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Evaluation of the genetic progress and changes in genome structure of sheep under community-based breeding programs in Ethiopia

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ABBREVIATION AND ACRONYMS

ADA: Austrian Development Agency

AGSBMC: Amed Guya Sheep Breeding and Multiplication Center

AI: Artificial Insemination

AIC: Akaike's Information Criterion

AI-REML: The Average Information Restricted Maximum Likelihood

ANRSBoARD: Amhara National Regional State Bureau of Agriculture and Rural Development

BCS: Body Condition Score

BHS: Black Head Somali

BLUP: Best Linear Unbiased Prediction

BOKU: University of Natural Resources and Life Sciences

CADU: Chilalo Agricultural Development Unit

CBBP: Community Based Breeding program

CGIAR: Consultative Group for International Agricultural Research

CSA: Central Statistical Agency

DBARC: Debre Birhan Agriculture Research Center

DBSBMC: Debre Berhan Sheep Breeding and Multiplication Center

DNA: Deoxyribonucleic acid

ESGPIP: the Ethiopian Sheep and Goat Productivity Improvement Program

FAO: Food and Agriculture Organization

F_{IS}: Inbreeding coefficient

F_{ST}: Genetic differentiation between subpopulations

GDP: Gross Domestic Product

GWAS: Genome-Wide Association Study

HWE: Hardy–Weinberg equilibrium

IBC: Institute of Biodiversity Conservation

ICARDA: International Center for Agriculture Research in the Dry Areas

ILCA: International Livestock Center for Africa

ILRI: International Livestock Research Institut

LRT: likelihood ratio test

NBE: National Bank of Ethiopia

NGO: Non-Governmental Organization

PCA: Population Component Analysis

RFLP: Restriction Fragment Length Polymorphism

RRA: Rapid Rural Appraisal

SNNPR: Southern nations' nationalities and peoples

SNP: Single Nucleotide Polymorphism

Abstract

Several pilot community-based breeding programs (CBBPs) were established since 2009 for various sheep breeds in Ethiopia. In these CBBPs, the main selection trait identified through participatory approaches was six-month weight (SMWT). The purpose of this study was to contribute to an understanding of the results of CBBP practices for two breeds (Bonga and Menz) by addressing (i) Estimation of the correlation between phenotypic based selection and BLUP-EBV; (ii) Assessment of the effect of selection based on SMWT on other productive and reproductive traits; (iii) Quantification of genetic trend for growth and reproduction traits; and (iv) Assessing the genomic changes induced by CBBPs. Data on 10877 lamb records from Bonga and 16245 from Menz sheep breed were collected between 2009 and 2018. Performance data from the breeding programs were analyzed using Average Information Restricted Maximum Likelihood Method (AI-REML). To understand how selection on weight traits impacted the genomic structure, we assessed genomic diversity, population structure, and signatures of selection of improved-under-CBBP and non-improved Menz and Bonga sheep populations using high density 600K SNP genotyping. A total of 182 animals of the two breeds were sampled from participating and non-participating flocks in CBBPs.

The correlation between the phenotype BV and the BLUP EBV correlation in both Menz and Bonga is high during all the years ranging from 0.77 to 0.92. For Menz, heritability estimates of 0.04, 0.18 and 0.39 were obtained for Birth Weight (BWT), Weaning weight (WWT) and (SMWT), respectively. For Bonga, the corresponding values were 0.17, 0.42 and 0.32. For Menz, genetic correlation estimates of 0.90, 0.53 and 0.88 were obtained between SMWT and WWT, SMWT and YWT and WWT and BWT, respectively. For Bonga, high to moderate genetic correlations of 0.97 and 0.42 were obtained between SMWT and WWT and litter size (LS) and SMWT, respectively. Over the years, there was a sustained genetic progress in SMWT for both breeds, being on average 0.12 ± 0.022 and 0.04 ± 0.003 kg/year for Bonga and Menz, respectively. Genetic progress in BWT was not observed in Bonga, but a significant increase occurred in Menz. For both breeds, WWT showed a significant increase reaching 0.09 ± 0.012 and 0.02 ± 0.018 kg/year for Bonga and Menz, respectively. Considering that there was no direct selection on WWT in the community flocks, the calculated increased weights were due to correlated responses. The genetic trend for LS over the years in Bonga was positive and significant ($P < 0.01$).

In Menz, the observed heterozygosity H_O and hxpected heterozygosity H_E were 0.31 and 0.32, respectively while for Bonga, a lower similar value of 0.3 was calculated for H_O and H_E. The average pairwise population differentiation (F_{ST}) between the two breeds was 0.083%, ranging from 0.078% to 0.087%, indicating their low to moderate differentiation. The F_{ST} within the same breed but between improved-under-CBBP and non-improved was 0.007%. PCA and ADMIXTURE analyses revealed a clustering pattern of the two sheep breeds according to their geographical distribution. The genomic regions under putative selection identified by FST approaches revealed genes associated with adaptation to environments, metabolism, immune responses, growth and reproduction traits.

Outputs of this study are to be used to develop optimum alternative improvement and dissemination schemes for Menz and Bonga sheep and a model scheme for other sheep breeds. Though preliminary, the genomic findings may represent in the future a breakthrough in improving the design of CBBP's for increased performance of local sheep breeds in Ethiopia.

***Keywords:** Sheep, Breeding, Weight, Genetic trends, Genetic correlations, Genomic diversity*

Resumen

Desde 2009 se establecieron varios programas piloto de cría basados en la comunidad (CBBPs) para varias razas de ovejas en Etiopía. El rasgo de selección principal para los CBBPs fue el peso a los seis meses (SMWT), el cual fue identificado a través de enfoques participativos. El propósito de este estudio fue el análisis de los resultados de los CBBPs en dos razas, Bonga y Menz. Para ello, se realizaron estudios genéticos y genómicos. Para el primero, la estima de la correlación entre la selección basada en fenotipos y BLUP-EBV, evaluación del efecto de la selección (SMWT sobre otros rasgos productivos y reproductivos), y cuantificación de la tendencia genética. Se recopilaron 10877 registros de corderos para Bonga y 16245 para Menz entre 2009 y 2018. Los datos de rendimiento de los programas de cría se analizaron utilizando el método de máxima verosimilitud restringida de información promedio (AI-REML). En los estudios genómicos, se evaluó la diversidad genómica, la estructura de la población, y la selección genómica entre las razas de ovejas Menz y Bonga. Se muestrearon un total de 182 animales de las dos razas en rebaños participantes y no participantes en los CBBPs y se utilizó un genotipado de SNP de alta densidad 600K.

Las estimas de heredabilidad para Menz, fueron de 0.04, 0.18 y 0.39 para peso al nacimiento (BWT), peso al destete (WWT) y SMWT, respectivamente. Mientras que, para Bonga, los valores correspondientes fueron 0.17, 0.42 y 0.32. Las correlaciones genéticas para Menz fueron de 0.90, 0.53 y 0.88 entre SMWT y WWT, SMWT y YWT, y WWT y BWT, respectivamente. Mientras que para Bonga, las correlaciones genéticas fueron de 0.97 entre SMWT y WWT, y 0.42 entre el tamaño de la camada (LS) y SMWT. A lo largo de los años, hubo un progreso genético sostenido en SMWT para ambas razas, siendo en promedio 0.12 ± 0.022 y 0.04 ± 0.003 kg /año para Bonga y Menz, respectivamente. No se observó progreso genético para BWT en Bonga, pero si un aumento significativo en Menz. Para ambas razas, el WWT mostró un aumento significativo, alcanzando 0.09 ± 0.012 y 0.02 ± 0.018 kg /año para Bonga y Menz, respectivamente. Teniendo en cuenta que no hubo selección directa de WWT en las parvadas de la comunidad, el aumento de peso calculado se debe a respuestas correlacionadas. La tendencia genética de LS a lo largo de los años en Bonga fue positiva y significativa (P <0,01). En los análisis genómicos, en Menz, la heterocigosidad observada H_O *y la heterocigosidad esperada* H_E *fueron de 0.31 y 0.32. En Bonga se obtuvo un valor similar, siendo este de 0.3 para* H_O *y* H_E*. La diferenciación poblacional por pares (FST) promedio entre las dos razas fue de 0.083% (variando de 0.078% a 0.087%), lo que indica una diferenciación entre baja y moderada. La FST dentro de la misma raza pero entre CBBPs y animales de control fue del 0,007%. Los análisis de PCA y ADMIXTURE revelaron un patrón de agrupamiento de las dos razas de ovejas según su distribución geográfica. Las regiones genómicas bajo selección putativa identificadas mediante enfoques FST revelaron genes asociados con la adaptación al medio ambiente, el metabolismo, la respuesta inmune, rasgos de crecimiento y reproducción.*

Los resultados de este estudio sugieren que es posible el desarrollo de esquemas alternativos óptimos de mejora y difusión para las ovejas Menz y Bonga, y un esquema modelo para otras razas de ovejas. Aunque preliminares, los hallazgos genómicos pueden representar en el futuro un gran avance en la mejora del diseño de CBBP para mejorar el rendimiento de las razas locales de ovejas en Etiopía.

Palabras clave: *Oveja, Cría, Peso, Tendencias genéticas, Correlaciones genéticas, Diversidad genómic*

Resum

Des de 2009 es van establir diversos programes pilot de cria basats en la comunitat (CBBP) per a diverses races d'ovelles a Etiòpia. En estos CBBPs, el tret de selecció principal identificat a través d'enfocaments participatius va ser el pes de sis mesos (SMWT). El propòsit d'este estudi va ser contribuir a la comprensió dels resultats de les pràctiques de CBBP per a dos races (Areca i Menz) a l'abordar (i) l'estimació de la correlació entre la selecció basada en fenotípics i BLUP-EBV; (ii) Avaluació de l'efecte de la selecció basada en SMWT sobre altres trets productius i reproductius; (iii) Quantificació de la tendència genètica dels trets de creixement; i (iv) Detecció de canvis genòmics induïts per CBBP. Les dades de 10877 registres de corders per a Areca i 16245 per a Menz es van recopilar entre 2009 i 2018. Les dades de rendiment dels programes de cria es van analitzar utilitzant el mètode de màxima probabilitat restringida d'informació mitjana (AI-REML). Per a Menz, es van obtindre estimacions d'heredabilidad de 0,04, 0,18 i 0,39 per al pes al nàixer (BWT), el pes al deslletament (WWT) i (SMWT), respectivament. Per a Areca, els valors corresponents van ser 0,17, 0,42 i 0,32. Per a Menz, es van obtindre estimacions de correlació genètica de 0,90, 0,53 i 0,88 entre SMWT i WWT, SMWT i YWT i WWT i BWT, respectivament. Per a Areca, es van obtindre correlacions genètiques altes a moderades de 0.97 i 0.42 entre SMWT i WWT i la grandària de la ventrada (LS) i SMWT, respectivament. Al llarg dels anys, va haver-hi un progrés genètic sostingut en SMWT per a ambdós races, sent com a mitjana 0,12 ± 0,022 i 0,04 ± 0,003 kg / any per a Areca i Menz, respectivament. No es va observar progrés genètic en BWT en Areca, però es va produir un augment significatiu en Menz. Per a ambdós races, el WWT va mostrar un augment significatiu aconseguint 0.09 ± 0.012 i 0.02 ± 0.018 kg / any per a Areca i Menz, respectivament. Tenint en compte que no va haver-hi selecció directa de WWT en les parvadas de la comunitat, l'augment de pes calculat es deu a respostes correlacionades. La tendència genètica de LS al llarg dels anys en Areca va ser positiva i significativa (P <0,01).

Per a comprendre com la selecció dels trets de pes va afectar l'estructura genòmica, avaluem la diversitat genòmica, l'estructura de la població i la selecció genòmica entre les races d'ovelles Menz i Areca utilitzant el genotipatge de SNP d'alta densitat 600K. Es muestrearon un total de 182 animals de les dos races dels ramats participants i no participants en les broques. En Menz, l'heterocigosidad observada H_O i l'heterocigosidad esperada H_E van ser 0,31 i 0,32, respectivament, mentres que per a Areca, es va calcular un valor semblant inferior de 0,3 per a H_O i H_E. La diferenciació poblacional per parixes (FST) mitjana entre les dos races va ser de 0.083%, variant de 0.078% a 0.087%, la qual cosa indica la seua diferenciació baixa a moderada. La FST dins de la mateixa raça però entre CBBP i animals de control va ser del 0,007%. Les anàlisis de PCA i ADMIXTURE van revelar un patró d'agrupament de les dos races d'ovelles segons la seua distribució geogràfica. Les regions genòmiques baix selecció putativa identificades per mitjà d'enfocaments FST van revelar gens associats amb l'adaptació als entorns, el metabolisme, les respostes immunitàries, els trets de creixement i reproducció. Els resultats d'este estudi s'utilitzaran per a desenrotllar esquemes alternatius òptims de millora i difusió per a les ovelles Menz i Areca i un esquema model per a altres races d'ovelles. Encara que preliminars, les troballes genòmiques poden representar en el futur un gran avanç en la millora del disseny de CBBP per a millorar el rendiment de les races locals d'ovelles a Etiòpia.

Paraules clau: *Ovella, Cria, Pes, Tendències genètiques, Correlacions genètiques, Diversitat genómica*

Introduction

Ethiopian livestock breeds are numerous, diverse and typically well adapted to the harsh environmental conditions under which they perform (Haile et al. 2019). Livestock are kept by householders across all wealth groups, but poorer households, more often, tend to have livestock as part of their asset portfolios than wealthier households (FAO, 2019). Sheep and goats are a mainstay of the agricultural sector in Ethiopia. They largely contribute to the livestock sub-sector and significantly contribute to livelihoods as well as food and nutritional security for poor households. By virtue of their lower capital, as well as feed requirements and shorter generation intervals than larger ruminants, sheep are suitable livestock assets for poor farmers. According to the Ethiopian Central Statistical Agency (CSA) (2017/2018), the total Ethiopian sheep population was estimated at 31.30 million. Therefore, the improvement of the sheep sector, and its profitability, is essential in lifting farmers out of poverty, changing the socioeconomic status of poor households and increasing the (GDP) of the country, through a more productive agricultural sector.

Efforts towards small ruminant genetic improvement started in Ethiopia in the early 1960s, with low and fragmented implementation (Tibbo, 2006). This is because almost all genetic improvement activities had focused on crossbreeding and were unsuccessful. Application, in Ethiopia, of the strategies and breeding schemes that have shown success in the developed countries did not yield the expected results, due to the absence of supportive infrastructure and the minimal participation of farmers as well as the incompatibility of the introduced genotypes and very often inadequate management practices (Kosgey, 2004). Centralized breeding schemes, usually run by governments, were attempted in developing countries. This top-down approach did not engage smallholder farmers who were the intended users. Subsequently, this approach also failed to provide sustainable solutions to improving small ruminant productivity. As a result, productive performance of small ruminants remained low where several previous attempts to improve it were met with little success. According to Gizaw et al. (2013), all the previous works of genetic improvements (crossbreeding) were disorganized, unstructured and unplanned, resulting in unsuccessful attempts and unsustainable results.

