-alpine sheep-barley and lowland pastoral systems

	Sub-alpine sheep-barley system				Lowland pastoral system			
		Flock size				Flock size		
	Overall	Large	Medium	Small	Overall	Large	Medium	Small
Ewes	20.1	42.4	15.8	7.1	27.4	39.7	18.8	7.4
Rams	2.9	5.5	2.4	1.5	8.5	13.9	3.2	2.6
Lambs (0-6 months)	7.5	15.5	5.7	3.1	9.9	14.3	6.5	3.1
Lambs (6-12 months)	4.5	8.9	3.7	1.9	8.7	13.4	4.6	2.5
Total	33.8	68.6	27.7	13.6	54.4	81.4	33.1	15.6

Table 7.2. Flock management in sub-alpine sheep-barley and lowland pastoral systems

Percent of respondents	Sheep-barley	Pastoral
Herding management		
Herding own flock separately		31.3
Herding own flock mixed with other flocks		68.7
Herding own flock always with same group of flocks	n.a.	66.7
Seasonal grazing management†		
Grazing in communal land during cropping season	59.9	
Grazing in own land during cropping season	40.1	
Grazing on village crop aftermath during non-cropping season	33.5	
Grazing on own crop aftermath during non-cropping season	66.5	
Flock mobility		
Sedentary		70.3
Nomadic		10.9
Transhumant††		18.8

† Some farmers use both communal or private grazing, and private or village crop aftermath. n.a., not available.

†† A form of nomadism where herders have a permanent home and only a subset of people necessary to tend flocks travel with the flocks.

More than one-third of the interviewed farmers and pastoralists stated that they can identify sires of animals born in the flock, either because they hand-mate some of the ewes or by associating physical appearances between the newborn lamb and rams in the flock. Almost all interviewees select a few of their best rams and ewes as replacements, but only half of pastoralists select replacement ewes. The information used for selecting replacement animals is presented in Table 7.3.

Table 7.3. Pedigree identification and selection practice in sub-alpine sheep-barley and lowland pastoral systems

Percent of respondents	Sheep-barley	Pastoral
Pedigree identification		
Sire	36.3	34.7
Dam	97.5	69.3
Selection practices		
Selecting replacement rams	96.3	82.2
Selecting replacement ewes	98.1	54.5
Primary source of information for selecting rams [†]		
Candidate's own performance or appearance	60.8	31.3
Sire	31.6	56.6
Dam	7.6	12.1
Primary source of information for selecting ewe		
Candidate's own appearance or performance	69.7	55.6
Sire	12.5	13.0
Dam	49.5	33.3

[†] In addition to the primary source, most farmers use the other sources as secondary sources of information.

Most of the farmers in the sheep-barley system use local Menz and Wollo rams, with only 8.9% of farmers crossing local ewes with imported Awassi rams. Crossbreeding is not practiced in pastoral system (Table 7.4). Nearly half the farmers (47.8%) and 61.8% of the pastoralists breed some of their ewes with one or more of their preferred rams, which occurs when ewes showing estrous signs are detected around the homestead after grazing time. However, farmers acknowledged that these ewes mated with preferred rams could also have randomly mated earlier in communal grazing fields.

Table 7.4. Mating practices in sub-alpine sheep-barley and lowland pastoral systems

Percent of respondents	Sheep-barley system	Pastoral system
Ram breed used		
Local	68.4	100.0
Exotic (crossbreeding)	8.9	
Both	22.8	
Mating method [†]		
'Controlled mating' using own ram	47.8	61.8
'Controlled mating' using neighbors' ram	8.1	0.0
Uncontrolled mating at grazing	44.1	38.2

[†] Percentage of the respondents who ranked the category as the 'mostly used' method.

3.2. Genetic gain and inbreeding

3.2.1. Within-village scheme

Predicted genetic gains (ΔG) in the breeding-objective traits and rates of inbreeding (ΔF) per generation under within-village schemes are presented in Table 7.5. With mass selection, ΔG were approximately zero for all traits studied under the random selection scheme ($P = 1.0$). The highest ΔG were obtained under Scheme-5% (highest proportion of rams selected, $P = 0.05$). The rate of inbreeding also increased from 0.0009 under random selection to 0.027 under Scheme-5%.

Table 7.5. Predicted aggregate response (H), genetic gains in breeding-objective traits, and increase in inbreeding (ΔF) per generation under different within-village selection schemes

		Breeding-objective traits ††					
Selection schemes †	H	YW	GFW	NLW	CG	FEC	ΔF
Random selection	1.88	0.001	0.0	0.0	0.00	-0.04	0.0009
Base scheme	540.1	0.411	0.013	0.003	055	-12.99	0.0041
Scheme-20%	647.0	0.492	0.016	0.003	0.66	-15.57	0.0064
Scheme-10%	801.9	0.609	0.019	0.004	0.82	-19.29	0.0135
Scheme-5%	928.9	0.704	0.022	0.004	0.95	-22.36	0.0270

† The schemes differ in the proportion of replacement rams selected. See text for details.

†† YW: yearling live weight, GFW: greasy fleece weight, NLW: number of lambs weaned per year per ewe joined, CG: chest girth, FEC: fecal egg count.

Aggregate responses and ΔF under mass selection and BLUP selection are depicted in Fig. 7.1. Under mass selection, aggregate responses increased from 0.30 to 0.52 as the proportion of rams selected decreased from 0.30 (base scheme) to 0.05 (Scheme-5%). Under BLUP selection, responses increased from 0.34 to 0.57. Correspondingly, ΔF increased from 0.0041 to 0.027 under mass selection, and from 0.0046 to 0.034 under BLUP selection. When the rate of inbreeding was constrained to an acceptable level of 0.01, the minimum possible P was found to be 0.149 and the aggregate response was 0.406.

3.2.2. Across-village scheme

Across-village schemes were evaluated based on mass selection and aggregate responses (Fig. 7.2). Aggregate responses showed only slight increases when the number of cooperating villages increased from one to five for a given P. However, ΔF declined substantially from 0.004 to 0.0008 under $P = 0.3$ and from 0.027 to 0.005 under $P = 0.05$ when the number of cooperating villages was increased from one to five. The trends in genetic response and ΔF under BLUP were similar to the trends under mass selection (data not shown).

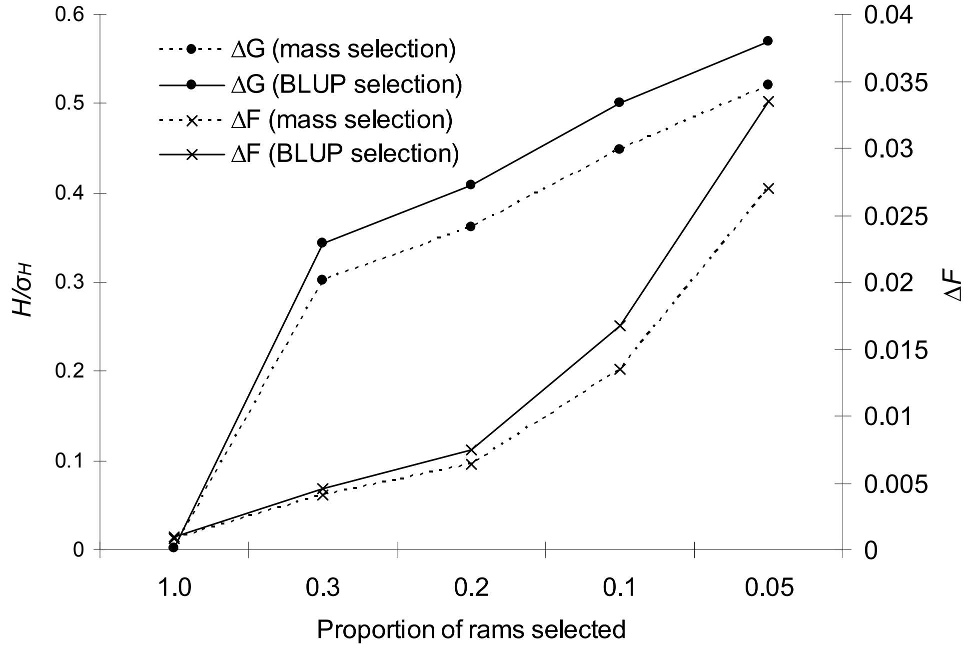

Fig. 7.1. Aggregate response as proportion of genetic standard deviation of the aggregate genotype (H/σ_H) and rate of inbreeding (ΔF) with decreasing proportion of rams selected (within-village selection schemes).