The failure of these programs led to a new approach aimed at genetic improvement of small ruminants, commonly referred to as community-based breeding programs (CBBPs). In Africa, CBBPs have been implemented across Ethiopia with the involvement of farmers, by using their knowledge, identifying their needs and understanding their perceptions. This was achieved through the active participation of smallholder farmers, from the initial design through to the implementation of the breeding programs (Haile et al., 2020). Community-based breeding program is an alternative approach that has also been implemented in Mexico, Argentina, Uganda and Malawi. It has gained global recognition and is considered a sustainable option for improving livestock production under smallholder conditions, and in low input systems. It is a recently advocated option for tropical, traditional low input livestock production systems (Sölkner-Rollefson, 2003; Baker and Gray, 2004; Wurzinger et al., 2011; Haile et al., 2020).

The first CBBP in Ethiopia, for sheep improvement, was implemented by the International Center for Agriculture Research in the Dry Areas (ICARDA), the International Livestock Research

Institute (ILRI), the University of Natural Resources and Life Sciences (BOKU) and Ethiopian national research institutes funded through an ADA project from 2007 to 2011 (Gutu et al., 2015). This program has been initiated, designed and implemented with four main sheep populations: Afar, Bonga, Horro and Menz, initially involving more than 8000 heads of sheep. Except for Afar, where CBBP was discontinued, in all the three locations, CBBP is underway in two communities, each organized as sheep-breeding cooperatives. Bonga is located in the southwest of Ethiopia, Horro in the west and Menz in the north-central highlands. In all sites, agriculture is the mainstay of the community and a mixed low-input crop-livestock farming system is practiced. Sheep production has always been an integral part of the traditional subsistence mixed crop-livestock production systems in these areas (Edea, 2008; Gizaw et al., 2014). Sheep are a source of cash to meet household basic needs, supplements crop production and represents a practice to mitigate the risk of crop failure in the harsh environment of the highlands.

Bonga and Horro sheep are characterized as fat long tailed breeds and are highly valued for their meat production. The Menz breed is raised for its coarse wool, used to weave traditional blankets and carpets, as well as for meat (Mirkena et al., 2012). Farmers in these locations largely depend on sheep farming for their livelihoods (Gizaw et al., 2014). Some farmers, including members of the CBBP, particularly in Menz, are food insecure and fall under the government food safety net program, meaning that they are heavily reliant on the potential of their sheep to improve their food security and livelihoods.

Community-based breeding program implementation is based on a shared participation between farmers, extension officers and scientists. Unlike the conventional hierarchical breeding approach, CBBP needs a detailed understanding of the community’s indigenous knowledge regarding breeding practices and objectives. After defining the production system and the breeding goal, animals recruited for CBBP are identified and this is followed by information collection related to phenotype, performance, pedigree, etc. This information contributes to estimate breeding values which are used to inform selection decisions. Depending on the breed and community preferences, the main traits that are included in these CBBPs are: growth traits, lamb survival, twining rate and fleece weight.

To date, the CBBPs in Ethiopia, through genetics and as a result of the improvement of management, have realized several achievements. For example, the negative selection has been reverted, as fast-growing lambs are being retained for breeding as opposed to being sold in markets (Gutu et al., 2015; Haile et al., 2020). Overall productivity has incrementally improved in many ways through more births (improvement of reproduction), bigger lambs at birth and weaning, reduction of mortality rates due to the combination of breeding with improved health care and feeding, better awareness about inbreeding and the need for improved breeding sires, formation of well-functioning cooperatives, general improvement of the performance of sheep and goats, and commercialization of breeding rams which is considered one of the major achievements of the CBBP (Gutu et al., 2015; Haile et al., 2020). Generally, CBBPs in Ethiopia have generated measurable genetic gains and impacted the livelihood of rural communities (Haile et al., 2020), though at a pilot scale. For these pilot programs to be taken to scale for larger populations of the indigenous sheep breeds, further optimization of the breeding programs is needed and more questions need to be answered.

In this study we addressed four research questions:

1) When CBBPs started in Ethiopia, selection was based on phenotype for breeding goal traits. This was so because, pedigree recording was rather difficult and enumerators who assist with collection of data did not have the skill to collect accurate data. However, as experience developed, selection was done based on estimated breeding values. Here we hypothesized that there is high correlation between rankings of sires based on phenotype and BLUP breeding values and such hypothesis needs to be tested using available datasets.

2) The main selection criteria of CBBP is the six-month weight, and through these past years, the selection was mainly based on this trait without taking in to account other traits. What we aim in this study is to assess the impact of continuous six-month weight selection on other productive and reproductive traits.

3) In any genetic improvement program, there is a need to track results and evaluate progress to make adjustments aimed at optimizing genetic gain and increasing farm profitability in the long term. One of the ways to perform such monitoring is through the assessment of genetic trends over time, which evaluates the changes brought about by the selection process. Another way would be to estimate genetic parameters which help to optimize programs. Furthermore, development of breeding objectives and effective genetic improvement programs require knowledge of the genetic variation among economically important traits, and accurate estimates of heritability, repeatability and genetic correlations of those traits. Genetic trends are usually calculated for the whole population. As selection in CBBP is based on sire selection, we also analyzed selection differential of sires.

4) Last but not least, it is known that intensive selection over years shapes the genome of sheep in the breeding program. Menz sheep are highly adapted to harsh environment in the highlands while Bonga are generally tolerant to many of the locally prevalent diseases (Haile et al., 2013). These two breeds were good candidates for CBBP and have potential for genetic improvement. Both breeds are raised in extensive production system with grazing as the main food source and thus natural and artificial selection are the evolutionary factors that have driven the genetic pool of both breeds. Based on the above considerations, one of the main objectives of our study was to assess the impact of artificial selection on the genetic pool of Menz and Bonga breeds through GWAS to understand the genetic basis of the local adaptation of the studied breeds and to decipher the genomic response caused by the long term selection in the framework of CBBP's.

The purpose of this study was to contribute to an understanding of the results of CBBP practices for two breeds (Bonga and Menz) of local Ethiopian sheep using the following four objectives:

1. Estimate correlation between animal ranking on phenotypic measurement and BLUP-EBV;
2. Assess the effect of selection based on six-month weight on other productive and reproductive traits;
3. Quantification of genetic trend for growth traits in the CBBPs;
4. To look for profound changes induced by CBBPs through genomic changes.

Literature review

Sheep production systems in Ethiopia

General overview of livestock production systems

Throughout their history, Ethiopians have constantly relied on livestock for their livelihood and different functions. Reports estimate that more than two thirds of the country population rely partly or entirely on livestock for their daily livelihood (FAO, 2019). This is concordant with the fact that Ethiopia, together with Sudan, is believed to have the largest livestock population in Africa (CSA 2013).

The livestock sector has been granting considerable benefits to the economy of the country and remains to be one of the most promising avenues for the government in its continuous efforts to pursue the economic development of the country. On a macro-economic scale and based on recent data, the livestock sector contributes up to 25.6% of agricultural GDP and 10.5% of total Ethiopian foreign exchange earnings (NBE, 2018). Beyond the fact that livestock species are important source of income, they also serve a wide variety of functions from cultural to subsistence purposes. Indeed, cattle, sheep and goats are source of food for the family household, transport, income generation, live savings and insurance during shocks (drought, crop failure) and are constantly present during religious and cultural events. Sales generated by animal products and live animals are the principal source of cash and means of savings, source of raw industrial material and foreign currency as well; Ethiopia being one of the main African countries exporting small ruminants to the Gulf countries mainly Saudi Arabia and the United Arab Emirates (Aklilu, Yacob & Catley, Andy. (2020)).

At the national level, sheep and goats account for about 90% of live animals/meat and 92% of skin and hide (FAO, 2019) export trade value. 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. They are also the drivers of crop production mainly as sources of drought power and provision of manure for soil fertility restoration. Dried animal manure is also used as fuel.

The diversity of Ethiopia's topography, climate and cultural conditions make it difficult to generalize about livestock production systems in the country (Alemayehu, 1985). Several approaches and criteria have been used to classify livestock production systems in the country and these criteria refer to the livestock species, climate, geography and topography, availability of resources particularly land, water and feed, the social factor, diseases' incidence, level of economic development, government economic support policies (inputs and services) and research support (Gizaw et al., 2011). More direct approaches have led to the identification of five main production systems based on integration of livestock with crop production, level of input and intensity of production, agro-ecology and market orientation. The emerging big clusters are the pastoral, agro-pastoral, mixed crop-livestock farming, urban and peri-urban systems (Solomon et al 2008).

Main sheep production systems

Sheep are an important component of most agricultural production systems in Ethiopia. Because of their high fertility, short generation interval, adaptation to harsh environment and their ability to produce when faced with limited feed resources, sheep are considered as more advantageous than other classes of livestock production (Gatenby, 2002) in generating investment and providing insurance (Tsedeke, 2007). Sheep have multipurpose functions providing meat, manure and as source of income (Mekuriaw et al., 2013). Moreover, they have special features, such as being small in size, which implies low initial investment in starting and expanding businesses and they can be efficiently integrated into marginal and small plots of land. Market openness is also much higher for sheep when compared for example to cattle (Nell AJ (2006)).

Sheep are produced under two major production systems; the sedentary mixed crop livestock production system and the nomadic pastoral or agropastoral system. Sheep husbandry is one of the few viable economic activities in pastoral areas. In highlands, crop production would nearly be impossible without livestock integration for draught power, the use of manure to benefit crops and to compensate for crop failures. In both systems, sheep play a significant role in stabilizing households and helps regional and federal governments to alleviate poverty.

The crop-based mixed farming system is often found in the highland agro-ecological zones (altitude between 1500-3000 masl). The mixed crop livestock system is found associated with different agricultural production systems. This diversity is reflected in the contribution of livestock to subsistence farming and to national economies as a whole. In the moist and sub-moist highland zones, livestock is owned by smallholders mixed sedentary farmers and the intensity of crop-livestock integration is variable. Meanwhile in humid and sub-humid zones, livestock is less important and crop production is the dominant activity. The grazing system of mixed species (cattle, sheep, goats…) is mainly practiced in such systems and sheep production remains secondary to crop production and it usually comprises small flock sizes to generate cash income from animal sales. Sheep production is characterized by low productivity due to nutritional stress and infestation by external and internal parasites. Small holder farmers allow their sheep flocks in a communal land for daytime grazing and depart during nighttime for enclosures. Flocks can be housed alone or with other species. The main feed resources for sheep are grazing on private and communal natural pasture, improved forage of oats grass (*Jerry oats*) and vetch (*Vicia sativa*) as well as supplementation with conventional and non-conventional feed types. Moreover, sheep have access to crop residues during harvesting times thus filling an important part of the annual feeding calendar. Farmers can also give supplementary feed (wheat bran, milling and local brewery by-products) to pregnant and nursing ewes, suckling lambs and castrated rams for fattening (Solomon et al., 2008)

Pastoralism occurs in the areas which are home to natural rangelands and is encountered in the arid and semi-arid lowland areas in the East, North-East, west and south of the country where the altitude is less than 1500 masl. Ethiopian pastoralists represent many different ethnic groups and are divided into the Somali pastoralists who constitute 53% of the pastoral population, followed by the Afar (29%), the Borana (10%) and the remaining 8% are found in Gambella and Tigray regions (Solomon et al., 2008)

Most small ruminants are concentrated in the pastoral and agropastoral areas and they constitute the major source of livestock products for the Ethiopian export market. However, herds in this system are multispecies and in some cases goats, cattle, sheep and camels co-exist. Since the main source of food is milk, pastoralists tend to keep large herds to ensure sufficient milk supply and generate income (IBC, 2004). This pastoral/agropastoral system is based on wide ranging communal grazing lands and pastoralist travel long distances in search of feed and water especially in the dry season. The pastoralists have an indigenous mechanism of coping with the problems of feed and water shortage during the dry season and during drought years. When grasses become depleted from the grazing land, they chop the leaves and branches of trees and feed to their animals. Acacia pods are also used as important sources of dry season feed. In the pastoral system, extensive livestock production including sheep is mostly the sole source of livelihood with little or no cropping (Tolera et Abebe 2007). Pastoralism is a way of life for 12 million Ethiopians who live in the remotest and most inaccessible areas of the country also in areas where the rainfall is unpredictable and erratic (The World Bank 2016). To adapt to these extreme climatic uncertainty and marginal landscapes of the dry land, pastoralists have sophisticated methods to optimize access to water and land, the use of different herd management strategies such as herd splitting and herd diversification to minimize the risk of livestock loss.

Other less dominant and secondary systems include urban/peri-urban and sheep/goat fattening and large-scale commercial livestock production (Gizaw et al., 2010). Gemeda et al. (2010) also reported the sheep-barley production system in Menz areas of Amhara region but such system can also be classified under the large mixed crop-livestock system. Urban and peri-urban production systems are developed in areas where the population density is high and agricultural land is shrinking due to urbanization around big cities like Addis Ababa and other regional towns. In this system, animals are kept in small to medium-sized farms. The main source of feed is both home-produced and purchased hay. In urban and peri-urban areas, there is a shortage of land and space due to expansion of towns, as a result crop production and rearing of large ruminants is likely to be more difficult than sheep rearing. Natural pasture, grass hay, by-product of local brewery making (Atela), by-products from legume grains (lentil, faba bean, field bean, check pea and *Lathyrus sativus*) processing, and wheat bran and Niger (Noug) seed cake are the major feed resources for this production system (Teklu, 2016)

Main sheep types and breeds in Ethiopia

The Ethiopian small ruminants' population is almost entirely composed of indigenous breeds (Table 1); a very small proportion of sheep population is represented by exotic breeds. The first introduction of exotic sheep breeds into Ethiopia trace back to 1944 when Merino sheep were introduced from Italy by an American aid organization. Other breeds like Romney, Corriedale, Hampshire, and Rambouillet were introduced from Kenya in 1967 and were kept at the government farm of Debre Berhan Sheep Breeding and Multiplication center (Getachew et al 2016). Dorper sheep was also introduced to the Somali region in the late 1980's. Awassi sheep were introduced from Israel in 1980; Awassi sheep have a similar phenotypic appearance to some local sheep, have improved growth performances and were well accepted by producers. These exotic sheep breeds were aimed for crossbreeding with local sheep, (Getachew et al., 2016) and the assessment revealed that growth and reproductive performance of crossbreds greatly vary and are influenced by many factors like management, location dam breed used for crossing, and breed composition level.

Table 1. Composition of the sheep population in Ethiopia according to origin

Origin	Number	%
Indigenous	30,612,976	99.72
Hybrid	66,277	0.22
Exotic	18,688	0.06
Total	30,697,941	100

Source: Computed from CSA (2009 E.C–2016/17) data.

There are about fourteen traditionally recognized sheep breeds named after their geographic location and/or the ethnic communities keeping them (Gizaw et al., 2011). The phenotypic traits are determined by ecological patterns while genetic characteristics are the results of interaction between historical patterns of migration, geographic isolation and interbreeding. One important attempt to categorize sheep in Ethiopia was published by Gizaw et al. (2007) and relying on the quantification of genetic differences among traditional sheep populations. The Bayesian cluster analysis using microsatellites markers and morphological divergence, gave a classification of Ethiopian sheep into six breed groups: short fat-tailed sheep, Washera, thin-tailed sheep, long fat-tailed sheep, Bonga, fat-rumped sheep and nine breeds (Table 2).

Table 2. Indigenous sheep types in Ethiopia

Breed group	Breed	Population	Tail type/shape
short fat-tailed sheep	Simien	Simien	Fatty and short
	Short fat tailed	Sekota, Farta, Tikur, Wollo, Menz	Fatty and short
Washera	Washera	Washera	Fatty and short
thin-tailed sheep	Gumz	Gumz	Thin and long
long fat-tailed sheep	Horro	Horro	Fatty and long
	Arsi	Arsi-Bale, Adilo	Fatty and long
Bonga	Bonga	Bonga	Fatty and long
Fat-rumped sheep	Afar	Afar	Fat rump with fat tail
	Black head Somali	Black head Somali	Fat rump/ tiny tail

Source: (Gizaw et al., 2007).

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 (Gizaw et al., 2007; Legese et al., 2008)

There is another categorization based on the ecological distribution, geographic proximity, tail type and shape of the various populations (Gizaw et al., 2008) which yielded four different groups namely the subalpine short fat tailed, highland long fat-tailed, lowland fat rumped and lowland thin tailed. The subalpine short fat tailed type is distributed over the central northern highland (2000-3600 masl) and includes seven sheep breeds (Menz, Sekota, Semien, Tikur, Wollo, Farta and Washera). These breeds are characterized by their short fat tail above the hocks, their small body size, coarse wool and low reproductive performance. The highland long-fat tailed type inhabits the south western mid highlands and exhibits a long fat tail which reaches the hocks; animals are large sized with short hair. The group includes Horro, Arsi-bale, Bonga and Adilo breeds. The lowland fat-rumped are mainly constituted by Afar and black head Somali (BHS) sheep. Finally, the lowland thin tailed is represented by only Gumz; animals are moderately prolific.

Sheep flocks' structure

Sheep flock structure by age group is a good indicator that can guide the use of targeted intervention options along the value chain. As indicated in Table 3, about 52% of sheep population in Ethiopia is two years and older, but about 26% of sheep population are under six months of age. About 11% are found in the age group six months to one year and one–two years 11%. This has been consistent over the last decade.

Table 3. Estimated numbers of sheep by sex and age in Ethiopia 2016/2017

Age	**Total**		**Male**		**Female**	
	Number	%	Number	%	Number	%
Total sheep	30,697,942	100	8,552,284	27.86	22,145,658	72.14
Under 6 months	8,050,597	26.23	3,912,226	12.74	4,138,371	13.48
6months – 1 year	3,330,041	10.85	1,460,876	4.76	1,869,165	6.09
1 year – under 2 years	3,352,705	10.92	1,238,304	4.03	2,114,401	6.89
2 years and older	15,964,599	52.01	1,940,878	6.32	14,023,721	45.68

Source: Computed from CSA (2009 E.C. 2016/17) data.

Table 4 illustrates how sheep over two years of age are utilized. More than 92% of sheep in this age category are kept for breeding purposes, while a small proportion (5%) of these animals is used for mutton production; and very few for milk and wool production.

Table 4. Purposes of keeping sheep aged two years and above in Ethiopia

Purpose of rearing	**%**
Used for Mutton	5
Used for wool	0.42
Used for breeding	92.3
Used for others	1.23

Source: Computed from CSA (2009 E.C. 2016/17) data.

Flock size at the household level is very small despite Ethiopia's large stock numbers. More than 62% of households own fewer than five sheep/goats and more than 87% of households own fewer than nine sheep/goat; the common holding is two sheep or two goats. Households may own both sheep and goats (Table 5).

Table 5. Number of holdings by flock size of sheep and goat in Ethiopia – 2016/17

Size of flock	Percentage of holdings of sheep	Percentage of holdings of goats
1-4 heads	61	57
5-9 heads	26	26
10-49 head	11	15
≥ 50	2	2

Source: Computed from CSA (2009 E.C. 2016/17) data.

Such a dispersion of the sheep as well as goat populations clearly indicate that small ruminants are mainly kept for subsistence. The small size of the flocks and their scattering across holdings, regions and geographies is one of the main challenges to design and implement development programs like mass vaccination and breeding. Any program for the development of the small ruminant sector in Ethiopia requires specific and novel approaches.

Growth performance of sheep in Ethiopia

Growth in animals is defined by an increase in body size by differentiation of body cells (Bathaei and Leroy, 1996). Growth-rate and body size in conjunction with changes in body composition are of great economic importance for efficient production of meat animals. Growth performance is a key production indicator which contributes to the determination of the overall productivity of the flock and the economic return from small ruminants' enterprises. In most sheep production systems, growth performance is often at the center of genetic improvement and management schemes. Growth performance has also implications for the reproductive efficiency of sheep. Fast growth rate entails reaching market weight early and brings a quicker income to the farmer and also allows sheep to breed early and contribute more lambs during their productive lifetime.

While heredity dictates the maximum amount of growth and development (commonly described by the genetic potential of animals), nutrition along with other environmental factors govern the actual rate of growth and extent to which development is attained. Nevertheless, any additional input that is required for normal physiological needs may not induce growth beyond the genetic potential of the animal. Growth rate of lambs or kids, particularly during the early stages of growth, is strongly influenced by breed, milk yield of the ewe, the environment under which the animals are maintained including the availability of adequate feed supply in terms of both quantity and quality (Awgichew, 2000; Taye et al, 2009). Parity, pre-lambing weight of the dam, type of birth, sex, season and month of birth are also known to be factors of variation of growth performances of small ruminants.

Birth weight

Recording of lamb birth weight can be important in breeding programs. Birth weight (BWT) can be determinant of lamb mortality; lambs with low birth weight experience higher levels of postnatal mortality, due to problems associated with low milk intake and hypothermia. Tibbo (2006) also reported that lambs born with lighter birth weight had high mortality rate. Conversely, lambs with high birth weights are associated with lambing difficulties (dystocia) which can lead to the death of the lamb, the ewe or both. Haile et al. (2020) reported no increase in birth weight of Bonga and

Horro breeds and claimed that this is particularly advantageous because improvement in this trait beyond a certain level may be associated with dystocia and loss of productivity. It is therefore important to be careful when considering growth traits that should be included in the breeding objectives.

Many studies have shown weak correlations between birth weight and later weights (e.g. Gürsoy et al., 1995; Duguma et al., 2002). However, other studies have shown that birth weight is also one of the important factors reported to influence the survival and pre weaning growth of the young small ruminants (Abegaz et al., 2000). According to E. Mukasa Mugerwa et al. (1991), there was a positive correlation between weaning weight and birth weight for Menz sheep of Ethiopian highlands. But weaker correlations were reported with later ages (Muir et al., 2000; Hanford et al., 2003). The higher weaning weight might be explained by the study of Petrovic et al. (2013) who indicated that higher body weight of lambs at birth gives greater possible speed for growth in early months of age, in contrast to lambs with less weight and thus less potential of growth. Ata and Hamed (2015) also stated that lambs born with greater weight at birth had a fast growth capacity and have higher mature body weight (Kasahun, 2000).

Demeke et al. (2004) compared the growth performance of the indigenous Menz breed and its crosses with Corriedale and Awassi breeds. They found that the effect of genotype was an important source of variation for body weight at all ages. In particular, it is well documented that birth weight of lambs is different among breeds (Yimam et al., 2004; Mesfin et al., 2014). Other research reports indicate that the birth weight of Ethiopian small ruminants is influenced by several factors like genotype, sex of lamb, birth type, season of birth, age of dam, nutritional conditions and production system (Wilson 1991; Mukasa-Mugerwa 1994; Awgichew 2000; Demeke et al., 2004; Berhan and Eik 2006). Lambs which are heavier at birth are usually singles or are those produced by ewes with larger body size and good feeding conditions. Male lambs are heavier than female lambs at birth and several researchers (Kassahun, 2000; Tibbo, 2006; Taye et al., 2009) have widely documented similar results. The differences in birth weights observed between the sexes might be due to differences in testosterone secretion between males and females. However, sexual dimorphism in body weight is more important during post-weaning than the pre-weaning period.

Dagnew et al. (2018) reported that the type of birth also has significant effect on birth weight, and commonly single born lambs (Gumuz breed) were heavier than their twin (3.42±0.04 kg versus 3.22±0.07 kg) born contemporaries (Table 6). This could be due to in-utero flow of nutriments through the placenta to the growing fetuses particularly during the last third of pregnancy. Other authors have also obtained similar results for Gumuz (Solomon et al., 2011) and Washera (Taye et al., 2009; Shigidafe et al., 2013) sheep. Lambs born in the wet season were significantly heavier than those born in the dry seasons. The significant influence of season on birth weight of lambs in the same study of Dagnew et al. (2018) was consistent with the results from previous studies (El-Hage et al., 2001; Gbangboche et al., 2011). The heavier birth weight during the wet season was attributed to the presence of feed due to short rainy season during pregnancy period and the beneficial effects on the nutrition of the dam and growth of its fetus.

Table 6. Body weight in kg at different ages of indigenous sheep in Ethiopia

Breed/type	BWT	WWT	SMWT	YWT	Reference
Adilo	2.29	11.18	-	-	Getahun 2008
Afar	2.7+0.02	11.5+0.08	17.2 +0.04	26.6+0.14	Yacob 2008
Arsi bale	2.89	12.23	-	-	Getahun 2008
BHS	2.5+0.03	11.3+0.12	16.4 +0.10	23.1+0.22	Yacob 2008
Bonga	2.86	11.6	-	-	Belete 2006
Gumuz	2.79+0.02	12.6+0.24	-		Abegaz 2007
Horro	2.34+0.05	9.9+0.4	11.8 +0.30	17.1+1.2	Tibbo 2006
Horro	2.6	12	-	24	Abegaz 2002
Menz	2.09+0.03	9.1+0.2	10.4 +0.22	17.3+0.4	Tibbo 2006
Menz	2.5	9.5	-	-	Demeke et al 2004
Menz	2.4	8.3	12.2	16.4	Niftalem 1990
Simien	2.97+0.03	11.76+0.16	15.78	-	Tegegne et al 2012
Washera	2.69+0.02	12.42+0.1	-	23.47+0.68	Mengistie et al 2010
Washera	2.83	13.3	19.6	-	DBARC 2006

BHS: black head Somali, BWT: birth weight, WWT: weaning weight, SMWT: six months weight, YWT: yearling weight.

Weaning weight (WWT) and Six months weight (SMWT)

Weaning is a crucial time in the management of ewes and lambs. Weaning is when lambs are no longer allowed to nurse their dams or they are no longer fed a milk diet. With the exception of artificially-reared lambs, weaning also includes separation from the dam. From the milk diet, lambs may consume forage, grain-based, or mixed diets. Weaning weight is a trait of great economic importance in meat sheep production since it is influenced by the survival of the lamb and its growth in the first weeks of its life and as such, it may determine the level of offtake from the flocks (Taye et al., 2009). Within breed, birth type and sex are sources of variation in lamb pre-weaning growth rate (Taye et al., 2009). The indication is that lambs heavier at birth have larger adult weight and higher growth capacity (Awgichew, 2000; Taye et al., 2009). Parity can also affect pre-weaning growth rate, from birth to 30 days of age. Lambs from second and third parity dams grew better than first and fifth parities (Tibbo, 2006).

For most indigenous Ethiopian sheep breeds, weaning weight (WW) often corresponds to the weight at the age of 3 months. Average figures reported by several researchers are summarized in Table 6. Data shows variation between 8 and 13 kg for WWT for most sheep breeds in Ethiopia. One of the main reasons for the variations in WWT are related to differences in growth potential between breeds (Gizaw 2002 Hassen et al., 2003, Lakew et al., 2014). Such differences were also shown to be related to differences in birth weight. Yilmaz (2007) has reported a positive correlation between birth weight and subsequent live body weight development in sheep. Similarly, in the work of Tibbo (2006) and Lakew et al. (2014), it was indicated that lambs heavier at birth grew faster than light weight lambs.

Weaning weight is also known to be affected by the mothering ability of the dam (Kassahun 2000). At early growth phases, there is more dependency on the milk production of the ewe as the lamb meets most of its requirement through suckling rather than on forage intake. A similar trend was observed (Laes-Fettback and Peters, 1995) for Egyptian goats in which breed and mothering ability of the doe have significantly influenced the pre-weaning daily weight gain. The environment under which the animals are maintained including the availability of adequate feed supply in terms of both quantity and quality are also important in determining levels of weaning weights (Bathaei et al., 1997).

Weaning weight is influenced by season of birth, sex of lamb and type of birth (Kassahun, 2000; Gbangboche et al., 2006); ram lambs and single born ones were heavier than their counterparts. Parity and postpartum ewe body weight had significantly influenced weaning weight. According to Frisch and Vercoe (1987), it is assumed that high growth potential is associated with enhanced resistance to environmental stressors (climatic factors, disease prevalence, etc.) and the nature of the relationship between the two factors need to be determined in order to enhance development of breeds that are tolerant or resistant to environmental stresses and which are economically productive. This could be realized through better management practices and selection of animals based on their weaning weight. The use of weaning weight as a selection index is reported by Van Wyk et al. (1993). They have stated that the animal's weaning weight indicates its value at the desired marketing age. Year of birth significantly affected the weaning and six months body weights as reported by Poonia et al. (1984) and Sharma et al. (1991). The year differences could be due to the varying availability of good fodder which directly affect the health, ewes milk production and thus the growth rate of the suckling lambs.

Sex of lamb had significant effect on body weights at weaning and six months age. Male lambs were significantly heavier at weaning and at six months of age (Haile et al., 2020 and Sharma et al. 2004). Table 7 shows that for both Bonga and Horro, the males were heavier than females at birth and at 6 months of age. In Menz, although males were heavier than females at birth, this difference was not significant (P > 0.05) at 6 months. Many reports in the literature (e.g. Tibbo, 2006; Saghi et al., 2007) concur with the observations that favor male sheep and could be related to inherent physiological differences in the growth in both sexes. Regression of dams' weight at lambing was observed to have significant effect on weaning and six-month body weights of their offspring (Dangi and Poonia 2006). Heavier lambs are born out of heavier dams and tend to maintain their vigor and growth. Similar findings were reported by Poonia et al. (1984) and Singh et al. (1987).

Table 7. Least squares mean (kg) for effects of lamb sex and birth type on birth weight (BWT) and 6-months weight (SMW) for Bonga and Horro sheep

	Sex		**Birth type**		
Site	**Male**	**Female**	**1**	**2**	**3**
Bonga					
BWT	3.34	3.24	3.57	3.28	3.03
SMWT	22.9	20.3	23.4	21.3	20.3
Horro					
BWT	2.55	2.47	2.66	2.53	2.34

SMWT	16.7	16.1	17.3	15.9	16.0

Source: Haile et al. (2020). 1,2 and 3 refers to single, twin and triples respectively.