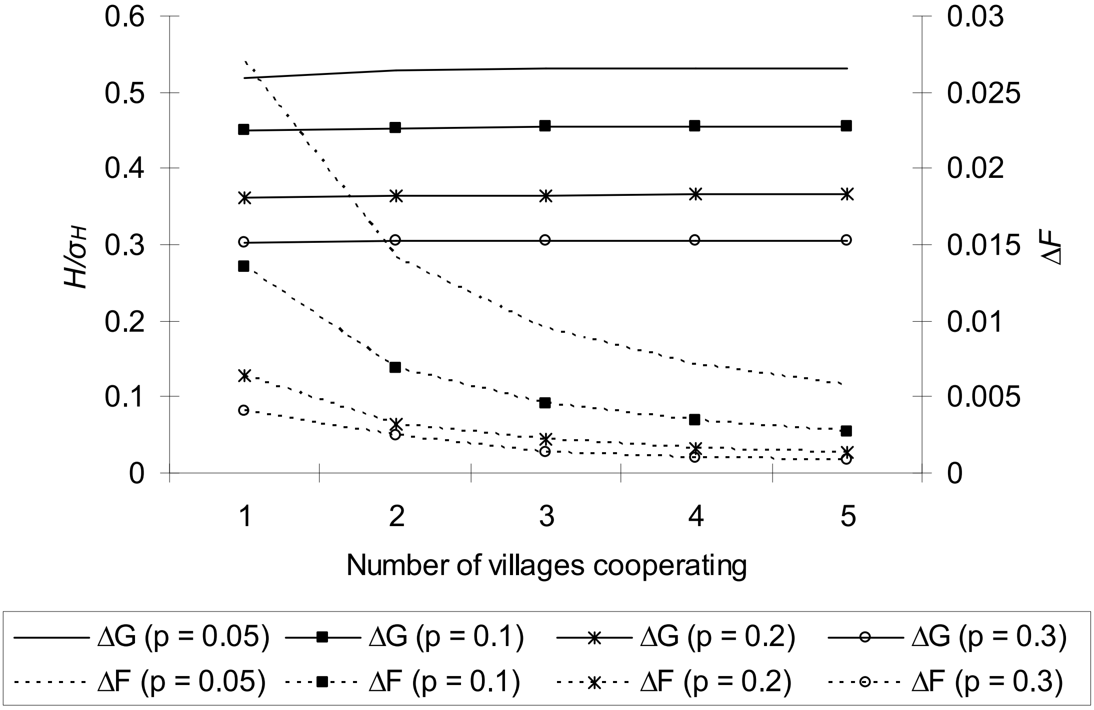

Fig. 7.2. Aggregate response as proportion of genetic standard deviation of the aggregate genotype (H/σ_H) and rate of inbreeding (ΔF) with increasing number of villages cooperating and different proportions of rams selected (P) under across-village selection schemes.

4. Discussion

The sheep breeding structure in developing regions can be best described as a one-tier structure, with farmers and pastoralists as both breeders and producers. Our survey showed that most farmers and pastoralists practice selection of replacement stock within their flocks, with a limited exchange of breeding stock between flocks (Table 7.4). A certain degree of uncontrolled mating occurs among animals of different flocks in a village due to communal grazing within the village. This uncontrolled gene flow between flocks in a village and the relatively small flock sizes hampers the efficiency of within-flock selection by individual producers.

Under smallholder livestock farming systems in Ethiopia, the structure of the village sheep breeding population should be viewed in relation to the structure of human population settlements. The smallest unit of human habitation is the *got* in the highland mixed crop-livestock system or the *jess* in the pastoral system (equivalent to village). Our results show that livestock feeding and breeding commonly occur in communally shared grazing lands within a *got* or *jess*. Although mixed at the village level, flocks within a village are almost completely separated from flocks of other villages, and thus village flocks can be regarded as largely closed populations. A technically and socially feasible option for designing breeding schemes under these conditions, therefore, would be to consider the village population as a breeding unit, as is done in the within-village schemes in our study.

Designing within-village schemes based on genetic evaluation across flocks within a village assumes uniformity of environmental effects within a village. Our survey on flock management practices showed that flocks within a village are mainly managed in communal grazing areas (Table 7.2). Furthermore, little variation is observed among farmers in the health care and supplementary feeding for sheep in the study area (Abebe, 1999). Flocks in such a village could thus be virtually considered as one large flock. Under these rather uniform conditions, selection of animals based on phenotypes recorded within a village seems appropriate. Correction of phenotypes for systematic environmental differences using an animal model BLUP for estimating breeding values is possible, but implementing such a system of genetic evaluation requires investments in infrastructure. However, we also evaluated the different schemes using BLUP selection which requires pedigree recording. Our results indicate that ΔG under the within-village scheme increased by 13% under BLUP selection compared to mass selection, but the rates of inbreeding also increased. In addition, comparing ΔG at equal rates of ΔF (0.01), we found only 2.5% more ΔG under BLUP selection compared to mass selection (see Fig. 7.1).

Based on our survey, a feasible village scheme is one based on mass selection, since pedigree recording is absent or incomplete under village conditions (Table 7.3).

We found that within-village schemes could result in reasonable genetic progress. However, with increasing ΔG, ΔF also increased to levels higher than acceptable (Table 7.5). Such relationships between ΔG and ΔF have also been reported in other studies (Toro and Silió, 1990; Quinton and Smith, 1995; Villanueva et al., 1995; Lewis and Simm, 2000). The predicted ΔF can be converted to effective population sizes (N_e) using the formula $\Delta F = 1/2N_e$ (Falconer and Mackay, 1996). The N_e ranged from 121.9 to 18.5 for within-village schemes varying in the proportion of rams selected (P) from 0.3 to 0.05. These N_e values are lower than the minimum acceptable N_e (500) suggested to maintain sufficient genetic variability for adaptation to the changing environment, or N_e of 50 to simply maintain short-term fitness, i.e., prevent serious inbreeding and its deleterious effects (Franklin, 1980 cited in Shaffer, 1981). Acceptable levels of ΔF reported in the literature vary from 0.01 (van Arendonk and Bijma, 2003) to 0.001 (Franklin, 1980). In this study we considered a ΔF of 0.01 as acceptable, as breeding schemes were designed at the village level, which implies that a population is divided in a number of subpopulations; thus, a higher rate of inbreeding can be accepted for a subpopulation.

Our study revealed that ΔF can be reduced without affecting ΔG by increasing the number of villages cooperating in the village breeding program (across-village schemes), thereby increasing the pool of candidates for selection. However, implementation of across-village schemes can be constrained by the absence of genetic links between sires in different villages needed for evaluating sires across villages. In this study, it is assumed that sire exchange between villages would be practical to establish the genetic links between sires across villages. Lewis and Simm (2000) suggested that once a sufficient proportion of ewes in flocks (10-20%) are mated to reference sires, a scheme effectively operates as large panmictic population, allowing for a more reliable genetic evaluation of animals across-flock, or across-village in our case. Ram exchange among cooperating villages was found to reduce the rate of inbreeding, which is consistent with earlier findings on various rotational ram exchange schemes (Caballero et al., 1996; Honda et al., 2004; Shepherd and Woolliams, 2004). In this study, we assumed that rams are exchanged randomly among villages with the flocks in the various villages considered as one big population where random mating of selected animals is followed. Planned exchange of males among subpopulations has been suggested to be more effective to limit rate of inbreeding (Yamada, 1980). The rates of inbreeding reported in the current study could thus be taken as the maximum that can occur under these conditions.

Evaluation of across-village selection schemes in this study indicates that an acceptable N_e of 50 (i.e. $\Delta F = 0.01$) with high ΔG could be attained by designing an across-village selection scheme involving three villages with the highest intensity of selection ($P = 0.05$). This optimal scheme involving three villages reduced ΔF by

64.8%, compared to within-village selection at similar *P*. However, the optimal scheme results in only a slight increase in ΔG (Fig. 7.2). Our results indicate that ΔG is more affected by *P* than by population size (i.e. number of cooperating villages) while ΔF is equally affected by *P* and population size. The importance of *P* has been emphasized by Quinton and Smith (1995).

The breeding scheme we propose could be referred to as a farmer-expert-managed selection program. That is, farmers and experts collaborate in data collection, evaluation of candidate animals, and practice of selection. Through this collaboration, traits (*e.g.*, fecal egg count) and data recording (*e.g.*, number of lambs weaned) that require assistance from livestock experts can also be included in the selection criteria. For implementation, it is important to minimize the number of traits that need to be recorded. Selection of traits to be recorded can be based on selection index calculations. Based on Solomon et al. (2008), the selection criteria in such a program is suggested to include measurements of chest girth and greasy fleece weight, both of which can be easily measured by farmers. Chest girth is highly correlated with body weight and is recommended as indirect selection criteria to improve body weight under village schemes (Solomon et al., 2008). Involvement of farmers in the design of breeding programs is essential, as Kosgey et al. (2006) revealed that lack of ownership is a main factor contributing to the failure of breeding programs.

5. Conclusion

Our survey of village sheep breeding provided insight into the existing flock structure and breeding management practices, and was used as a starting point for designing village breeding schemes. We designed a village sheep breeding scheme that can be used for sheep breeding in Ethiopia, as well as to design village breeding schemes in similar situations.

Our study revealed that a within-village selection scheme involving 200 ewes can be effective in creating genetic gain. However, the rate of inbreeding is relatively high. The most optimal scheme involves across-village selection with at least three villages cooperating, resulting in a rate of inbreeding well below acceptable levels and reasonable genetic gain. Such a scheme requires a combined ewe flock of at least 600 joined to 15 rams each generation, corresponding to an effective population size of 50. The scheme, however, requires that exchange of rams between cooperating villages is practiced. Our results also indicate that genetic response with mass selection is fairly comparable with BLUP selection, especially comparing schemes at equal rates of inbreeding.