Yearling weight YWT

Weight at one year of age has little interests for selection of sheep breeds. Indeed, lambs from most sheep breeds reach the economic weight (slaughter age) at much younger ages. For this reason, genetic parameters for weight at 12 months of age such us heritability are rarely reported in literature. Animals reaching 12 months are about to initiate their reproductive life and one would assume that weight at one year of age is more relevant in linking body development and yearling reproductive efficiency. Taking the example of the Barbarine sheep thriving under harsh, dry conditions of North Africa, it was shown that changes in live weight of young growing females leading to weight at 12 months are more important in determining the level of reproductive performance than the absolute weight at 12 months (Ben Salem et al., 2009). Some data on weight at 12 months is available for Menz sheep and shows very important effects of year and flock on the phenotypic variability (Gizaw et al., 2007). According to the authors, the fluctuations are not related to genetic trends in breeding values, but most likely there was a high management input and\or favorable environment in particular years. It was demonstrated that there has been a significant genetic improvement in weight at 12 months in response to selection. The same authors also demonstrated that high positive genetic correlations were found between weight at 3 and 6 months with the weight at 12 months.

Al Subaihi et al. (2018) reported a high genetic correlation between weight at SMWT and YWT (0.94) for Omani sheep in Oman. This shows that these traits are genetically controlled by the same set of additive genes. This also means that if selection is targeted at yearling weight, farmers could cull animals based on their weight at 6 months without having to wait for recording yearling weight. Such culling could save valuable time and resources at the level of the farm without negatively influencing the overall genetic progress associated with any selective breeding program in place.

Reproductive performances of indigenous sheep in Ethiopia

The reproductive performance determines the production efficiency. Levels of reproductive performance are often the main determinant of biological and economic efficiency of animal production in the tropics whether under intensive or extensive production systems. Fertility is one of the most important parameters of sheep productivity; the litter size per lambing is a good indicator of both the genetic potential of the breed for prolificacy and the nutritional status while lambing interval and age at first lambing indicate the non-seasonal potential and the sexual maturity of the breed, respectively and are also economically important traits in sheep production enterprises (Gizaw, 2002). Lifetime productivity of the ewe is a composite trait related to longevity. Biological and economic efficiency of sheep production enterprises are both improved with high levels of flock reproduction rate; in other words, biological efficiency of sheep with regards meat, milk and wool production is conditioned by reproductive performances. Reproductive traits have low heritability, discrete phenotypic expression and are expressed only in sexually mature ewes. Low heritability of reproductive traits is probably due to the greater proportional influence of environmental effects as well as little genetic variability for fertility, litter size, lamb survival and lambing frequency and other reproductive traits (Turner and Young, 1969). Several studies have revealed the existence of differences in reproductive performances between indigenous sheeps in Ethiopia. Finding out actual levels of reproductive and productive performances and their variations between and within small ruminant populations and management systems would therefore be important to identify options for improvement.

Conception rates and fertility

Fertility is one of the most important parameters of sheep productivity, for any product yield to be recorded, females should first give birth. Fertility is commonly defined by the proportion of females successfully lambing in comparison to the number of ewes presented to rams during the mating season. At the individual level, fertility is usually expressed as a binomial variable taking the values 1 or 0. Genetic factors and all environmental factors whether associated to the animal (age of the dam, parity, weight at mating and dynamic of weight) or the environment itself (feeding, changes in photoperiod, management standards at the flock level, health status) are all known to be important factors of variation of fertility in sheep. It is further important to point out that fertility of the female is also conditioned by the fertility of the rams, their libido and the males to female ratio in the flock.

Nutrition is one of the most important factors that influence the fertility of sheep. Fertility is usually unaffected under normal feeding conditions. However, severe undernutrition may cause ovulatory cycles to stop and induces perturbations in the oestrus cycle all of which negatively affect fertility. Supplementary feeding prior to mating (flushing effect) is a well-known management practice in sheep flocks and is aimed at improving conception rates and causing a moderate increase in ovulation rate and litter size.

Research shows that lambing rates, which is another expression of fertility rate (ewes lambing/ewes mated), are impacted by breed. For example, In Menz ewes, Mukasa-Mugerwa and Lahlou-Kassi (1995) reported high conception rates (>= 90%) (Table 8) and 81 percent lambing rate compared to 76 percent experienced by Horro ewes (Berhan and Van Arendonk, 2006). Differences between conception and lambing rates can be explained by early and late embryo losses. There is a lack of information on reproductive losses in the literature on Ethiopian sheep breeds and one study in Menz sheep reported that abortion rates are high and variable (3.7 to 40 percent) among breeding females (Abassa, 1995).

Conception and lambing rates in Horro ewes were found to increase with ewe parity and ewe weight at mating, up to a certain limit (Gizaw et al, 2002). Indeed, extremely high ewe weights at mating and advanced ages of the ewes were shown to be associated with declines in conception rates. On the other hand, under weight of ewes at mating (as a result of poor nutrition) depresses fertility.

Rekik et al. (2015), reported that slaughtering of pregnant ewes in the highlands also contributes to depressed conception rates. Most farmers in the Ethiopian highlands sell their sheep to generate income. In a related study, Mukasa-Mugerwa and Tekelye (1988) found that 70.1 percent of the females slaughtered for market consumption were pregnant and 24 percent were carrying twins. A high proportion of these females were pregnant in their third to fifth month of gestation.

Table 8. Conception rate of Ethiopian indigenous sheep breeds/types

Breed/type	Conception rate (%)	Reference
Horro	91.6	Berhan and Van Arendonk, 2006
Afar	82	Yebrah 2008
Black head Somali	63	Fekerte 2008
Menz	>90	Mukasa-Mugerwa and Lahlou-Kassi 1995
Arsi-bale	54.04	Deribe 2009

Age at first lambing (AFL)

Age at first lambing is one of the factors influencing lifetime reproduction and is thus recommended for inclusion in the selection program (Schoeman, 1991). Early sexual maturity is a desirable trait in intensive production systems because it allows producers to cull infertile animals earlier and to distribute the maintenance costs of the ewe flock over a larger number of lambs (Kutluca and Emsen, 2018). Early maturing females are known to have a relatively long and fruitful reproductive life, resulting in more offspring produced and faster return on investment.

Among the most important parameters affecting AFL, genotype (breed effect) and various management components are reported below. Management, regarding whether breeding is controlled or uncontrolled tends to affect the age at first parturition (Wilson 1989). It is also observed that AFL is commonly longer in sheep that are bred in controlled breeding systems compared with sheep reared under uncontrolled systems, where rams are free to run with females and serve them at the earliest possible display of estrus. Poor nutrition and disease can also lead to delayed AFL through limiting early animal growth and maturation of the reproductive axis. AFL is also affected by season of lambing; lambs born during the rainy season attain their puberty at earlier age. Year and season of birth in which the ewe lamb was born influence age at first lambing through their effect on feed supply and quality. In temperate latitudes where there is a clear distinction between breeding and anoestrus seasons, it is well established that attainment of puberty and AFL significantly differ according to the season of birth and the influence of photoperiod. The type of birth of the ewe significantly affects the age at which the maiden ewe first lambs. Age of the dam is another factor of variation; offspring of young and old ewes mature later than those from dams in the intermediate age group (Wilson, 1984).

Age at first lambing can be recorded easily in a farmer's flock and at farm levels. There is a big variation among production systems and breeds for this trait (12-24 months). Profitability of the flocks and lifetime productivity are reduced if AFL is delayed beyond 2 years of age. The data on average AFL for most of indigenous sheep in Ethiopia ranges between 11 and 16 months (Table 9). Ethiopian sheep breeds have acceptable age ranges for first lambing comparable or slightly delayed compared to temperate breeds that reach puberty at the age range of 5-12 months. However, this finding should be treated carefully since there are many other factors governing the age at puberty and the age at first lambing. For example, age at first lambing for Menz Sheep breed ranges between 15 and 17.4 months (Gautsch 1987, Abebe 1999 and Getachew et al., 2013). The reported average ages of lambing for Washera were 15.5 and 15.47 months as reported by Mengistie et al. (2011) and Taye (2008), respectively. Age at first lambing is usually delayed in animals living in harsh environments. For the pastoral black head Somali breed, AFL is nearly 24 months.

Table 9. Age at first lambing of Ethiopian indigenous sheep breeds/type

Breed/Type	**AFL**	**Reference**
Local Sheep in Adaa Liban	17.07	Samuel (2005)
Thin-tailed sheep	13.70	Mukasa-Mugerwa et al. (1986)
Adilo	12.4	Fsahatsion et al. (2013)
Adilo	14.6	Getahun (2008)
Wollo	14.5	Getachew et al. (2013)
Menz	16.5	Gautsch (1987)
Menz	17.41	Getachew et al. (2013)
Menz	15.22	Abebe (1999)
Washera	15.5	Mengistie, et al. (2011)
Washera	15.47	Taye (2008)
Gumuz	13.76	Abegaz, et al. (2011)
Horro	10-11	Dhaba, et al. (2013)
Horro	13.3	Zewdu (2008)
Arsi-bale	12.4-12.7	Deribe, et al. (2009)
Bonga	14.9	Zewdu (2008)
Bonga	13	Belete (2009)
Afar	13.5	Tesfaye et al. (2008)
Black head Somali	23.6	Fekerte (2008)

Litter size (LS)

Litter size, the number of lambs born per parturition, is one of the major determinants of reproductive efficiency and of the productivity of a dam and thereby the profitability of a farm. Positive relationships between LS and age and LS and parity have been noted. Dibissa (2000) reported that ewes in a higher parity had higher litter sizes than ewes in a lower parity; litter sizes increased with parity from 1.26 at the first parity to 1.44 for parities five and above. Age of the dam can have significant effect on number of lambs per lambing. Litter size is reported to increase until the age of five years or fourth parity and decreases slightly thereafter (Wilson et al., 1984, Berhanu and Haile, 2009). However, other reports show peak prolificacy is generally achieved between 4 and 8 years of age.

Litter size is a trait that largely depends on ovulation rate and is affected by the number of fertilized oocytes. The higher the ovulation rate, the more oocytes will be available for fertilization during estrous and the possibility of the dam to yield large litters. Litter size can also be presented as being the difference between ovulation rate and total reproductive wastages which are the sum of unfertilized ova and embryonic and fetal losses (Gatenby, 2002). Ovulation rate is dependent on breed, level of nutrition, season and age (Haresign, 1985). Sheep breeds are usually classified as low, moderate and high prolific breeds depending on their inherent ovulation rate (Table 10). With reference to West African sheep breeds, average litter size was estimated at 1.24 ± 0.33 lambs (Musa et al., 2005). Also, litter size in sub-Saharan African sheep was 1.01 to 1.487 (ILCA 1995) with Arab sheep in the semi-arid zone of Chad showing the lowest values. It is also affected to a large extent by ewe body weight at mating which itself is linked to nutrition. Nutrition is one of the main factors affecting ovulation rate and poor nutrition during service period leads to reduced ovulation rates and increased embryonic mortality and consequently depressed litter size.

Table 10. Litter size of Ethiopian indigenous sheep breeds/types

Breed/type	LS	Management	Source
Adilo	1.42	Traditional	Getahun et al. (2008)
Adilo	1.3	On farm	Fsahatsion et al. (2013)
Arsi-bale	1.2	Traditional	Getahun et al. (2008)
Arsi-bale	1.52	On farm	Deribe (2009)
Arsi bale	1.7	Traditional	Tsedeke (2007)
Menz	1.02	On farm	Nitfalem (1990)
Menz	1.14	On farm	Agyemang et al. (1985)
Menz	1.03	On farm	Abebe, M. (1999)
Menz	1.13	On station	Mukasa-Mugerwa (2002)
Menz	1.1	Traditional	Dibissa (2000)
Menz	1.08	NA	Gautsch (1987)
Washera	1.1	Traditional	Taye (2008)
Washera	1.1	On farm	Mengistie et al. (2011)
Bonga	1.4	Traditional	Belete (2009)
Bonga	1.36	On farm	Zewdu et al. (2009)
Horro	1.4	On farm	Zewdu et al. (2009)
Horro	1.34	On station	Abegaz et al. (2000)
Horro	1.21	On farm	Belay and Aynalem (2009)
Horro	1.34	On station	Abegaz et al. (2002)
Black head Somali	1.04	On station	Tibbo (2006)
Black head Somali	1.01	On farm	Aden (2003)
Gumz	1.17	On farm	Abegaz et al. (2011)
Afar	1.03	NA	Wilson (1982)
Afar	1.05	NA	Ibrahim (1998)
Thin tailed	1.30	NA	Mukasa-Mugerwa (1998)

The significant effect of the farm management has been described in several studies (Anel, et al., 2005, Paulenz et al., 2002), and the percentage of ewes having twins in tropical sheep breeds, generally ranges between 0 and 50% (Gatenby, 1986) while under traditional management conditions, the percentage tends to fall below 10%. Table 10 summarizes levels of LS for Ethiopian sheep breeds in the literature. According to Zewdu (2008), breed differences for LS are also very wide. Twinning rates of 39.9 and 36% corresponding to litter sizes of 1.40 and 1.36 were obtained for Bonga and Horro sheep breeds, respectively. However, for Menz sheep, LS's are smaller than the values documented for most of the indigenous sheep in Ethiopia. Low twining rate was reported for both Menz (1.03-1.13; Abebe 1999, Mukasa-Mugerwa et al. 2002) and Afar sheep (1.03; Wilson, 1984) and it appears to be one mechanism of adaptation to the harsh environmental conditions and to the seasonal scarcity of feed resources.

Effect of body condition score (BCS), live weight (static effects) and changes in BCS and live weight (dynamic effects) before mating, during mating and after mating period, on LS of different breeds of sheep in the different rearing systems were studied (Cam et al., 2010; Aliyari et al., 2012; Ibrahim, 1998) and point out to an increase of 10% to 40% in litter size by improving the nutritional management of the pre-mating ewe or by treatment with gonadotropins. According to Abegaz et al. (2002) and with respect to weight of Horro ewes at mating, litter size increased by 2.5% for each kilogram increase in weight at mating time, hence suggesting the importance of breed and interactions with nutritional and physiological conditions and its impact on reproductive efficiency as measured by LS in this case (Gunn, 1983; Koycegiz et al., 2009).