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CHAPTER 8

General Discussion

General discussion

In developing regions, farm animal genetic resources are a vital component of the genetic and ecosystem biodiversity. Anderson (2003) pointed out that complex, diverse and risk-prone rural livelihood systems need animals that are flexible, resistant and diverse. Such requirements can best be met through rational utilization of adapted indigenous livestock genetic resources. Sustainable utilization of livestock diversity requires characterization of the available resources and development of sustainable genetic improvement strategies that consider the needs and perceptions of target groups and that minimize loss of genetic diversity. In chapters 2-7 of this thesis, we presented approaches for characterizing livestock diversity, setting conservation priorities, and designing sustainable pure-breeding programs for low-input systems. In this chapter, we discuss the significance of assessing neutral genetic diversity, alternative approaches for setting conservation priorities, and options for conservation through utilization of livestock breeds.

1. Significance of neutral genetic diversity

Molecular genetic markers have recently become the preferred tool for phylogenetic reconstruction of species. Molecular markers, particularly microsatellites, are also recommended by FAO (2005) for assessing genetic diversity in farm animal species. Genetic diversity assessed based on microsatellite markers merely reveals genetic distinctness and evolutionary relationships of populations at neutral loci. This is because molecular evolution is thought to arise from nucleotide substitutions that occur by random fixation of neutral or nearly neutral mutations rather than by natural selection (Nei, 1975). Thus microsatellite variations may not reveal genetic diversity with respect to variation in production and adaptation traits between populations.

The benefit of characterizing (economic) farm animal species based on genetic markers that have little or no connection with production and adaptation traits may not be immediately apparent. Ruane (1999) argues that it is the protein-coding loci and not those representing neutral non-coding DNA segments that are most relevant for livestock breed conservation and for the ability of the surviving genetic resource to produce in the future production environment. On the other hand, some authors (Li et al., 2004 and references therein) argue that anonymous markers such as microsatellites may also provide indirect information on functional genes since some of these markers are located in transcribed regions of genomes. In our study, patterns of microsatellite genetic variation among Ethiopian sheep breeds (Chapter 2) were found to be more associated to geographical distances between the breeds rather than to variation in their ecological locations or in the breeding management practiced by the different communities who rear them. Genetic differentiation of populations due to genetic drift resulting from isolation by geographical distance is known to be neutral. This raises the question of whether conservation decision for livestock breeds based on variation at neutral loci regardless of their adaptive ability is appropriate. This issue is particularly relevant for breeds with special merits such as adaptation to marginal environments and low-input systems (*e.g.*, Menz sheep in this thesis). In conservation decisions for farm animal species, emphasis should be given to variation in especial traits and current merits of breeds, particularly in regions with food security problems in developing regions. Chapter 3 and Reist-Marti et al. (2006) working on African cattle breeds adopted such approaches.

Currently it is not possible to characterize livestock breeds based on variation at quantitative trait loci because of absence of sufficient knowledge on polymorphisms causing functional genetic variation in production and adaptation. Neutral genetic markers can be used to characterize farm animal populations, but that should not be the end by itself and neutral variation should not be the only criterion to classify populations and base conservation decisions. The emphasis in earlier livestock characterization works has been to assess neutral genetic diversity per se, and presenting genetic characteristics of populations at neutral loci (e.g., genetic distances). Such information alone is of little relevance to livestock production in the developing region. In Chapter 2, an approach was presented to characterize livestock breeds combining molecular genetic variation with information on ecological adaptive variation, the history of the breeds and the role of the communities raising the breeds. In such an approach, characterization of livestock populations needs to be extended beyond quantifying (neutral) genetic variation. It should include classification of the populations into management units (breeds), which is commonly neglected in characterization works. Classification of populations into management units should consider ease of management of the genetic resources and their adaptive characteristics. For instance, classification into several groups based on neutral genetic variation alone may be required from methodological point of view. However, populations need also be classified into broader and manageable categories (*e.g.*, Chapter 2) considering neutral genetic variation as well as other relevant factors important for the management of the genetic resources (e.g., ecological variation and affiliation of populations to communities). Understanding the historical pattern of diversification of the populations, the role of the communities maintaining the populations, and adaptive variation among populations including the causes of adaptive variation will have important implications for conserving and developing the populations. Morphological characterization could provide indirect information on adaptive variation. Toro and Caballero (2005) suggest that morphological variation could be a quite attractive tool for screening overall adaptive genetic diversity since morphological traits usually show low levels of non-additive genetic variation. This is in agreement with the results in Chapter 2 where morphological variation among the

14 traditional sheep breeds in Ethiopia was found to follow ecological variation in Ethiopia. It should however be stressed that maintaining diversity at neutral loci could contribute to meet our needs in the unknown future.

Morphological characters are also an important tool to classify traditional breeds of livestock into broad categories or breed groups (eg: Epistein 1971; Rege, 1999a; Rege and Tawah, 1999; Solomon et al., in press; Chapter 2). Detailed morphological description as presented for example in Table 8.1, together with information on geographic distribution (Fig. 8.1), is also required to physically identify, describe, and recognize distinct animal populations that are identified based on genetic markers. In our study, categories of traditional sheep breeds classified based on morphology and geographic distribution also roughly correspond with classification on neutral markers (Chapter 2). Hanotte et al. (2000) also observed that distribution of Y specific alleles among traditional African cattle breeds corresponds with their classification into breed groups. These results may suggest that morphological classification of livestock populations into major management categories could meet conservation arguments both for maintaining most of the neutral genetic diversity and for current sustainable utilization of diversity to sustain livelihoods of the communities keeping the populations. This argument is supported by the data presented in Chapter 2 where most of the variation is between the major breed groups and most of the breeds within the breed groups are genetically similar. In addition, each breed group is maintained by a specific community or adjacent and culturally similar communities, which facilitates management of the genetic resources at community level. Morphological diversity assessment could be considered as an alternative to molecular characterization for developing regions where resources for molecular characterization are limited. However, morphological characterization could not discern variation between populations within breed groups, as shown in Chapter 2. Such detailed analysis of populations requires use of neutral markers which are the complete genetic markers currently available. It should also be mentioned that assessment of within-breed variation at neutral loci is of value in providing information on relatedness or level of inbreeding of a population when pedigree information is incomplete or absent. It can be concluded that morphological characters should be used as a complementary tool to neutral molecular genetic markers for characterization and conservation of farm animal species.

2. Approaches to conservation priority

In chapter 3, an approach for setting priorities for conservation of livestock breeds was presented which combined contribution of breeds to genetic diversity and to farm livelihoods. With regard to contribution of breeds to genetic diversity, two alternative approaches have been suggested in the literature. The first is based on between-breed genetic diversity (Weitzman, 1992), and the second accounts for both between- and within-breed genetic diversity (Eding et al., 2002 and Caballero and Torro, 2002). In Chapter 3 we used Eding's marker estimated kinship/core set approach. Here we discuss the relative priorities of breeds when Weitzman and Eding approaches are compared, using the data on sheep breeds of Ethiopia (Chapter 3).

Weitzman diversity is based on genetic distances between populations. Pair-wise Nei's (1983) genetic distances (D_A) between breeds based on microsatellite allele frequencies were calculated using DISPAN software (Ota, 1993). Total Weitzman's (1992) diversity V of a set of breeds S can be estimated as,

$$V(S) = \max_{i \in s} [V(S \setminus i) + d(i\, S \setminus i)]$$ Thaon d'Arnoldi et al. (1998),

where $V(S \setminus i)$ is diversity of S excluding breed i and $d(i\, S \setminus i)$ is the distance between i and S excluding i, using WEITZPro (Derban et al., 2002).

The marginal diversity (partial contribution) of breeds (or the loss of diversity caused by the extinction of a particular breed) can be computed as,

$1 - V(S - i)/V(S)$, where $V(S - i)$ is diversity of the set excluding breed i.

Weitzman's approach is known to favour the conservation of genetically distant breeds (Thaon d'Arnoldi, 1998; Tapio et al., 2006). Our result on conservation priorities for Ethiopian sheep breeds using Weitzman approach (Table 8.2) is in agreement with the above findings as the breed with the highest marginal diversity (Bonga) is one of the most genetically distant breeds, i.e. the breed has very low kinship with the other breeds (Chapter 3, Fig. 3.1). It has also been argued (Caballero and Toro, 2002; Eding et al., 2002; Simianer, 2005) that the Weitzman approach does not account for within-breed diversity, which might lead to favouring the conservation of more inbred populations. This is supported by our results because Bonga breed also showed the lowest within-breed diversity (highest within-breed kinship, and lowest heterozygosity and allelic richness; Chapter 3, Table S3.1).

In contrast to Weitzman approach, the breed that contributes most to Eding diversity (Simien sheep) showed high between-breed as well as high within-breed diversity (Chapter 3). This is in agreement with the claims by Eding et al. (2002) and earlier findings (Mateus et al., 2004) that Eding's approach favours the conservation of breeds with high within- as well as between-breed variation.