Lambing interval (LI)

This refers to the number of days between successive parturitions and it is only relevant in flocks where rams and ewes are kept together all year around under a free mating regime. Through the provision of satisfactory nutrition and proper management in the tropics where sheep breeds have an attenuated reproductive seasonality due to photoperiod, it is practically possible to attain three lambings in two years (Agyemang et al., 1985; Gautsch et al., 1987). For this to be realized, lambing/kidding interval should not exceed 8 months (245 days). Lambing interval has an important influence on a sheep production enterprise. Lambing interval is one of the main components of reproductive performance which is affected by nutrition and early weaning. Tests on an eight-month lambing interval under controlled mating in Horro sheep have shown acceptable results in both ewe and lamb performance (Abegaz et al., 2000). The LI has three phases: the gestation period, the postpartum anoestrus period and the service interval. As the major component of lambing interval is post-partum interval (PPI), accelerated lambing or kidding revolves around manipulating PPI because a shorter PPI will result in a shorter parturition interval.

Genetic and environmental differences led to wide variation of lambing interval among different sheep breeds. This interval is influenced by several factors, such as previous litter size, parity, suckling intensity (number of lambs suckling and duration) and lambing season. Mengiste (2008) working on Washera sheep reported shorter lambing interval for ewes lambing during the wet rather than the dry season of the year. This may be related to more forage availability and a better postpartum nutritional status of the ewes lambing during the wet season (Magaña-Monforte et al. 2013). As parity increases, the lambing interval showed a decreasing trend in Washera ewes (Taye, 2008). Management practices and restrictions on mating also prolong the interval between lambing (Suleiman et al., 1990). Oliveira et al. (2014), indicated that LI extends (linear effect) with the age of weaning, and it is believed that the lack of early weaning in extensive systems is the cause of long LI's. Another factor that influences LI is the ewe's age; as ewe's age increases until the age of 8 years, the LI also increases. Beyond this age, LI become irregular and with wide variability (Aguirre et al., 2016). The litter size of the previous lambing can have an effect on LI, as twins or triplets have more milk demand. Indeed, the ewe is stimulated to produce more milk for its lambs, so she draws on her body reserves, hence depressing body condition and resumption of ovarian activity is delayed (Magaña-Monforte et al. 2013). It appears also that ewes with higher post –partum weights showed reduced lambing intervals (Gautsch, 1987). Coop and Devendra (1982) stated that frequent lambing put more stress on the ewe unless provided with appropriate diet. In the Shale type sheep, the interval following the birth of male lamb was on average longer than that following female animal (Wilson and Durkin, 1988). Lambing interval for different Ethiopian sheep breeds is summarized in Table 11.

Table 11. Lambing interval of Ethiopian indigenous sheep breeds/types

Breed/type	Lambing Interval	Source
Adilo	7.3	Getahun et al. (2008)
Arsi-bale	7.8	Tesfaye (2008)
Arsi-bale	9.1	Deribe (2009), Tsedeke (2007)
Menz	8.5	Tesfaye (2008)
Menz	11.9	Niftalem (1990)
Menz	8.4	Mukasa-Mugerwa (2002)
Menz	8.6	Getachew et al. (2013)
Menz	8.5	Dibissa (2000)
Washera	9.03	Mengistie et al. (2011)
Washera	9.5	Taye (2008)
Bonga	8.0	Belete (2009)
Bonga	8.9 ± 2.1	Zewdu et al. (2009)
Horro	9-10	Dhaba et al. (2013)
Horro	8.7	Belay et al. (2009)
Horro	7.8 ± 2.4	Zewdu et al. (2009)
Black head Somali	10.46	Fikrte (2008)
Black head Somali	11.2	Aden (2003)
Gumz	6.64 ± 1.13	Solomon (2007)
Gumz	6.6	Abegaz et al. (2011)
Afar	9.01	Tesfaye (2008)

Reports of lambing interval of local sheep in Ethiopia from field studies are highly variable and ranged from 6.6 to 12 (Table 11). Menz, Washera and other local breeds were reported by many authors to give 3 lambing within 2 years (Taye 2008; Mukasa-Mugerwa *et al.,* 2002). According to Solomon (2007), Gumuz breed had an average lambing interval of 6.64 ±1.13 months so the breed can also produce three lambing in two years even under the traditional management system while Belete (2009) and Zewdu (2008) indicated that lambing intervals of Bonga and Horro ewes were around 8 and 7.8 ± 2.4 months respectively. Among other breeds of sheep in Ethiopia that had short lambing intervals were Menz (8.5 months) and Afar sheep (9 months) (Getachew et al. 2008). Similar to Ethiopian sheep, three lambing in two years are reported for West African Dwarf, Djallonke, sheep (Gbangboche et al 2006) and Balochi sheep in Pakistan (Jahan et al 2013).

Sheep breeding programs in Ethiopia

Livestock productivity can be increased through genetic improvement. Strategies for genetic improvement of livestock mainly involve the decision on the use of genetic variation within a breed (selective breeding) or between breeds (crossbreeding) (FAO, 2007b; Philipsson, 2000).

Crossbreeding

To improve sheep productivity, crossbreeding with exotic breeds is considered as the most rapid way of improving levels of performance of indigenous sheep breeds due to its quick benefits in terms of breed complementarity and heterosis effects (Leymaster, 2002; Hayes et al. 2009, Yimam, 2004). Different governmental (research organizations and universities), non-governmental institutions (example FARM AFRICA) and projects (examples Chilalo Agricultural Development Unit (CADU) and Ethiopia Sheep and Goat Productivity Improvement Project (ESGPIP)) in Ethiopia focused on importing exotic breeds for cross-breeding since the early 1940s (Tibbo, 2006; Solomon et al., 2013; Getachew et al., 2016). These have included importing exotic sheep breeds such as Bleu du Maine, Merino, Rambouillet, Romney, Hampshire, Corriedale, Dorper and Awassi sheep as well as Saanen goats. After the importation of these improved genotypes, comes the multiplication of the introduced purebreds, the crossbreeding with indigenous sheep and finally the distribution of both crossbred and pure exotic animals to sheep producers. To accomplish the crossbreeding program, the Ethiopian Sheep and Goat Productivity Improvement Program (ESGPIP) took the responsibility for importation of improved genotypes, multiplication of purebreds, crossing with indigenous sheep and distribution of both crossbred and pure exotic animals to sheep producers. Four nucleus and ten Breeding, Evaluation and Distribution (BED) sites were established in different regions of Ethiopia (Ayichew et al. 2019).

The first introduction of exotic sheep breeds into Ethiopia dates back to 1944 when Merino sheep were introduced from Italy by an American aid organization and were maintained at Entoto sheep breeding station. Romney, Corriedale, Hampshire, and Rambouillet were introduced from Kenya in 1967 and were kept at the government farm Debre Berhan Sheep Breeding and Multiplication Center (DBSBMC) which was located at Debre Berhan town. The introduction of these breeds was aimed at crossing them with local Menz sheep in order to supply wool for the Debre Berhan blanket factory established in 1967. Nevertheless, they were not preferred by farmers due to their physical characteristics like the face, which was covered with hair, absence of horn in males, thin tail and fatty nature of wool making it difficult to spin in the traditional way. The program was terminated and none of the exotic breeds can be traced except for a few Corriedale animals in a South Wollo village with a high contribution from local breeds.

Awassi sheep were introduced from Israel and kept at DBSBMC and Amed Guya Sheep Breeding and Multiplication Center (AGSBMC). Awassi breed has been well accepted by Ethiopian farmers due to its similar physical appearance to that of local breeds and was crossed with Menz dams. In the first four years of Awassi ram distribution, individual smallholder farmers were targeted. While the program has a clear crossbreeding scheme for the multiplication of crossbred rams in the multiplication ranches, the strategy for dissemination of genetic improvement to villages and sustaining crossbreeding at the village level is not well defined. Extensive and indiscriminate distribution of crossbred rams across the country for the last three decades yielded virtually no impact on the sheep industry (Gizaw and Tesfaye 2009). There have also been repeated outbreaks of viral diseases (*Maedi visna*) that forced the elimination of purebred Awassi and crossbreds.

Dorper sheep were introduced into the Jijiga area (Somali Region) in the late 1980s. On-station performance of crossbred was very good however there was no on-farm evaluation during that time (Awgichew and Gipson, 2009). All sheep were looted from the ranch during the political instability in 1991 (Awgichew and Gipson, 2009).

Crossbreeding among indigenous breeds has also been practiced at Debre Birhan Agriculture Research Center (DBARC) as an alternative to the use of exotic genotypes for crossbreeding. Indigenous Washera rams were distributed in the highlands of North Shewa, South Wollo, North Wollo, and Gondar areas (ANRSBoARD, 2006). In 2005, a village-based Farta × Washera sheep crossbreeding program has been started (Mekuriaw et al., 2013) with the aim to increase productivity of medium sized indigenous Farta (Gizaw et al., 2008a) by crossing or introducing male and females of indigenous Washera sheep.

In developing countries, the adoption of new livestock technologies including crossbreeding programs has been low due to lack of adaptation of the crossbreds to harsh production environments (i.e. in terms of climate, diseases and feed availability) and low complementary socio-economic support in some regions (Iñiguez, 2011). The proportion of exotic and crossbred sheep populations in Ethiopia remains low, only 0.06% (CSA, 2016-2017), indicating that research and development efforts of sheep crossbreeding in Ethiopia did not deliver the anticipated benefit to smallholder farmers so far. There is no comprehensive study showing the performance of crossbreds, both biologically and economically, to substantiate the argument on the benefit of sheep crossbreeding for smallholder farmers. Some studies of Solomon et al. (2013) and Getachew et al. (2010) indicated that in sheep, the impact of decades of crossbreeding is negligible. This has been due to poor involvement of stakeholders and implementing livestock improvement programs without taking into consideration the needs of farmers (Tibbo, 2006; Gemeda et al., 2010 and Tadelle et al., 2012). The distribution of the improved genotypes of these programs was indiscriminate and unplanned, resulting in failure of the breeding programs and threatened to dilute the sheep genetic diversity in the country (Solomon et al., 2011). One of the reasons why the production of crossbred animals has been occasionally reported to be lower than expected is that those animals have not been offered the possibility to express their genetic production potential. For instance, Hassen *et al*. (2003) reported that crossbred lambs did not perform better than Ethiopian indigenous lambs in daily gain, probably owing to the fact that dams were unable to produce enough milk to fulfill the growth potential of first generation (F1) lambs, either because of insufficient nutrition or low genetic capacity for milk production. Feed availability to sustain more productive animals and the extra feeding cost are among the major factors limiting the interest of using improved animals, especially in resource-deprived systems.

Central nucleus-based breeding programs

Sheep production in developing regions is generally characterized by small flock size, uncontrolled mating, and the absence of pedigree and performance recording (Tibbo, 2006; Solomon and Tesfaye, 2009). Such limitations limited the implementation of effective genetic improvement programs. To overcome these constraints, nucleus breeding schemes have been suggested for tropical countries, in which genetic improvement is centrally organized in a population maintained in research institutes or government farms. The objectives of the central nucleus-based breeding research projects have been to evaluate the genetic response and potential of local breeds to selection and to establish elite nucleus flocks as sources of improved rams. The research projects included Afar, BHS, Horro, Menz, and Washera sheep selection projects/programs. The breeding programs have mostly targeted growth performance of local breeds. The selection criteria were post-weaning growth rates, six-month and yearling weights.

The open nucleus breeding scheme offers a simple procedure for producing and disseminating breeding stock of high breeding value. Based on breeding values for the breeding goal traits, ewes born to superior rams would be selected and bought for transfer to nucleus flocks. Nucleus flocks will be set-up in the governmental breeding ranches. Subsequent genetic evaluations and selection for superior rams would be undertaken in the nucleus flocks where animals from different sources are evaluated in the same environment. Dissemination of superior rams to participating farmers will be made on cost recovery basis. Tibbo (2006), has also presented a plan for the indigenous Horro sheep open-nucleus breeding scheme in Ethiopia. This scheme could be utilized for conservation of genetic resources (including breeds, desirable genes, genotypes, etc) through improvement and proper utilization (Tibbo, 2006; Philipsson, 2000). This scheme can serve for both pure-breeding and crossbreeding and dissemination of improved genetic materials allowing conservation and improvement of the indigenous sheep breeds.

Despite decades of research, projects based on open nucleus breeding scheme generally yielded unsatisfactory results. Selection in the Horro sheep nucleus flock did not result in appreciable genetic improvement and the breeding program showed no progress (Solomon and Duguma, 2000; Solomon et al., 2007a). The reasons for the failure could be lack of documented selection procedures, high turnover of breeders managing the nucleus flocks, lack of skills in quantitative genetics particularly the accurate estimation of breeding values, budgetary constraints, lack of vision and commitment from researchers, and bias in the livestock development strategy towards crossbreeding with less emphasis on the recurrent selection program. Results of selection in the nucleus flocks of Afar and BHS sheep remain unreported and the initial breeding programs were discontinued with a strong likelihood that any achieved genetic improvement was lost with the disposal of the flocks. Moreover, implementation of nucleus breeding schemes in low-input environments has proven to be difficult because of requirement of long-term commitment of sponsors and involvement of farmers (Gizaw and Getachew, 2009; Kosgey et al., 2008). Since genetic improvement is a long-term venture, sustaining sheep breeding programs in Ethiopia has proved to be difficult.

Community-based breeding program

Genetic improvement of livestock species is a high input oriented, labor intensive and long-term program. Due to lack of resource personnel, supportive infrastructure and institutional arrangements, genetic improvement still remains a challenge in developing countries. Indigenous livestock populations in developing countries, are being reared predominantly by smallholders under traditional husbandry practices.

Genetic improvement in Ethiopia started in the 40’s with solutions like within breed selection programs and importation of exotic breeds for breed replacement and/or crossbreeding. Nevertheless, most crossbreds, except the Awassi from Israel, were later neglected because they were not accepted by farmers as they did not meet their phenotypic preferences (Tibbo, 2006; Gizaw and Getachew, 2009).

The Ethiopian Institute of Agricultural Research (EIAR) also initiated characterization and genetic improvement studies largely on indigenous sheep types in 1975 (Galal, 1983). This too failed to impact the traditional and extensive sheep production systems and the productivity remained low. Main reasons for the failures were lack of involvement or inadequate participation of sheep producers in the design and implementation of the breeding programs in addition to the poor infrastructural and institutional arrangements (Duguma et al., 2009; Tibbo et al., 2010). The gap between farmer’s perception and researcher’s interest is one of major hindrance for successful implementation of breeding programs. Therefore, success of breeding program is largely related to the level of involvement of the community in the design, implementation and operation of the program (Mueller, 2006) suggesting a need for new, more suitable methods for the developing world.

The community-based breeding program (CBBP) is believed to be a more viable and sustainable way for conservation and simultaneous genetic improvement of indigenous livestock under smallholders farming system (Philipsson et al., 2006; Wurzinger et al., 2011). The concept of community-based breeding (CBB) is not new, formally used as a tool in agricultural research since 1970 (Omore et al., 2008). Community-based breeding programs are based on bottom-up participatory approaches and typically relate with the farmers of low-input production systems within a certain geographical area of those having a common interest to work together for the improvement of their genetic resources (ICAR-FAO, 2000; Mueller et al., 2015). Community-based breeding program increases the productivity and profitability of indigenous breeds or strains without compromising their resilience and genetic integrity using easy to access interventions (Haile et al., 2010).