Weitzman's approach targets conservation of individual breeds separately. It is thus suited to meet conservation arguments that aim to maintain individual breeds with current economic, ecological and cultural merits. Eding's core set approach involves maintaining an interbreeding population composed of individuals selected from breeds contributing to the core set (Eding et al., 2002). This may be appropriate for conservation arguments directed to preserving genetic diversity as insurance against future uncertainties with little consideration to current merits of specific breeds, e.g. conservation of wild animal species. Insurance arguments focus on conservation at the species level. Extinction of livestock species is unlikely (Rege and Gibson, 2003), and conservation at the species level may not thus be the focus of farm animal biodiversity conservation. In addition, livestock breeds in developing regions have specific breed merits and highly affiliated to specific communities (see Chapter 2 and 3), which necessitates their separate management. In conclusion, Edings approach appears to be more appropriate for prioritizing breeds as it considers both between- and within-breed genetic diversity. Though the approach assumes formation of interbreeding core sets, it can still be used to rank breeds based on their relative contributions to the core set and maintain the breeds separately (as is done in Chapter 3).

3. Conservation through utilization

3.1. Selective breeding

The theme of this thesis is conservation-based selective breeding. It has been argued (Rege, 1999b; FAO, 2007; Hiemstra et al., 2007) that the most rational and sustainable way to conserve livestock genetic resources is to improve their competitiveness through sustainable breed improvement programs (i.e. conservation through use). Adapted local breeds are perceived by their owners to be of low productivity and could easily be replaced by supposedly more productive breeds (Chapter 3). Woolliams et al. (1998) rated selection within local breeds as having higher or equal chance of sustainably reversing such reasons for breed decline, compared to other options such as crossbreeding, improving management, providing incentives to producers, and developing novel or niche products of the breed. It is well established that selective breeding of local sheep breeds can result in substantial long-term genetic improvement (Chapter 4 and 5; Biniam, 1992; Abegaz et al., 2002; Solomon and Joshi 2004a, 2004b). Despite the availability of such overwhelming information on the advantage of selective breeding, genetic improvement in local breeds is mostly sought through crossbreeding.

The impact of crossbreeding on erosion of indigenous livestock genetic diversity is well known. The most undesirable aspect of crossbreeding activities in developing regions is the indiscriminate crossing of local breeds with supposedly improved breeds without considering the existing production systems and the environment. Local breeds could be more advantageous than exotic breeds when compared under low-input production systems, which is often the case in developing regions, and marginal environments. Crossbreeding programs in developing regions lack stratification of production, appropriate crossbreeding methods, and effective dissemination schemes that enable maintenance of desired exotic blood levels in the commercial population. Some crossbreeding programs in developing regions, e.g., dairy cattle crossbreeding in Ethiopia seems to be effective. This program targets largely peri-urban commercial production systems in high potential areas. The program is also largely confined to production of dairy cows, maintaining the adapted local bulls which are required for ploughing. However, other crossbreeding programs, e.g. sheep crossbreeding program in Ethiopia, lack focus and targets, and effective dissemination schemes. As a result, the program virtually failed resulting only in dilution of the adapted sheep genetic resource.

Selection for high production efficiency only is also associated with undesirable correlated effects with respect to metabolic, reproduction and health traits (see review by Rauw et al., 1998). Such undesirable effects have more important implications under low-input systems and in marginal areas. Consequently, definition of broader breeding goals addressing both production and adaptive traits has been emphasized (Solkner et al. 1998; Olesen et al., 2000; Nielsen et al., 2005, 2006; Fimland, 2007). Breeding goals of farmers and pastoralists in traditional low-input production systems were found to be broader than commonly assumed based on expert technical knowledge (Chapter 4 vs. Chapter 6). Intensive selection can also result in loss of within-breed diversity in terms of increased rate of inbreeding unless methods to limit the rate of inbreeding are implemented. Dynamic selection tools that balance maintenance of genetic diversity with genetic progress have been developed (*e.g.*, Meuwissen (1997). Such dynamic tools, however, require pedigree recording which may not be feasible under the conditions of developing countries, particularly under village breeding. The above mentioned limitations of selective breeding can be overcome and selection can still be considered as a conservation-based breeding option in developing countries. The problem of narrow breeding objectives can be overcome by involving farmers when defining breeding objectives (Chapter 6). Regarding maintenance of within-breed diversity, we demonstrated in Chapter 7 that it is possible to design breeding schemes that balance genetic gain and rate of inbreeding also in the absence of pedigree recording.

3.2. Community-based (in-situ) management of genetic resources

Conservation strategies are broadly grouped into *in-situ, ex-situ in vivo* and *in vitro. In-situ* is the method of choice for conservation of farm animal genetic resources (Gibson et al., 2006). This is particularly the case where farm animal genetic resources are the best available livelihood options for farmers (Woolliams et al., 1998).

Conservation could be equivalent to preservation when the concept is applied to wild animal species or rare livestock breeds on the brink of extinction. In such cases *ex-situ in vivo* or *in vitro* maintenance of the population may be the best option. On the other hand, *in-situ* conservation of livestock breeds is primarily the active breeding of animal populations and their continued use as part of an ongoing livelihood strategy (Woolliams et al., 1998; Gibson et al., 2006). In such a context, community- or village-based breeding programs, as presented for example in Chapter 7 of this thesis, can be viewed as part and parcel of a comprehensive conservation plan, and not as a separate genetic improvement activity that entails significant additional costs.

Community-based breeding programs need to be designed based on breeding objectives of the community. Conventionally, breeding objectives are defined based on economic efficiency of livestock enterprises using profit equations. The breeding objectives of subsistence farmers in low-input systems go beyond economic efficiency and the primarily focus is on long-term sustainability of the system (e.g., farmers prefer more adapted than more productive animals). However, it can be argued that relative weights farmers attach to traits (Chapter 6) are based on economic rationale and thus reflect implicit economic values of traits. Consequently, definition of breeding objective for subsistence farmers should also consider current profitability of farm enterprises, not only long-term sustainability as it is commonly advocated.

Ex situ in vivo conservation is the maintenance of pure-bred nucleus flocks in organized government farms or research farms which can form a repository of the pure breed. However, maintenance of *ex-situ* flocks needs to be linked to farmer livelihoods in order to be feasible, for instance through closed or open nucleus breed improvement schemes. For alternative nucleus breeding schemes and their efficiency reference is made to Kosgey (2004). Although *in-situ* conservation or village breeding schemes are more advantageous in terms of contribution to biodiversity, maintenance of adaptive fitness, sustainability, and cost of establishment and maintenance (Woolliams et al., 1998), the few livestock pure-breeding programs in developing regions are mainly based on *ex-situ* nucleus breeding schemes. Nucleus breeding schemes enable implementation of efficient selection methods such as BLUP selection and result in higher genetic gain compared to *in-situ* schemes (Chapter 5 and 7; Kosgey, 2004). However, centralized nucleus breeding programs are disconnected from the community and require long-term commitment from implementing bodies (Kosgey et al., 2006), and are commonly designed based on a given set of breeding objective traits. On the other hand, farmers breeding objectives vary even among groups of subsistence farmers (Chapter 6; Solkner et al., 1998). It is obviously not possible to establish nucleus programs for each group of farmers. Village breeding program is suited to such situations since it enables to organize farmers with similar objectives.

Centralized nucleus programs could focus on the production of breeding animals that meet the needs of specialized commercial producers. There could be discrepancies in breeding objectives of subsistence and commercial systems in developing regions. For instance definition of breeding objectives using bio-economic model (data not shown) for susbsistence and emerging commercial (export) systems in Ethiopia shows that for the subsistence systems the most profitable production trait is number of lambs weaned per ewe joined, while for commercial systems it is carcass dressing percent. Such discrepancies pose a problem of defining an overall industry breeding objective and nucleus selection program for some breeds. This indicates that breeding objectives need to be tailor-made to the specific needs of different production systems, and nucleus and village programs could serve different but complementary purposes. Nucleus programs could focus on commercial farmers and also more marketed-oriented subsistence farmers (e.g., fatteners). Village programs could focus on susbsistence farmers. This is because genetic improvement at community level is supposed to target multipurpose animals that meet low-input systems and with a view of conserving the breeds.

Centralized nucleus breeding programs could be linked to village programs, targeting particularly market-oriented farmers. This could be in the form of an open nucleus scheme where there is gene flow between the nucleus and the village flocks. Alternatively, the nucleus center could serve as a central testing station for the village program. In such a scheme, there could be two stages of selection. First, animals are selected at village level for traits that can be measured at village level and then, at a second stage at nucleus center, they will be evaluated for traits that need more facilities and skills. For instance, animals can be selected for their size, conformation and other farmers' preferences such as color at village level, and then transferred to central station to be tested for finishing and carcass traits.

In conclusion, conservation of livestock breeds should not be viewed as preservation, and need to focus on improving the livelihoods of the communities maintaining the breeds. This can best be achieved by fully involving farmers in the design and implementation of breeding programs. To this end, village selective breeding schemes appear to be the best option to start with.

Research on development of breeding programs suitable to the conditions of developing regions is required, particularly regarding the practical implementation of breeding programs. This could include evolving village programs to more organized programs and linking village breeding scheme with nucleus breeding program, which is currently the approach in most developing countries. Other aspects of research include ways of developing village schemes into village ram breeding nucleus centers which can serve as a source of improved breeding stock for other villages not participating in the scheme. Scaling up village programs from cooperating villages to district levels also needs to be considered.

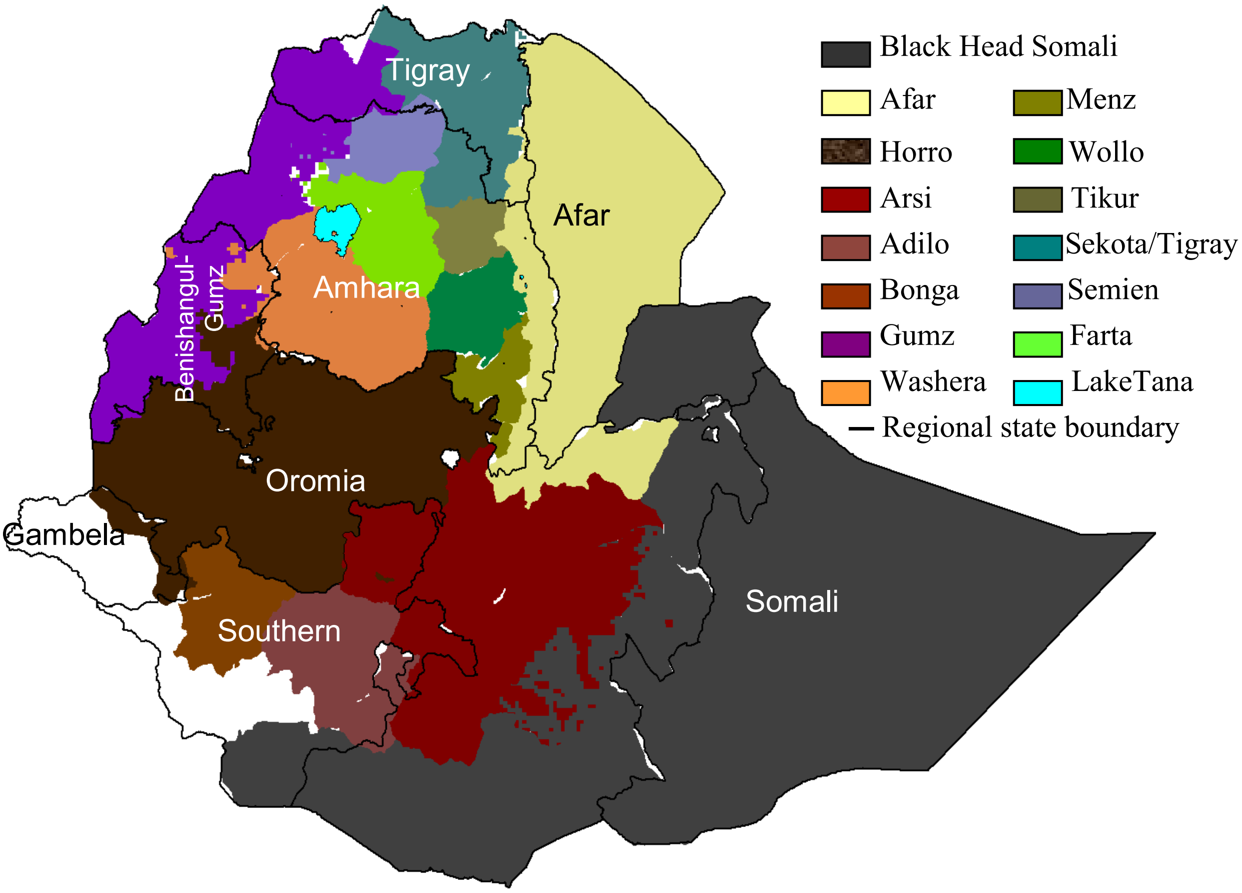

Fig. 8.1. Geographic distribution of sheep types in Ethiopia.
Source: Solomon et al. (in press)

Table 8.1. Sheep types and their ecology, geographic distribution, distinguishing physical features and population sizes ('000')

Types	Other names	Ecology	Geographic distribution	Important physical features*	Population
Sub-alpine short-fat-tailed group					
Menz	Legegora, shoa, Abyssinian, Ethiopian highland sheep	Sub-moist/dry, sub-alpine highlands (2500 and 3200 m);	North Shoa zone of Amhara state	Short fat tail turned-up at end; small body size; short-legged; long fleece with coarse wool; commonly black with white patches, white, brown, white with brown patches; straight-faced; horned males; short semi-pendulous ears with 12% rudimentary ears in the population. Kept by Amhara community	971.4
Sekota	Tigray highland, Abergelle	Cool, dry/sub-moist highlands (2000 m); semi-arid river valley	Wag Himra zone of Amhara State and Tigray State	Short fat tail turned-up at end and fused with main part; medium-sized; Predominantly brown or white coat, few blacks with brown belly; white animals have finer hair or wooly udder-coat; semi-pendulous or rudimentary ears in Wag Himra and Tigray, predominantly rudimentary in Tekeze valley. Reared by Agew, Tigray and Amhara communities	732.3
Simien		Alpine mountains (3000-4000 m) including Semien Wildlife park;	North Gondar zone of Amhara state (Debark, Dabat, Janamora, Wegera)	Short fat tail; well developed wooly undercoat; plain brown, plain white, brown/white with white/brown patches, plain black and black with brown belly; unique long laterally spiral horn in males and short horns in most females; largest of the highland wooled sheep. Reared by Amhara community	347.6
Tikur		sub-alpine highlands (3000 m)	North Wollo zone of Amhara state	Short fat tail; wooly undercoat; Predominantly black (60%) coat; small body size; majority short semipendulous ears, 24% rudimentary ears. Reared by Amhara communities	525.3
Wollo		Cood highland (2000-3200 m)	South Wollo zone of Amhara state	Short-fat-tail with short twisted/coiled end, occasionally turned up at end; Small size; well developed wooly undercoat; Predominantly black, white or brown, either plain or with patches of white, black or brown; long hair with wooly undercoat; horned males. Reared by Amhara communities	1395.9
Farta		Sub-moist highland (2000-2500 m)	South Gondar zone; Gondar zuria, Belesa, Dembia districts	Short fat tail; medium size; wooly under coat; Commonly white (37.5%), brown (27.5%) and black with brown belly (15%), white/brown with brown/white patches; males are horned. Reared by Amhara communities	555.6
Washera	Agew, Dangilla	Wet, warmer mid-highlands (1600-2000 m)	West and East Gojam and Agew Awi zones of Amhara state; Dangur, Madura and Alefa Takusa districts	Short fat tail; Large body size; short-haired; predominantly brown; both males and females are polled; reared by Amhara and Agew communities	1227.7

Highland long-fat-tailed group					
dilo		Wet, warmer mid-highland (1800-2000 m)	North Omo, Derashie, Gedio and Amaro zones of Southern state; some northern Borena districts (1300 – 2400 m)	Long fat tail; Large size; short-haired; males are short-horned and 18.4% of ewes are horned; predominantly brown (943%), brown with white patches (32%), black (16%), black (19%) and black with brown patch (9%). Reared by southern nationalities	407.7
Arsi-Bale		Mainly wet, cool and warmer highlands (2000-3300); sub-moist lowlands	Arsi, Bale, E. Shoa, W. Harerghie zones, some districts in Borena zones of Oromia; Hadya, Gurage, Kembata & Sidama zones	Long fat tail with twisted end in some animals; medium size; hairy fiber, especially in adult ewes, males have minor wool growth in some parts of body; Males and most females (52%) are horned; Large size; coat colors are brown (35.1%), brown with white patches (24.3%), black, white, and combinations of above colors. Reared by Oromo communities	6345.1
Horro		Cool, wet highlands (2991 m) to humid mid-highlands (1600 m).	East Welega, West Welega, Illubabor, Jimma and West Shoa zones of Oromia, and some bordering Gambella and Benishangul districts	Long fat tail extending below hock, either straight (51.4%) or coiled/twisted (48.6%) at the tapering end; prominent fat tail in males; Large, leggy and prolific; dominant colors are brown and fawn, belly is lighter especially in adult ewes, less frequent are black, white, brown with white patches; both sexes are polled. Reared by Oromo, Benishangul and Gambella communities	3409.3
Bonga	Gesha, Menit	Humid mid-highland zone (1200 – 2500)	Keffa, Sheka and Bench zones of Southern State	Long fat tail with straight tapering end (98.4%); hair sheep; Large size; predominantly plain brown (57.9%) or with black (.9%) or white (5.3%) shade, plain white (10.5%) or with brown patches (10.5%), and black (2.6%); both sexes are polled. Reared by Keffa, Sheka and Bench communities	517.5
Lowland fat-rumped Group					
Afar	Adal, Danakil	Mainly arid lowland(<1000 m); mid-highland (1200–1900 m)	Afar state; boardering Tigray, Amhara; E. & W. Harerghe and E. Shoa of Oromia	Wide fat tail, in some large fat tail reaching below the hock; hair fiber; medium size; characteristically uniform creamy white/ beige coat; rudimentary ear; polled; dewlap. Reared by Afar, Amhara, Tigray communities	681.9
BHS	Wanke, Ogaden, Berbera black head	Mainly arid lowlands (215-900 m); highlands (up to 2000 m)	Somali state; lowlands of Bale, Borena and south Omo zones; part of east Harerghe	Short fat rump with a stumpy appendage; uniform white body and black head and neck; polled; convex face, especially in males; short, outward forward drooping ear; well developed dewlap. Reared by Somali and Oromo, Konso and south omo communities	906.2
Lowland thin-tailed Group					
Gumz		Moist lowlands (< 1000 m)	Benishangul-Gumz state; lowlands of North Gondar	Long thin tail; some what dwarf; convex face profile; long pendulous ear; commonly plain brown or with patch (39.4%), white with brown or black patch (21%), black (15.8%), white, black with white patch, brown with black patch; polled. Reared by Gumz and Amhara communities	50.9

* Coat colors are in order of frequency in the population. Source: Solomon et al. (in press).