*Community-based breeding programs **in Ethiopia***

The community-based breeding program was first introduced in Ethiopia in 2009 by ICARDA together with the International Livestock Research Institute, Boku University, and the Ethiopian National Agricultural Research System (NARS). Community-based breeding programs combines selective breeding programs based on production parameters, such as body weight and higher reproductive efficiency with expert local opinion as to what constitutes a good ram/buck and communal use of selected rams/bucks, to increase productivity and reduce mortality of sheep and goats. Since, then more than 40 programs have sprung up.

Rather than relying on centralized staff management, these programs train and hire local students, technicians and other community members to carry out critical functions like collecting and maintaining animal records. Local hires provide a direct link between farmers and researchers in the formative stages of the program and in the delivery of extension services to disseminate best breeding practices.

Breeding programs were implemented in four sites (Bonga, Horro, Menz, and Afar) across four regional states of Ethiopia. After the end of the project, the more successful breeding programs in Menz, Horro, and Bonga continued under the CGIAR Research Program on Livestock and Fish and expanded to two new sites, Doyogana and Atsbi (for sheep) and another one in Abergelle for goats.

Steps for setting up the Community based breeding program

1- Selecting target breeds and communities

1.1 Selection of breed

There are a number of criteria to follow when selecting breeds. They should:

- be Genetically heterogenic and diverse;
- be among the most populous in the country;
- be kept by resource poor farmers/ pastoralists;
- have potential for genetic improvement;
- be easily accessible and available within reasonable reach from research/ development centres;
- have a good background information to facilitate the design of the improvement breeding program.

1.2 Selection of community

The success of CBBP (Annex 1) depends highly on the right selection of the community. Factors to be considered when selecting communities are:

- Market accessibility, transportation means and road quality;
- Negative/positive selection of other projects in the same region;
- Government support, since the availability of good extension services are an important support for CBBP;
- Availability of inputs and services (feed, veterinary services and drugs).

The factors mentioned above are mainly external factors affecting the community selection. There are also community-related factors like:

- Willingness of the community to participate;
- The community should possess a large and equitable distribution of sheep/goat flocks;
- Existence of communal resources or institutional arrangements (communal grazing area, watering points…);

- Presence of community leaders who are important during community selection to facilitate the work with the project’s team.

When selecting the communities, it is advisable to follow the following steps to facilitate the process:

- Consulting the extension representatives and researchers from the area;
- Seeking advice from former livestock specialists or NGOs and development project staff;
- Visiting the community accompanied with people who have developed trust within this community;
- Organizing a participatory workshop (consider to include people from different sectors and backgrounds, consider gender balance, choose a good timing to set up the workshop and it also should be facilitated by someone who understands the language and the culture of the community);
- Continuous documentation of the process by communication experts.

2- Characterization of target sites and breeds

2.1. Description of the production system

Description of the production system depends on both, primary and secondary sources. Assuming the secondary sources are already available through articles, Rapid Rural Appraisal (RRA) and previous projects, the characterization of the production system should mainly concentrate on:

- Identifying the importance and different use of livestock in the system
- The economic evaluation of production
- The current breeding practices, rams’ management, herd structure, and previous crossbreeding/improvement projects
- The available marketing channels for live animals and their products

2.2 Breed characterization

Preliminary identification of sheep breeds is based on phenotypic characterization and the genomic characterization

2.2.1 Phenotypic characterization

- Qualitative variables such as, coat colour, fibre type face profile presence of horn tail type
- Quantitative variables such as, body weight at different ages, withers height, body length and heart girth.
- Daily milk yield, lactation length, reproductive performance such as lambing rate, ewe/doe fertility, prolificacy, pre weaning survival rate and lambing interval

2.2.2 Genomic characterization

Genetic markers used in this type of analysis include biochemical (protein) polymorphisms, micro- / minisatellite markers, restriction fragment length polymorphisms (RFLPs), mitochondrial DNA and Y-chromosome specific markers. Genetic characterization can provide an objective assessment and understanding of the genetic relationships and differences within and between the target populations. Genomic data can provide information on rare variants segregating within and between populations and investigate the genetic architecture underpinning quantitative and qualitative traits through selection sweep analysis, genome-wide association mapping (GWAS) and QTL-mapping. Phenotypic recording and genotyping/genome sequencing are done for all the individuals making up the reference population. This provides the training datasets that can be used to build statistical models and prediction equations to estimate SNP/marker effects viz:

$$Yi = \mu + X1ib1 + X2ib2 + \ldots\ldots. + X5000ib5000 + ei;$$

Where Yi = phenotypic record of animal i; μ = average phenotypic performance; X1i = random polygenic effect (genotype) of animal i for SNP/marker 1 with values 0, 1, 2 (homozygous, heterozygous, alternate homozygous); b1= random effect for a paternal (k = 1) or maternal (k = 2) haplotype at locus j of animal i; ei = residual.

Once the prediction equations have been developed, selection candidates which are either offspring from the reference populations or from the base populations (selected by farmers based on their own criteria) are genotyped. The genotype data from the selection candidates is then combined with the estimated SNP/marker effects to derive their genomic breeding values (GEBV).

3- Definition of breeding objectives

The success of CBBPs depends on understanding livestock keepers' breeding objectives and selection criteria. To do so, homogeneity and heterogeneity of breeding objectives and selection criteria need to be assessed among community members and between neighboring communities. Uniform and consistent views among farmers facilitate the creation of a common understanding and a clear formulation of common objectives. Different participatory approaches can be used to describe community breeding objectives:

- Personal interviews with farmers to list and describe the traits that are of economic interest
- Workshops where groups of farmers can discuss their opinion on breeding objectives and selection criteria.
- Choice cards experiment where respondents are asked to choose from a series of choice sets, each containing five to six traits and alternative traits
- Ranking experiments of live animals by the farmers according to their own preference

4- Developing adequate breeding structures

There are different breeding structures needed for the implementation of CBBP. Population selection is where best animals are selected from the whole population as a replacement breeding stock. The recording of performance and pedigree, monitoring and screening is applied to all animals and the rearing of male candidates is undertaken in central governmental test stations or entrusted to one or more members of the community

In the nucleus system, the best animals that fit to fulfil the specific function of producing the 'best' next generation for the whole population are identified, selected and bred separately. Nucleus farmers concentrate on maximizing genetic gains while the remaining can concentrate on production.

The nucleus can be either open or closed. The closed one means no upward gene flow is allowed from base to nucleus while the open nucleus allows the best animals to enter the nucleus from the base population (Figure 1). One of the important features of open nucleus is that adaptation traits and other breeding objective preferences in the base population can be secured in the males produced assuming that such traits are used in the selection of the best females from the base. Another feature of the open nucleus, is the low inbreeding rate compared to the closed one.

The performance testing station is where male candidates selected at weaning age, are gathered and kept together in one common station. These males are monitored under the same conditions for a fixed period of time. The station might belong to community or can be facilitated by external organizations such as a university or a governmental body. There are examples of breeding programs which start with a centralized nucleus and then develop into a dispersed one. It means that the nucleus is managed by several farmers but all following the same management and selection process. Such dispersed nuclei may develop into reference sire schemes and eventually into population wide evaluation scheme.

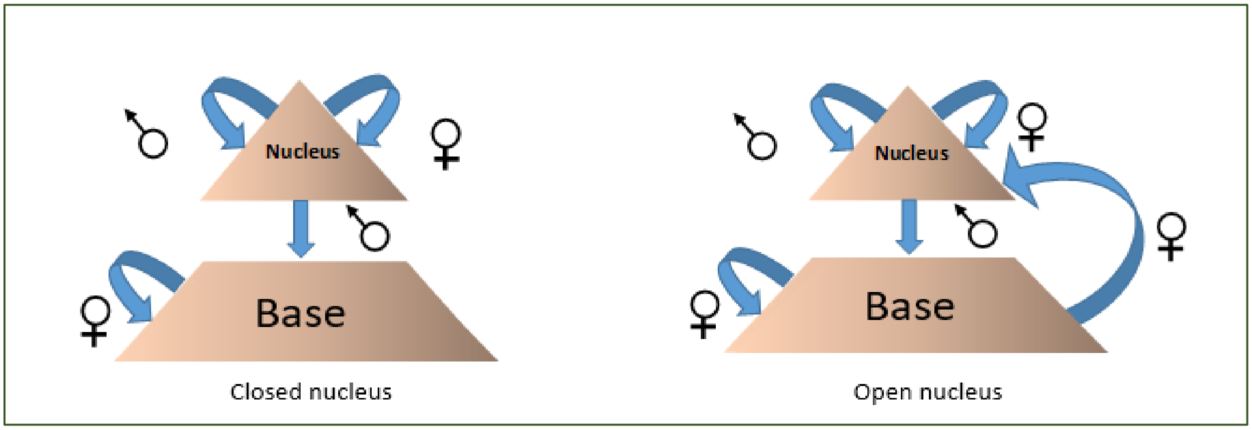

Figure 1. Open and closed nucleus schemes

4.1 Performance recording

4.1.1 Animal identification

In genetic improvement programs, identification is an essential process to keep track of animals, as well as their performances and respective pedigree. Combining performance and pedigree records enables more precise computations of the genetic worth and makes the estimation of the breeding value more accurate and therefore used for selection.

There are different methods of identification: ear tags, collars, tattoos branding and ear notches. Unique numbering should be embraced in a manner that no two animals in the breeding program can have the same identity.

4.1.2 Data recording and management

In CBBP, recording formats are simple and practical for easy use and adoption. After a thorough discussion with the community, two recording templates for ewes are available. The first one has detailed information and kept for the enumerator while the second with little information, is kept with the household. There is a designated template for lambs which is used to record information about its identity and performance.

The data and traits that should be recorded are: ID, sex, dam ID, sire ID, birth date coat colour and tail. As for the performance data we have, weight at different ages (birth weight, weaning weight, six months weight and yearling weight), number of lambs born, lambing interval, age at first lambing, post-partum weight, mating date and parity.

The type of data and its frequency need to be decided in close consultation with the community and must be based on the agreed breeding objectives and selection traits. Support in data entry and processing should be provided by the extension and research group.

4.1.3 Selection of candidate rams

The selection of young rams is based on its own performance and the maternal one. There are different stages of selection, the first stage can involve discriminating of some animals that possess undesirable phenotypic characteristics or clearly observable defects. The retained ones are judged based on body weight and conformation traits. The selection is sometimes based on traditional practices (what farmers usually do) which in this case will improve the probability of acceptance by the community. It is important that the selected young males are effectively used for breeding before they are sold off in order to avoid negative selection. Animal models can be used to rank rams. If breeding values cannot be computed for whatever reason, rams can be selected based on simple index values that are computed from the available recorded data from the site population.

4.1.4 Management and use of breeding rams

In most mixed crop livestock systems, smallholders share the selected best rams between them. However, in other communities, members may be reluctant to share rams outside their established social network. The best way to use rams communally is by forming “ram -user-groups.” This can be based on criteria such as number of breeding ewes, settlement patterns and use of communal grazing areas. In order to minimize inbreeding, a ram rotation strategy among the ram groups has to be established through a consultative process. The best way is to use a ram in the flocks for one year, after which it is rotated to another group within the community. Ram rotation records must be diligently kept to avoid inbreeding.

The management of selected breeding rams to be used by the community should be based on pre-agreed modalities. Some of the options include:

- Managing the ram in rotation;
- Keeping the ram in one agreed household and those who use the ram pay an agreed amount for the service;
- Keeping the ram in one agreed household and other community members contribute in kind (e.g. feed and veterinary drugs) to keeping the ram.

5- Use of selected rams in artificial insemination

It is well known that improved rams bring genetic progress where they are used. Whether the ram is placed at the level of the household or used collectively at the level of the community under common natural mating practices, a ram with a high-breeding value may only mate with a very limited number of females (20–30) during the mating season. Furthermore, collective use of the selected rams may represent a very high risk of sexually-transmitted diseases. Artificial insemination (AI) is universally represented as being the most common process through which the products of the primary breeding activities are out and upscaled. In this regard and with reference to the context of CBBPs in Ethiopia, Mueller et al. (2019) have identified AI, in complementarity of natural mating, as one strategy to further increase genetic progress and dissemination relying on a more intense use of sires. Fixed-time AI using fresh, cooled semen is the most widely used method in sheep (Mueller et al.2019, Palacín et al. 2012).

Available data on the reproductive history of the females is important during selection. Ensuring normal fertility in the flocks is essential for productivity and, therefore, care should be taken to ensure that females that do not conceive are mated naturally, even if the males used are not selected within the CBBP.

6- Creating an enabling environment

6.1 Community–implementers' relationships

A continuous interaction between farmers, researchers and extension staff is crucial for the success of a CBBP. To maintain a steady and stable relationship between all the mentioned actors for full commitment, some measure should be taken:

- Regular workshop meetings to discuss every step of program design and implementation;
- Open discussion with farmers about their perceptions, fears, doubts or any idea that can help with the program;
- Informal consultations with community elders to disseminate information about the program;
- Giving farmers regular feedback to track performance of their flock;
- Consideration of the culture, religious and ethical values of the community.

6.2 Government support

To ensure sustainability of the breeding program, government support is essential. This can be achievable through some actions like:

- Providing farmers with start-up costs for initial costs of performance recording and animal identification;
- Allocation of funds for technical personnel (researchers and extension staff) and infrastructure;
- Government should facilitate access to credit, land and other resources (e.g. watering points, rural access roads, livestock auction yards and market information on livestock and livestock products).

6.3 Market access

One of the initial steps of setting up CBBP, is the study of market, its local, national and international demand and also the accessibility to it. Farmers are encouraged to form cooperatives or farmers associations to ensure better access to markets and stronger negotiation power, which also means a larger number of animals and/or quantity of livestock products can be brought to market regularly.

6.4 Links with other projects/activities

A positive synergy can take place when linking breeding programs to other ongoing development initiatives and activities in the local area. Such cooperation reduces redundancies, ensures convergence of objectives and strengthens the project.

7- Monitoring and evaluation

Different authors (FAO, 2010; Haile et al., 2011, and Mueller et al., 2015) mention the importance of a systematic evaluation of the performance and impact of CBBPs to monitor if the promised changes have been actually achieved. An evaluation of a breeding program can serve two major purposes. Firstly, as a quality management tool for implementing institutions to monitor and evaluate on-going activities of a CBBP and to identify possible challenges in the execution of a program. Secondly, the evaluation can serve as a guide for (external) funding bodies to measure impact on the livelihoods of farmers and other stakeholders. By regularly monitoring the breeding program, corrective measures can be taken to improve it. Showing the impact of the breeding program will be essential for ensuring continuous support of the program.

The monitoring can be divided into three main domains:

- Evaluation of CBBP implementation;
- Monitoring of implementation outputs;
- Evaluation of CBBP-associated impacts on livelihoods of farmers and the environment.