Table 8.2. Weitzman [32] total diversity† conserved from the full set of breeds and diversity conserved after exclusion of each breed [$V(S - i)$] with the corresponding percentage contribution [$d\ V(i)$] of the excluded breed to the full set

Breed (i)	$V(S - i)$	$d\ V(i)$ Percent
	1.2715 †	
Farta	1.2347	2.89
Menz	1.2229	3.82
Sekota	1.2179	4.22
Simien	1.1157	12.25
Tikur	1.2103	4.81
Wollo	1.2140	4.52
Afar	1.1968	5.87
BHS	1.1672	8.20
Adilo	1.2034	5.36
Arsi-Bale	1.1751	7.58
Horro	1.1861	6.72
Bonga	1.0624	16.45
Gumz	1.1206	11.87
Washera	1.1887	6.51

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Summary

Summary

Twenty percent of the world domestic animal breeds are classified as being "at risk" of extinction. Seventy percent of the mammalian breeds, for which no risk status data are available, are found in the developing world. This is a serious constraint to effective prioritization and planning of sustainable breed conservation measures. Ethiopia is an ideal case for studying livestock diversity and conservation in the context of developing regions. The country has a highly diverse population of sheep breeds spread across diverse ecological regions, communities and production systems. However, no information is available on the genetic variation, threat status and relative importance of these breeds for smallholder livelihoods. There is also no strategy for conservation and/or genetic improvement of these breeds. In this thesis, these two aspects of sustainable sheep breeding are addressed. In the first part, an improved method for characterization of sheep resources in Ethiopia is presented. The second part of this thesis describes the development of sustainable conservation-based breeding strategies for sheep breeds under smallholder traditional systems, taking Ethiopia as a case study.

Characterization of sheep resources

Populations of livestock species in developing regions are traditionally recognized as distinct types or traditional breeds, and named after the geographical locations or the communities keeping them. However, the relation between traditionally recognized populations and patterns of genetic and morphological variation among most livestock populations in developing regions is mostly unknown. In **Chapter 2**, we investigated molecular genetic and morphological variation and patterns and causes of population structuring among 14 traditional sheep populations in Ethiopia using 17 microsatellite markers and 12 morphological characters. We hypothesized that geographical isolation, ecological variation and community isolation are associated with the current population structure in Ethiopian sheep populations. Sheep breeds were initially classified as fat-tailed, thin-tailed and fat-rumped sheep. This classification is thought to correspond to three consecutive events of sheep introductions from the Near-east into East Africa. Analysis of microsatellite and morphological variation showed that current population genetic structure in Ethiopian sheep is strongly associated with historical patterns of sheep migration from Asia into Africa. Investigation of factors associated with genetic variation showed that an isolation-by-distance model (which reflects neutral causes of variation), independently of other factors, could explain most of the observed genetic variation. However, there is a strong indication of adaptive divergence in morphological characters. Using a combination of microsatellite analysis and morphological divergence, we propose a classification of Ethiopian sheep into six breed groups and nine breeds.

The objective of characterizing animal genetic resources is to facilitate decisions on prioritization in conservation of these resources. The primary objective of livestock conservation for developing regions is conservation for sustainable use and thus conservation decision should be based on both genetic and non-genetic aspects contributing to the survival of breeds. In **Chapter 3** , a maximum-utility-strategy is described, which is used to prioritize the 14 traditional sheep breeds based on their threat status, contributions to farmer livelihoods (current breed merits) and to genetic diversity. Contributions of the breeds to genetic diversity were quantified using Eding's marker-estimated kinship approaches. Non-genetic aspects included threats (*e.g.* low population size, low preferences by farmers) and current merits (economic, ecological and cultural merits). The results on threat status, current breed merits and contributions to genetic diversity were combined to produce a ranking of the 14 breeds for conservation purposes. This approach balances the trade-offs between conserving breeds as insurance against future uncertainties and for current sustainable utilization, and provides a basis for conservation strategies for Ethiopian sheep.

Sustainable breeding strategy

A commonly cited obstacle to the design and implementation of conservation-based selective breeding programs in developing regions, is the lack of estimates of genetic parameters to predict genetic gains and of actual responses to selection under low-input production systems and in marginal environments. In **Chapter 4** results of a selection experiment on Menz sheep under such conditions are presented. The selection criteria were yearling live weight (WT12) and greasy fleece weight (GFW) combined in an economic index. Realized genetic trends were 0.49 kg for WT12, 0.01 kg for GFW, and € 0.46 for the aggregate breeding value. Results also show that there has been improvement in correlated traits (weights at birth, weaning and six month). It can be concluded, based on estimates of genetic parameters and observed genetic trends, that selective breeding can lead to significant genetic improvement under low-input systems and marginal environments.

Genetic improvement of yearling weight in Menz sheep is relevant as most farmers in the Menz area market their sheep around yearling age (12 months). The Menz sheep nucleus selection program presented in Chapter 4 was based on measurement of live weight. However, measurement of live weight under village conditions is difficult. Alternative selection criteria to improve live weight under village breeding programs were investigated in **Chapter 5**. In this chapter, estimates of genetic parameters and realized responses for live weight (LW) and linear size traits using data from the Menz sheep nucleus selection program are given. A simulation study was conducted to compare predicted responses from indirect selection on linear size traits and direct selection on LW under simulated nucleus breeding program and village-based

breeding program. The moderate heritability estimates for some of the linear size traits (0.27 – 0.48), and the high genetic correlation between linear size traits and LW (up to 0.98) indicate that indirect selection on linear size traits can result in improvement of LW. Predicted responses in LW from indirect selection on chest girth, wither height and body length were 94.8% (nucleus program) and 92.6% (village program) of the responses to direct selection. Ease of measurement of linear size traits is of particular significance in village breeding programs where measurement of live weight can be difficult.

Sustainable animal breeding strategies require a broad definition of breeding objectives that emphasize maintaining adaptation to local circumstances and biodiversity, in addition to profitability. The breeding objectives assumed in Chapter 4 and 5 were identified by research experts without consultation of stakeholders. In **Chapter 6**, a farmer participatory approach was used to define breeding objectives and selection indexes for sheep breeding under traditional subsistence farming in sheep-barley and pastoral systems in Ethiopia. Breeding-objective traits were identified based on producers' preferences for traits collected during survey interviews. The desired gains in the resulting traits were calculated and were used to derive relative weights of traits in the breeding objective using desired gain selection index method. Producers' preferences showed that adaptive traits are more important than or as important as production traits. Results of the survey also showed that there are differences in the breeding objective of groups of farmers within a production system, such as those producing and marketing yearlings (subsistence farmers) and producing and finishing yearlings (subsistence+). The low correlation (0.31) found between selection indexes constructed for subsistence and subsistence+ producers demonstrates that breeding objectives need to be tailored to the specific needs of the different groups of farmers. Finally, in this chapter, an approach to incorporate producers' preferred breeding objectives into conventional selection tools is presented.

Sustainable animal breeding strategies also require community- or village-based management of the genetic resources. Accordingly, optimal village breeding schemes require consideration of both short-term (high rate of genetic gain) and long-term (maintenance of genetic variance and avoidance of inbreeding depression) effects of selection decisions. In **Chapter 7**, genetic responses and rates of inbreeding from alternative village sheep breeding schemes are evaluated. Schemes were designed based on a survey of existing flock structure and breeding management in a typical sheep-barley production system in Ethiopia. This survey showed that individual flock sizes are small, and that the majority of farmers practice mixed grazing and uncontrolled mating of their flocks in communal grazing lands within villages. This was found to be a limitation to the efficiency of within-flock selection under village conditions. Within-village schemes (selection across flocks within a village) and across-village schemes (selection across villages) were subsequently compared at different intensities of ram selection (i.e. proportions of rams selected, *P*). Results indicate that under within-village schemes, intensity of selection could not be increased (i.e. *P* could not be decreased below 0 .149) when rate of inbreeding was constrained to an acceptable level of 0.01, resulting in low genetic gain. The most optimal scheme was found to be across-village selection with at least three villages cooperating and an intensity of selection of 5 % of the yearling rams.

The salient points of the thesis are discussed in a general context in **Chapter 8**. It is argued that the benefit of characterizing (economic) farm animal species based on genetic markers that have little or no connection with production and adaptation traits may not be immediately apparent. Neutral genetic markers can be used to characterize farm animal populations, but that should not be the end by itself and neutral variation should not be the only criterion to classify populations and to base conservation decisions on. In conservation decisions for farm animal species, emphasis should be given to variation in special traits and current merits of breeds, particularly in developing regions with food security problems. Approaches that combine molecular genetic variation with information on ecological adaptive variation (which can be inferred from morphological variation), the history of the breeds and the role of the communities raising the breeds should be adopted to characterize livestock breeds. It is also argued that the most rational and sustainable way to conserve livestock genetic resources is to improve their competitiveness through sustainable breed improvement programs (i.e. conservation through use). To this end, community- or village-based selective breeding schemes appear to be the best option to start with.

Samenvatting

Twintig procent van alle gedomesticeerde landbouwhuisdier rassen kunnen worden geclassificeerd als zijnde bedreigd met uitsterven. Zeventig procent van de rassen, waarvan geen gegevens voorhanden zijn, komen uit ontwikkelingslanden. Dit is een belangrijke beperking bij het prioriteren en plannen van duurzame conservering programma's. Ethiopië is een ideaal land voor de studie naar diversiteit en conservering van landbouwhuisdieren in de context van ontwikkelingslanden. Het land heeft een zeer diverse populatie van schapen rassen verspreidt voorkomend over zeer diverse ecologische zones, gemeenschappen en productiesystemen. Er is echter geen informatie beschikbaar over de genetische variatie binnen en tussen deze rassen, de mate waarin ze bedreigd worden met uitsterven, en de belangrijkheid van deze rassen voor de levensomstandigheden van kleine boeren. Er is ook geen strategie met betrekking tot conservering en / of genetische verbetering van deze rassen. In dit proefschrift worden deze aspecten van duurzame schapenteelt in ontwikkelingslanden behandeld. In het eerste deel wordt een verbeterde methode voor het karakteriseren van schapenrassen in Ethiopië gepresenteerd. Het tweede deel van dit proefschrift beschrijft de ontwikkeling van duurzame, op conservering gebaseerde, fokstrategieën voor schapen (rassen) gehouden onder kleinschalige, traditionele omstandigheden. Hierbij wordt Ethiopië als casestudy gebruikt.

Karakterisering van schapenrassen

Populaties van landbouwhuisdieren in ontwikkelingslanden worden traditioneel herkend als afzonderlijke populaties of traditionele rassen, en worden benoemd naar de regio van herkomst of de traditionele gemeenschappen die ze houden. De relatie tussen deze verdeling in traditionele rassen en de patronen van genetische en morfologische variatie in de populatie als geheel is echter, in de meeste ontwikkelingslanden, grotendeels onbekend. In **hoofdstuk 2** beschrijven we, gebruikmakend van 17 microsatelliet merkers en 12 morfologische kenmerken, de moleculair genetische en morfologische variatie in, en patronen en oorzaken van, de populatiestructuur van 14 traditionele schapen populaties in Ethiopië. De hypothese was dat geografische isolatie, ecologische variatie en isolatie van gemeenschappen geassocieerd waren met de huidige populatie structuur van schapen in Ethiopië. Schapen rassen werden eerst onderverdeeld in 3 groepen: "fat tail", " thin tail" en "fat rump". Deze kwalificatie wordt geacht overeen te komen met drie achtereenvolgende introducties van schapen vanuit het Midden Oosten, via Ethiopië, naar Oost Afrika. De analyse van de genetische en morfologische variatie liet zien dat de huidige populatie structuur in Ethiopië sterk geassocieerd is met de historische patronen van schapen migratie vanuit

Azië naar Afrika. Het “ isolatie door afstand” model, wat vooral oorzaken van neutrale genetische variatie reflecteert, verklaarde hierbij, onafhankelijk van andere factoren, de meeste genetische variatie. Er zijn echter ook sterke aanwijzingen voor adaptieve diversificatie in morfologische kenmerken. Op basis van de combinatie van microsatelliet analyse en waargenomen morfologische diversiteit stellen we een classificatie van de 14 traditionele populaties in 6 ras groepen en 9 rassen voor.

Het doel van het karakteriseren van genetische bronnen is het faciliteren van beslissingen ten aanzien van prioritering en behouden van deze bronnen. Het primaire doel van conservering van landbouw huisdieren in ontwikkelingslanden is het behouden voor duurzaam gebruik, nu en in de toekomst. Beslissingen ten aanzien van conservering moeten derhalve gebaseerd zijn op zowel genetische als niet-genetische aspecten die bijdragen aan de overleving van deze rassen. In **hoofdstuk 3** wordt een maximaal-nut strategie beschreven welke gebruikt werd om tot een prioritering te komen van de 14 traditionele populaties. Hierbij wordt gebruik gemaakt van de mate waarin een ras bedreigd wordt met uitsterven, hun (huidige) bijdrage aan het levensonderhoud van kleine boeren, en hun bijdrage aan de genetische diversiteit van de schapen populatie als geheel in Ethiopië. De bijdrage aan genetische diversiteit werd gekwantificeerd met Eding’s “ marker estimated kinship “ benadering. Niet-genetische aspecten waren risico factoren zoals kleine populatieomvang en waardering door boeren, en huidige economische, ecologische en culturele waarden van een ras. Deze benadering laat zien dat het mogelijk is een evenwicht te vinden tussen het behouden van een ras als verzekering voor een onzekere toekomst en het huidige duurzame gebruik van dat ras.

Duurzame fokstrategie

Een vaak genoemd obstakel bij het ontwerp en implementatie van een fokprogramma in ontwikkelingslanden, is het ontbreken van schattingen van genetische parameters. Hiermee kan de genetische vooruitgang en werkelijke vooruitgang voorspeld worden van selectie onder marginale condities. In **hoofdstuk 4** worden de resultaten van een selectie experiment met Menz schapen onder marginale condities gepresenteerd. De selectiecriteria waren lichaamsgewicht op twaalf maanden (WT12), en wolgewicht (GFW), gecombineerd in een economische index. Gerealiseerde economische trends waren 0.49 kg voor WT12, 0.01 kg voor GWF, en € 0.46 voor het gecombineerde fokdoel. Resultaten laten ook zien dat er vooruitgang was in de gecorreleerde kenmerken geboortegewicht en gewicht na 6 maanden. De conclusie is dat, gebaseerd op de schattingen van de genetische parameters en de gerealiseerde vooruitgang, selectie onder marginale condities tot goede resultaten kan leiden.

Genetische verbetering van het gewicht op 1 jaar in Menz schapen is zeer relevant aangezien de meeste boeren in het Menz areaal hun schapen op 1 jaar vermarkten. Het nucleus fokprogramma is echter gebaseerd op het meten van levend gewicht en dit kan in veel dorpen een probleem vormen. Daarom werden in **hoofdstuk 5** een aantal alternatieve selectiekenmerken om gewicht te verbeteren onderzocht. In dit hoofdstuk worden schattingen van genetische parameters voor lineaire kenmerken en de gecorreleerde gerealiseerde respons voor levend gewicht op 12 maanden voor een nucleus fokprogramma gepresenteerd. Ook voerden we een simulatiestudie uit om de voorspelde respons na indirecte selectie op lineaire kenmerken en de respons na directe selectie op levend gewicht te vergelijken onder de condities van een nucleus fokprogramma en een fokprogramma met actieve participatie van boeren in de deelnemende dorpen ("village-based breeding program"). De redelijk hoge erfelijkheidsgraden voor sommige lineaire kenmerken (027-0.48) en de hoge correlatie tussen lineaire kenmerken en levend gewicht op 12 maanden (0.98) laten zien dat indirecte selectie op lineaire kenmerken kan resulteren in verbetering van het lichaamsgewicht. De voorspelde respons in lichaamsgewicht via indirecte selectie op borstbreedte, schofthoogte en lichaamslengte waren 94.8 % bij een nucleus programma, en 92.6 % bij een participatief programma, van de respons na directe selectie op lichaamsgewicht.

Het meten van eenvoudige lichaamsmaten is met name relevant voor participatieve fokprogramma's in dorpen, waar het enigszins nauwkeurig bepalen van het gewicht lastig kan zijn.

Voor duurzame fokprogramma's zijn brede definities van het fokdoel nodig, waarin naast economisch rendement ook het behoud van adaptatie aan lokale omstandigheden en bijdrage aan biodiversiteit zijn opgenomen. De fokdoelen genoemd in hoofdstuk 4 en 5 waren gedefinieerd door onderzoekers, zonder consultatie van de directe belanghebbers. In **hoofdstuk 6** werd een participatieve benadering gebruikt waarbij boeren werden betrokken bij het formuleren van fokdoelen en selectie indices voor een schapen fokprogramma in traditionele, marginale schaap-gerst productie systemen en seminomadische omstandigheden in Ethiopië. Kenmerken voor het fokdoel werden geïdentificeerd op basis van voorkeuren van boeren en producenten welke werden verzameld met behulp van enquêtes en interviews. De verlangde vooruitgang in de resulterende kenmerken werden berekend en gebruikt om relatieve gewichten toe te kennen aan de index kenmerken in het fokdoel. De voorkeuren van de producenten (boeren, nomaden) lieten zien dat de adaptieve kenmerken belangrijker, of net zo belangrijk, werden gevonden als productie kenmerken. De resultaten van de enquête liet ook zien dat er verschillen zijn in het fokdoel van de verschillende groepen boeren binnen een productie systeem: er zijn boeren die alleen 1 jaar oude lammeren produceren en vermarkten, en er zijn boeren die deze lammeren ook afmesten. De lage correlatie (0.31) tussen de twee selectie indices gemaakt voor deze twee groepen boeren laat zien dat fokdoelen op maat gemaakt dienen te worden naar de behoeften en specificaties van de doelgroep. In **hoofdstuk 6** wordt een manier gepresenteerd waarop dat gedaan zou kunnen worden.