Optimization of Breeding Schemes

In order to overcome some of the constraints of smallholder sheep production, CBBPs are an alternative approach for achieving genetic and husbandry improvements as well as sustainable institutional development around the breeding plans. The economic role of sheep for the poor households significantly contribute to livelihoods as well as food and nutritional security, as tangible benefits (cash income, manure...) as well as intangible socioeconomic benefits (insurance, finance...). Identifying breeding objectives traits and their relative economic importance, along with a comprehensive understanding of trait preference from producers and market perspectives, can help in designing adapted CBBP and is a promising entry point to achieve sustainable genetic progress (Mueller et al., 2015). Furthermore, sustainable genetic improvement program does not focus on technical feasibilities only, but also analyzes the organizational aspects of the breeding scheme under specified conditions.

The basic design of a typical CBBP under the conditions of smallholder sheep farming systems in Ethiopia is a one-tier breeding structure where selection is implemented in the whole village sheep population (considered as one flock). All six months lambs are evaluated as cohorts. No selection on ewes, and the best rams are selected by a farmer committee based on their 6 months weight. The weight of selection candidates is adjusted for age of weighing, season of birth and dam parity. Rams are organized to be owned, used and managed communally. Beyond the definition of the breeding objectives, there are key choices in designing breeding programs for smallholder systems that are related to breeding schemes/structures to be suitable for the low-input, smallholder farming system. Available options should be simulated and evaluated for their bio-economic efficiencies including genetic gains and profits. Such an optimization exercise may prove to be crucial in the initial design of village-based breeding programs in low-input systems.

The literal meaning of optimization is making the best or most effective use of resources. When that is brought to the context of animal breeding, this implies how best resources needed for animal breeding are most effectively used in such a way that optimal gains are secured both in terms of genetic gains and profits. Therefore, designing an optimized CBBP that considers sheep breed characteristics, producers' trait preference, market demand and organizational framework by taking into consideration the diverse sheep production systems is crucial for the long-term viability and success of this program.

Tatek (2016), reported that in order to optimize breeding programs several steps should be followed:

- Study of factors affecting contributions of sheep farming to household economy and dietary diversity in different production systems;
- Identification of sheep breeding objectives and economic values of traits based on revealed and stated preference information;
- Formulation of alternative breeding options while taking into consideration the economic values of traits in different production system;
- Identifying major stakeholders, organizational networks and other elements of organization and their influence on the establishment and successful operation of community-based small ruminants breeding.

Owners or farmers usually use their experience for optimizing their farm income. Sometimes, however, their experience does not guarantee their intended results (Alsheikh and El-Shaer 2009; Tsukahara et al., 2011). Accordingly, linear programming should be used as an effective technique to address the limited production resources among different agricultural (cultivation and livestock) activities to provide optimal results for these owners (Alsheikh et al., 2002). According to Tsukahara et al. (2011), simulation models can provide a logical understanding and predictions of outcomes of the production systems including genetic, managerial or environmental variables under different sets of conditions. In small ruminants for instance, biological production efficiencies were estimated and crossbreeding systems were evaluated under tropical conditions using a deterministic simulation model (Tsukahara et al., 2011). Bosman et al., 1997 developed a simulation model to assess the efficiency of small ruminants' production. Oishi et al. (2008) used the simulation method to estimate the effect of culling age of does on productive efficiency.

A deterministic simulation model is said to be appropriate for the optimization of alternative breeding plans for livestock. ZPLAN (Willam et al., 2008), the computer program, was used to model the alternative livestock breeding programs. Breeding programs and their parameters are defined by users and the program calculates results such as annual genetic gain for the breeding objectives, genetic gain for single trait and returns for investment periods adjusted for costs (profit). The program is based on a pure deterministic approach. Compared to stochastic simulation models, its advantage is multi-trait including return on costs over a given time horizon and runtime is fast (Willam et al., 2008).

To optimize the village-based breeding program in Menz, Gizaw et al. (2013) simulated, three scenarios of controlled breeding. Each scenario of controlled mating was evaluated under the nine levels of participation. The first scheme had two tiers, where they establish a village-based nucleus. Farmers contribute their best females to the nucleus, and the selected rams will be used to supply the village. In the second scheme (one tier), selection is carried out in the whole village sheep population. The farmers select breeding rams from across all the sheep population and then used communally. Scheme 3 assumes a dispersed village-based nuclei scheme. This scheme involves establishing a nuclei breeding village where genetic improvement is generated, which then serve as sources of improved rams to the whole population of a village.

Another three central nucleus-based schemes were considered for optimization. Scheme 4 (Two-tier central nucleus scheme) is the conventional central nucleus scheme (e.g. Bondoc & Smith 1993; Gicheha et al. 2006) where genetic improvement is generated in a central nucleus flock located in a research/government farm which supplies improved rams to villages. The central nucleus could be operated by a private breeding company. During the first few years of the program, the central nucleus flock was planned to remain closed to gene inflow but would be opened to accept elite ewes from village nuclei as operational feasibility of such a scheme is ascertained, and some performance recording takes root in the base flocks. Scheme 5 (Three-tier central nucleus scheme) is similar as Scheme 4, but the central nucleus is linked to village-based multiplier nuclei. The village nuclei are operated by cooperative village breeding groups. Scheme 6 is same as Scheme 5, but the village nuclei also practice selection of rams to be supplied to the village production unit. However, rams selected in the village nuclei are not used for breeding in the nuclei.

As a part of the optimization process, the two sets of sheep breeding schemes (village-based and central nucleus based) were evaluated (Gizaw et al., 2013). It was concluded that the 6th scheme, the one linking central nucleus flocks with village-based nuclei is the most feasible option and could overcome the operational difficulties of the conventional central nucleus breeding scheme. Also, the second scheme was reported to be suitable as a breeding program addressing the whole sheep population.

The literature review section has reviewed establishment, growth and expansion of the approach of CBBP’s as applied in the context of Ethiopia for the selection of indigenous sheep and goats. The review highlighted the main milestones, the valuable achievements and identified some gaps mainly related to the actual genetic progress and to possible interactions between selected traits and other important functional and economic traits. Further, there have been no studies related to the possible changes at the genome level as incurred by selection on the economically-important traits. The literature review also addressed in a comprehensive way a phenotypic and genetic analysis of the main weight and reproductive traits that are relevant in the context of Ethiopian sheep breeds in the light of availbale international literature. Our study has been made possible at this stage valorizing a valuable 10-year database of records on animals and their pedigrees.

Materials and methods

Study Area and characteristics of the production system

The study was conducted in two areas, Bonga and Menz (Figure 2). Agriculture in Bonga area is dominated by mixed crop-livestock production system, coffee production, exploitation of forest resources and honey production. It has one major rainy season that extends from May to October and dry season lasts from November to April (Mirkena *et al.,* 2012). The data was collected from two villages in Bonga, Boqa and Shuta of Adiyo Kaka district of Kaffa zone, Southern nations' nationalities and peoples' region of Ethiopia.

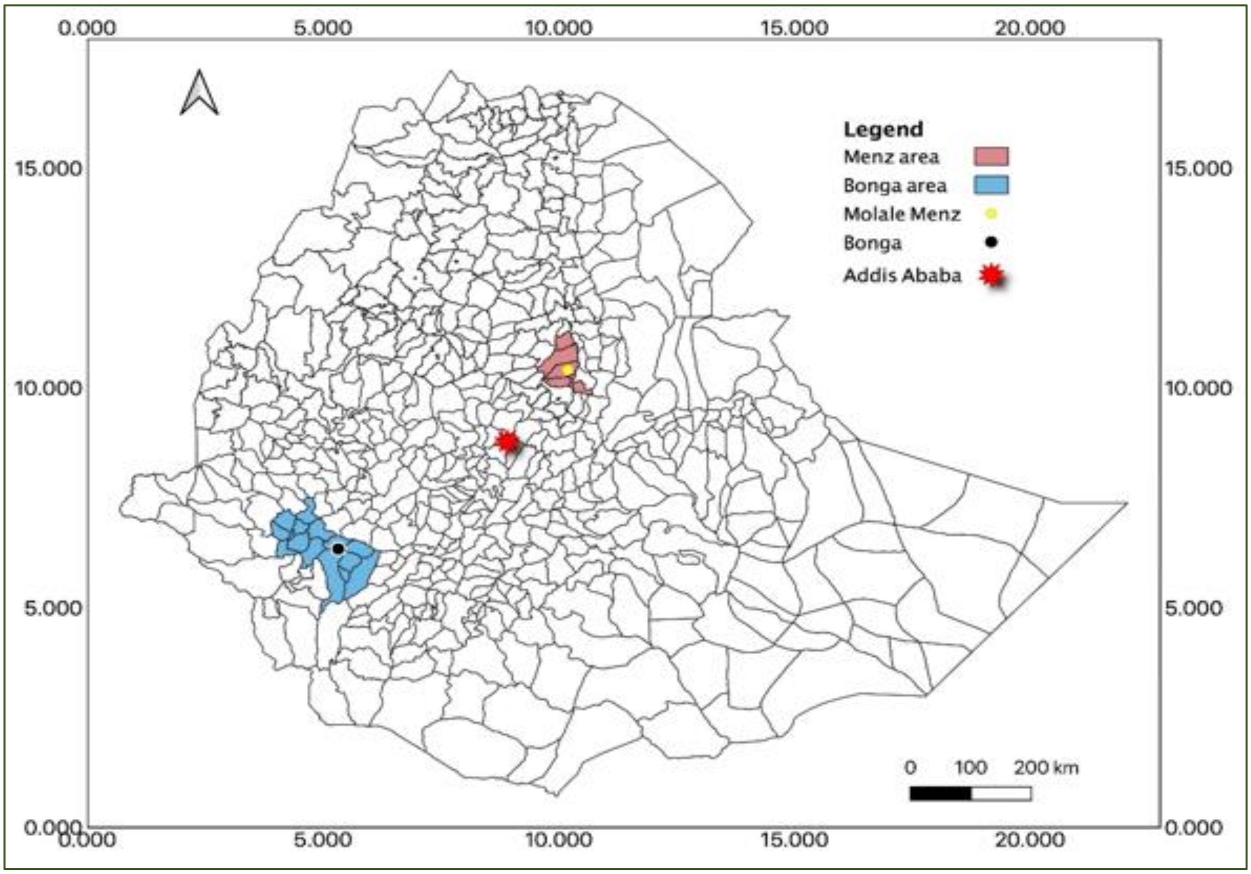

Figure 2. Map of the study areas

Boqa-Shuta is located at 509 km South West of Addis Ababa ($7^0 17^'$ N latitude and $36^0 24^'$ E longitude). It has a wet humid agro ecology with an average altitude of 2511 masl and with mean annual temperature ranging between 17.5-22.5 ^{0}C. The area is covered by a large evergreen natural forest receiving year-round rainfall; the recorded minimum and maximum rain fall within the period of data collection (2008-2018) was 1079 and 2032 mm per year with an average of 1617 mm (Figure 3).

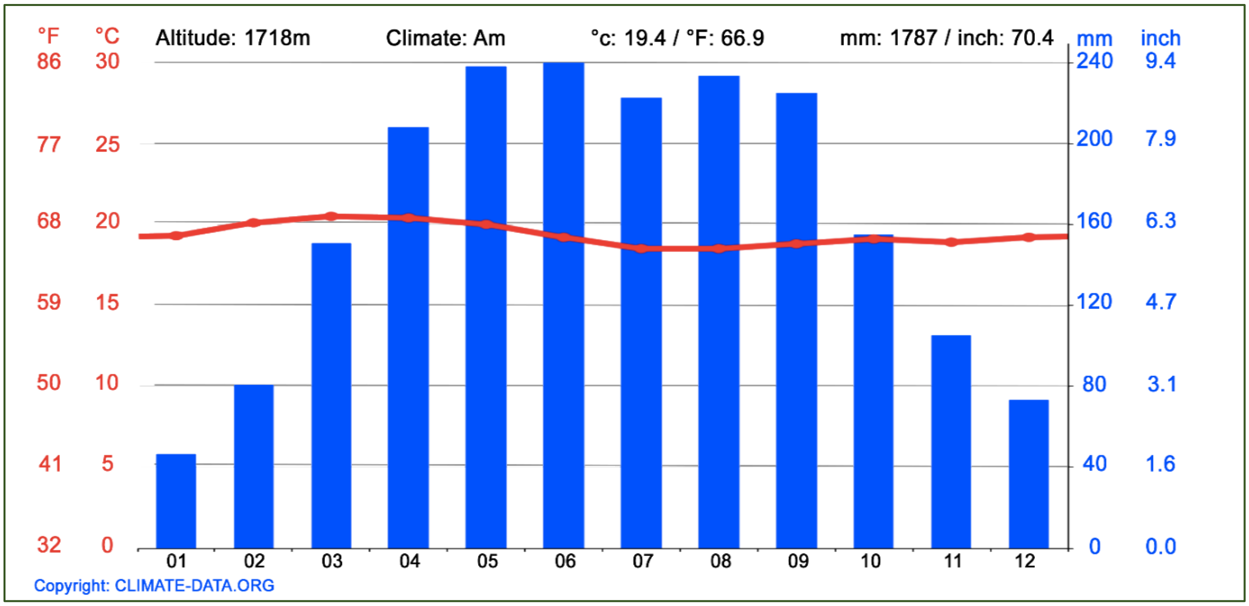

Figure 3. Average monthly rainfall and temperature in Bonga area during the period 2009-2018 (source: climate-data.org)

The other study area, Menz is located at an altitude of 2800 to 3100 meters above sea level and about 280 km north of Addis Ababa. The area is characterized by bi-modal rainfall with a main rainy season (June to September) and an erratic and unreliable short rainy season (February to March, Figure 4). Based on the meteorological data obtained from Debre Berhan Agricultural Research Centre for the year 1985 to 2005, the annual rainfall at Menz was about 900 mm and the minimum and maximum average temperatures were 6.8 ^{o}C and 17.6 ^{o}C, respectively. The cool highland parts of Menz are believed to be the main habitat of Menz sheep.