Duurzame participatieve fokprogramma's vereisen ook dat de genetische bronnen op gemeenschapsniveau beheerd worden. Dienovereenkomstig moeten in dergelijke fokprogramma's overwegingen van korte termijn (veel genetische vooruitgang) en lange termijn (behoud van genetische variatie en voorkomen van inteelt) in de selectie beslissingen meegenomen worden. In **hoofdstuk 7** worden de genetische respons en mate van inteelt van een aantal participatieve fokprogramma's vergeleken en geëvalueerd. De fokprogramma's werden ontworpen op basis van kudde structuren en beheer van genetische bronnen in een bestaand schaap-gerst productie systeem in Ethiopië. In dit systeem zijn de individuele kuddes klein en beoefenen de meeste boeren een praktijk van gemende begrazing en ongecontroleerde paring in hun kuddes die op gemeenschappelijke gronden binnen de dorpsgrenzen worden gehouden. Dit beperkt de mogelijkheden voor een "binnen-kudde" selectieprogramma op dorpsniveau. "Binnen-dorp" selectieprogramma's (selectie over alle kuddes binnen 1 dorp) en "tussen-dorp" selectieprogramma's (selectie over alle dorpen) werden vergeleken met verschillende intensiteiten van ram selectie (het aantal rammen dat geselecteerd wordt uit de totale hoeveelheid beschikbare rammen, P). De resultaten laten zien dat in "binnen-dorp" selectie schema's de intensiteit van selectie P niet hoger dan 0.149 kan zijn als de snelheid waarmee inteelt toeneemt wordt beperkt tot 1% per generatie. Dit resulteert in een geringe genetische vooruitgang van het selectie kenmerk. Het meest optimale schema was een fokprogramma waarbij drie dorpen betrokken waren en jaarlijks 5 % van alle beschikbare rammen geselecteerd worden.

De meest pregnante punten van dit proefschrift worden bediscussieerd in **hoofdstuk 8**. Hierin wordt betoogd dat het karakteriseren van populaties van landbouwhuisdieren in ontwikkelingslanden met genetische merkers zonder dat daarbij productie en adaptieve kenmerken betrokken worden, van beperkt nut kan zijn. Neutrale genetische merkers kunnen gebruikt worden landbouwhuisdier populaties te karakteriseren, maar het mag niet het enige criterium zijn waarop populaties worden geclassificeerd en waarop beslissingen ten aanzien van behoud en conservering zijn gebaseerd. De nadruk dient juist te worden gelegd op het karakteriseren van de variatie in speciale adaptieve kenmerken en de lokale waarden van de rassen, vooral in regio's / ontwikkelingslanden met een onzekere voedselvoorziening. Rassen dienen gekarakteriseerd te worden door combinatie van moleculaire genetische variatie met informatie over ecologische adaptatie (af te leiden uit morfologische variatie), de geschiedenis van een ras / traditionele populatie, en de rol van het ras / populatie voor lokale gemeenschappen. De meest duurzame manier om dergelijke rassen te behouden is ze op te nemen in een participatief fokprogramma, om zo de productiviteit te verhogen en daarmee de concurrentie met geïmporteerde (gekruiste) rassen te verhogen. Het hier beschreven "tussen-dorp" fokprogramma lijkt voor Ethiopië de beste manier om hiermee te starten.

General conclusion and recommendation

1. Local breeds that are traditionally recognized as distinct types in developing regions may not all be genetically distinct. The 14 traditional sheep breeds in Ethiopia can be classified into six genetically distinct breed groups and nine breeds. Traditional breeds that do not differ genetically (*e.g.* the sub-alpine short-fat-tailed group comprising Menz, Farta, Sekota, Wollo and Tikur) can be managed as a single breed.

2. Morphological description is an essential component of breed characterization. It can be used to physically identify, describe, and recognize a breed, and also to classify livestock breeds into broad categories. Morphological characterization can not discern genetic variation between populations within breed groups. Such detailed analysis of populations requires use of molecular genetic markers such as microsatellites. Genetic markers are essential to assess within-breed variation (relatedness or level of inbreeding), particularly in situations where pedigree information is mostly incomplete or absent. Morphological characters should be used as a complementary tool to molecular genetic markers for characterizing animal genetic resources.

3. The emphasis in the conservation of livestock breeds in developing regions should be to maintain diversity to meet current and future livelihood requirements. Conservation priorities should be set in consultation with the farmers. Conservation actions need to be geared to within-breed genetic management and increasing utility of the local breeds through improvements in genetic performance levels, management, and marketing.

4. Conservation and improvement programs need not be seen as separate and competing activities. Village-based selective breeding programs designed with full participation of the farmers are suitable for low-cost *in-situ* conservation of indigenous animal genetic resources.

5. More research on development and practical implementation of breeding programs suitable to the conditions of developing regions is required. Future research may focus on evolving village programs to more organized programs, linking village breeding scheme with nucleus breeding programs, ways of developing village schemes into village ram breeding nucleus centers serving as a source of improved breeding stock for farmers not participating in village breeding programs, and scaling up village programs to district levels.

Curriculum vitae

Personal profile

Solomon Gizaw GebreMichael was born of his father Gizaw GebreMichael and mother Abebech Mersha on 13 December 1963 in Dire Dawa, Ethiopia. He attended elementary and Secondary schools in Dire Dawa, obtained BSC degree in 1986 in Animal Sciences from Alemaya Univeristy, MSc degree in Animal Breeding and Genetics from NDRI, India in 2002. He has been working in livestock research all through. He is married to Yeshihareg Mammo and is a father of son Henock Solomon and daughter Yordanos Solomon. He joined Animal Breeding and Genomics Centre of Wageningen University in September 2004 to work on a collaborative PhD project between ILRI and Wageningen University.
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21. **Solomon Gizaw**, Solomon Abegaz and Yohannes Gojam. 1995. Factors affecting preweaning survival of Horro lambs at Bako Research Center. Third ESAP conference, 27-29 April 1995, ESAP Proceedings, pp140-145.
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27. Sisay Lemma, **Solomon Gizaw**, Assefa deressa and Yimam Hassen. 1998. Sheep and goat research in the Amhara region. In: Beyene Seboka and Abera Deressa (eds), Agricultural Research and Technology Transfer Attempts and Achievements in Northern Ethiopia. Proceedigs of the fourth Technology

Generation,Transfer and Gap Analysis Workshop, 18-21 March 1997, Bahir Dar, Ethiopia.

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29. **Solomon Gizaw**. Livestock production sub-system in Yeku watershed. In: Kindu Mekonnen and Solomon Gizaw (eds), Integrated Watershed Development in the Amhara Regional state . September 1999, Bahir Dar Ethiopia.

Training and supervision plan

Name	Solomon Gizaw GebreMichael
Group	Animal Breeding and Genomics Center
Supervisor	Prof.Dr.ir. Johan Van Arendonk
Co-supervisor	Dr ir. Hans Komen, Dr. Olivier Hanotte(ILRI)
Project term	01 Sept. 2004 - 30 Aug. 2008

The Graduate School
WAGENINGEN INSTITUTE of ANIMAL SCIENCES

The basic package	ECTS
WIAS Introduction course	1.5
Biology underpinning Animal Science: Broaden your horizon	1.5
Subtotal	*3.0*
Scientific exposure	
International conferences	
Conservation genetics of animal populations, Wageningen 2006	0.3
18 symposium on reproductive technology for conservation, Utrecht 2008	0.3
Plant breeding for organic and sustainable low-input agriculture, Wageningen 2008	1.5
59th conference of EAAP, Lithuania, August 24-47, 2008	1.2
Wotro annual conference, Amsterdam 2004	0.3
Seminars and workshops	
Dairy cattle production and breeding, Wageningen 2007	0.15
Thermal programming in chickens, Wageningen 2007	0.15
Poultry and people, Wageningen 2007	0.15
Personalities in animals: implications for welfare, Wageningen 2007	0.15
WIAS Science Day, Wageningen 2004	0.3
Various seminars at ILRI	0.15
WIAS Science Day, 2008	0.3
Presentations	
Conservation genetics of animal populations, Wageningen 2006 (oral presentation	1.0
Sheep genetic resources of Ethiopia (oral)	1.0
WIAS Science Day (poster)	1.0
Conservation and utilization of livestock resources in developing countries, June 2008 (oral)	*1.0*
Subtotal	*9.2*
In-depth studies	
Disciplinary and interdisciplinary courses	
Bioinformatics course, ILRI Nairobi, 2005	1.5
Linear models in animal breeding, Wageningen, 2007	2.0
Understanding genotype x environment interaction, Wageninegn 2007	2.0
Longitudinal data analysis, Utrecht 2006	0.6
Factor and cluster analysis, Utrecht 2006	0.6
Advanced regression analysis, Utrecht 2006	0.6
Participation in quantitative genetics discussion group (QDG)	0.5
Mathematical modeling in biology, 2008	2.0
Undergraduate courses	
Genetic improvement of livestock	6.0
Animal breeding and genetics	6.0
Advanced statistics for life science	6.0
Subtotal	*27.8*
Professional skills support courses	
Techniques for writing and presenting scientific paper, 2006	1.2
Project and time management, 2005	1.5
Scientific publishing, 2004	0.3
Subtotal	*3.0*
Research skills training	
External training period at ILRI	2.0
Supervising MSc student	1.0
Subtotal	3.0
Education and training total (min 30 ECTS)	**45.9**