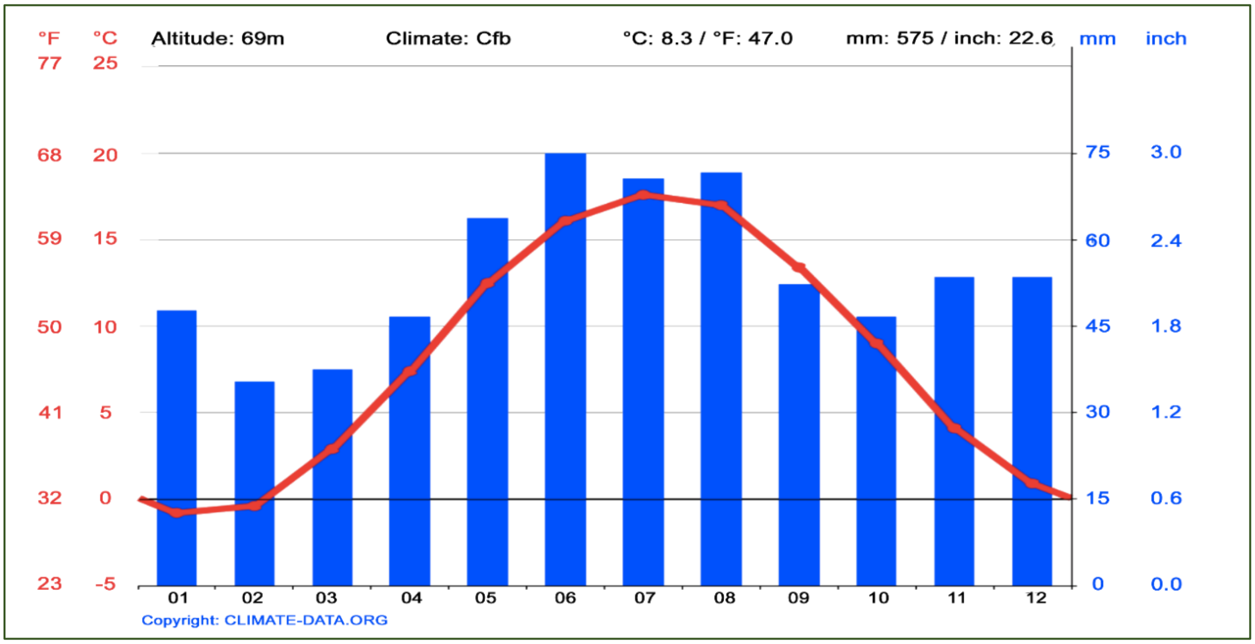

Figure 4. Average monthly rainfall and temperature in Menz during the period 2009-2018 (source: climate-data.org)

The potential of the area for sheep production is well documented (MOA, 1998; Abebe, 1999). The major crops by coverage are barley (52%), wheat (23%), beans (15%) and other crops (10%). Based on figures published by the Central Statistical Agency (CSA, 2019), the Menz area has an estimated total human population of 324,705 and 93.7% of its population lives in rural areas and depend mostly on agriculture. With an estimated area of 2,689.38 square kilometers, the Menz area has an estimated population density of 120.7 people per square kilometer. The farming system of the study area is largely characterized by mixed crop-livestock production system. Crop production is limited due to severe frost, poor soil fertility and unreliable rainfall. Thus, the area is characterized as one of the drought prone areas of the Amhara National Regional State.

Farmers largely depend on sheep farming for their livelihoods (Gizaw et al., 2014). Some farmers, including members of the CBBP, in this area are food insecure and fall under the government food safety net program implying the potential of sheep to improve farmers' access to food.

Breeds' description

The Bonga sheep breed is characterized by a wide and moderately long tail; both males and females are mostly polled, have long ears and short and smooth hair (Edea et al., 2009) (Figure 5). The breed is judged good for traits such as growth rate, meat quality, fattening potential, twinning rate and temperament (Edea et al., 2009). Bonga sheep are native of Kaffa zone of Southern Ethiopia and one of the 14 indigenous sheep breeds of Ethiopia reared in highlands of Kaffa, Shaka and Bench Maji zones of Southern Ethiopia. The commonly used name 'Bonga sheep' was derived from the town of Bonga where the breed is marketed (Metsafe et al., 2017). They are of mutton type breed and have a higher body weight at maturity and the ewes are moderately prolific. The skeletal frame of the Bonga sheep is larger as compared to other Ethiopian sheep breeds and they are generally tolerant to many of the locally prevalent diseases (Haile et al., 2013). Currently, it has a total sheep population of 725,572 heads (approximately 75% of total are females) of which 66% of them are being reared in Kaffa zone (CSA, 2019). However, it has been widely spread to the neighboring areas of Southern nations' nationalities and peoples (SNNPR) and Oromia that share the same geographical boundary and markets and are important source of animal proteins.

Figure 5. Bonga sheep in Boqa

The Menz area is considered the epicenter of distribution of the Menz breed. The Menz breed is raised for its coarse wool, used to weave traditional blankets and carpets, as well as for meat (Mirkena et al., 2012). Menz sheep are adapted to the high-altitude precipitous terrain characterized by scarcity of feed and low crop production due to extreme low temperatures and drought in the cool highlands. This is a hardy small breed which has a good level of tolerance to internal parasite infections and is productive under low-input production circumstances of the degraded ecosystems (Getachew et al., 2010).

Figure 6. Menz sheep

The Menz sheep have a characteristic short fat tail (Figure 6), which drops to the hocks and has a slight upward twist/curve at the end. The fleece is semi-open and made up of locks of coarse hair and a woolly undercoat. Dewlap and wattles are absent and the ears are small with a downward-forward inclination. The body is compact, and the neck is short. Both rams and ewes have a very nervous disposition.

The dominating color seems to be black or dark brown with some white spots on the head, neck and legs. Males have mostly long and twisted horns while females are predominantly polled. The Menz sheep are small, short and compact; mature body weight is estimated to be between 30 and 35 kg (Galal, 1983).

Breeding program description

Community-based breeding program, has been implemented in Menz and Bonga. These two sheep CBBP sites are among the four oldest sheep CBBP sites established by ICARDA-ILRI-BOKU joint project in collaboration with NARS in 2009 (Haile et al., 2020). The CBBPs are carried out to improve Bonga and Menz sheep breeds with active participation of farmers. Community-based breeding program focuses on indigenous stock and consider farmers' needs, views, decisions and active participation, from inception through to implementation, and therefore provide a participatory and bottom-up approach. Ethiopian CBBP combines selection of breeding rams based on careful recording of important production parameters, such as body weight at 6 months and ewe litter size at birth (for Bonga only), with expert local opinion as to what constitutes a good ram. Selection of male lambs during the initial stages was carried at six months of age but subsequently the final selection for admission to breeding at 12 months age. Screening of superior lambs was carried out based on their estimated breeding values (EBVs) for selection trait/s. Animal conformation and phenotypic characters were checked by a breeding ram selection committee elected by the community. Lambs or rams that have good breeding values were culled if morphological characters like horn, coat colour and tail type were not preferred by the breeding ram committee of the CBBP.

Phenotypic, pedigree and genetic data collection

Phenotypic and pedigree data

The phenotypic and pedigree data used in this study were archived from data collected in Bonga and Menz CBBP's between 2009 and 2018. For both breeds of sheep, growth records were available for weight traits measured from birth to yearling age of the lambs. These included birth weight (BWT), weaning weight (WWT), six months weight (SMWT) and yearling weight (YWT). For each lamb, sex and birth type were also recorded as well as litter size and lambing interval of the dam. Weights of lambs were recorded soon after birth and then at 3, 6, 9- and 12-months age. At birth, lambs are identified by individual ear tags. Body weight was measured using a spring balance (50 kg capacity) where the animals were held in a sac and hanged by the balance. The pedigree data was also recorded by CBBP's enumerators who are employed for each sheep-breeding community for record-keeping. These enumerators live within the community and closely follow-up the breeding program. The detailed data structure and number of records for the pooled data of studied traits is indicated in Table 12. Reproductive data (litter size) of Menz was not included as ewes of this breed - because of the harsh environment - are managed on an annual basis for their reproduction and litter size is uniformly equal to 1. Only 2 to 3% of the ewes produce twin litters.

Table 12. Descriptive statistics for body weight and reproductive performance traits of Menz and Bonga sheep

Site	**Menz**				**Bonga**					
Trait	BWT	WWT	SMWT	YWT	BWT	WWT	SMWT	YWT	LS	LI
No. Records	4637	4013	3455	2464	10877	8453	4623	456	8416	2854
No. animal with known sirew	2817	2490	2132	1584	8298	6584	3943	307	6984	2367
No. animal with known dam	4470	3897	3354	2389	10681	8311	4550	427	8259	2847
No. Animals with both known parents	2716	2413	2065	1529	7446	6471	3863	305	6860	1989
No. sires	218	177	162	113	687	519	283	36	563	257
No. dams	1713	1506	1225	951	3993	3012	1565	164	2989	114

BWT: birth weight, WWT: weaning weight, SMWT: Six months weight, YWT: yearling weight, LS: litter size, LI: lambing interval.

Genetic data

A total of 217 animals (117 from Bonga and 100 from Menz) were used for genomic analysis. Animals were selected based on their EBV for the CBBP participant sheep, but randomly for the non-participant ones (Table 13). Whole blood (10 ml) was collected via jugular venipuncture into EDTA vacutainers, were conserved in cold, and then frozen at -20 °C in laboratories of the International Livestock Research Institute (ILRI).

DNA was extracted using Qiagen kit (Qiagen Inc. USA) following the manufacturer instructions. Genomic DNA was obtained from these samples using phenol-chloroform extraction. All 217 DNA samples were genotyped with the Ovine Infinium HD Bead Chip (Illumina San Diego, CA, USA) at GeneSeek Inc (https://genomics.neogen.com/en/) which included 606,006 genomic SNP variants.

Table 13. Description of collected blood samples

Breed/location	Number of blood samples	CBBP participant	Non-CBBP (control)
Menz			
Molale	100	56	44
Bonga			
Boqa	64	64	6
Shuta	53	53	6

Data management and Analysis

Fixed effect analysis

Data collected from each site were coded for further analysis. Phenotypic and quantitative data were entered into Microsoft EXCEL, 2007 software. Preliminary data analysis like homogeneity test, normality test and screening of outliers were carried using R software (R Development Core Team, 2013) and SAS PROC UNIVARIATE (SAS, 2012 ver. 9.4) before conducting the main data analysis. The data were checked for pedigree structure using pedigree viewer software version 6.5. To obtain accurate estimates of genetic parameters, non-genetic factors which influence the phenotypic expression of different genotypes should be either controlled experimentally or accounted for statistically. For animal breeding applications, the inclusion of fixed effects is used to protect against downward bias in heritability estimates. PROC GLM of SAS (SAS, 2012) was carried out to examine the significance of fixed effects (sex (2 levels), year (10 levels, 2009-2018), parity (6 levels, from parity one till parity 6), birth type (2-3 single, twin and triple) and season(2 seasons; Dry/Wet for Bonga and for Menz; four seasons: heavy rain (1), harvest (2), dry (3) and small showers(4)) on growth and reproductive traits and to determine which fixed effects should be included in the final models.

Model selection

Best fitting genetic model were identified after testing different models, using AIC and LRT tests, and was used for the genetic analysis. For each trait, a series of six univariate linear animal models were considered (See below) to identify best fitting model. The models differed in the (co)variance components fitted to assess the importance of maternal effects. The models expanded from a simple animal model (model 1) which included only a random direct additive genetic effect to a comprehensive maternal effect model which included direct and maternal genetic effects (model 6). The general representation of the most complete linear animal model (model 6) partitions growth rate of an animal into a linear sum of different fixed effect (as determined by least square analysis significance) and random effects (direct additive genetic, maternal additive genetic, maternal permanent environment).

The Average Information Restricted Maximum Likelihood method (AI-REML) of WOMBAT (Meyer, 2007) was used to fit a univariate animal models for each trait to estimate breeding values (EBV), (co) variances, and heritability. While the bivariate and multivariate models were used to estimate genetic correlation among the traits. The fitted models accounted for effect of parity (with all parities above 6 grouped as one class), year (2009-2018), season (heavy rain, harvest, dry and small showers season for Menz rainy season from June to September, dry season from October to May for Bonga) and birth type (for Bonga, single, twin and triplets). Random effect for animal, maternal (m) and permanent environmental (pe) effects were fitted. The six models fitted were as follows:

(1) $y = \mathbf{X}\beta + \mathbf{Z}\alpha + e$

(2) $y = \mathbf{X}\beta + \mathbf{Z}\alpha + \mathbf{Z}_m + e$ with $\mathrm{Cov}(\alpha, m) = 0$

(3) $y = \mathbf{X}\beta + \mathbf{Z}\alpha + \mathbf{Z}_m + e$ with $\mathrm{Cov}(\alpha, m) = A\,\sigma_{am}$

(4) $y = \mathbf{X}\beta + \mathbf{Z}\alpha + \mathbf{Z}_{pe} + e$

(5) $y = \mathbf{X}\beta + \mathbf{Z}\alpha + \mathbf{Z}_m + \mathbf{Z}_{pe} + e$ with $\mathrm{Cov}(\alpha, m) = 0$

(6) $y = \mathbf{X}\beta + \mathbf{Z}\alpha + \mathbf{Z}_m + \mathbf{Z}_{pe} + e$ with $\mathrm{Cov}(\alpha, m) = A\,\sigma_{am}$

Where y is a vector of observation on specific trait of the animal, β is a vector of fixed effects; α, m, pe are vectors of random effects describing additive genetic, maternal additive and permanent environment effect. **X** and **Z** are corresponding incidence matrices relating to each effect to y and e is the vector of residuals. **A** is the numerator relationship matrix between animals and σ_{am} is the covariance between additive direct and maternal genetic effect.

The (co)variance structure for the random effects is:

$$V(a) = A\sigma^2_a,\ V(m) = A\sigma^2_m,\ V(pe) = I_d\sigma^2_{pe}\ \ V(e) = I_n\sigma^2_e,\ \ \mathrm{Cov}(a, m) = A\sigma_{am}$$

$$E[y] = [X\beta],\quad V\begin{bmatrix}\alpha\\ m\\ pe\\ e\end{bmatrix} = \begin{bmatrix} A\sigma^2_\alpha & A\sigma_{am} & 0 & 0\\ A\sigma_{am} & A\sigma^2_m & 0 & 0\\ 0 & 0 & I\sigma^2_{pe} & 0\\ 0 & 0 & 0 & I\sigma^2_e\end{bmatrix}$$

σ^2_a = direct additive genetic variance

σ^2_m = maternal additive genetic variance

σ^2_{pe} = maternal permanent environmental variances

σ^2_e = residual variances

A = additive numerator relationship matrix created from the pedigree structure.

I_d, I_n = Identity matrices with order equal to the number of ewes and records respectively

For the reproductive traits, the variance components for the investigated traits (lambing interval, LI and litter size, LS) were also estimated by AI-REML method of WOMBAT (Meyer, 2007) program following the repeatability animal model. Repeatability (r) was calculated as:

$r = \sigma^2_a + \sigma^2_{pe} / \sigma^2_p$ where:

σ^2_a = additive genetic variance

σ^2_{pe} = permanent environmental variance

σ^2_p = phenotypic variance

In order to determine the most appropriate model, Akaike's information criterion (AIC) and log likelihood ratio test (LRT) were used (Akaike, 1974): $AIC_i = -2 \log L_i + 2p_i$ where $\log L_i$ is the maximized log likelihood of model i at convergence and p_i is the number of parameters obtained from each model; the model with the lowest AIC was chosen as the most suitable model. Model with different random components were also compared using the log likelihood ratio test (LRT), calculated as twice the difference between the log L of each model. The LRT was given by $D = 2\log(l_{R2}/l_{R1}) = 2[\log(l_{R2}) - \log(l_{R1})]$, where l_{R1}=log likelihood of restricted model and l_{R2}=log likelihood of the more general model.

Heritability was calculated as σ^2_a/σ^2_p using the estimated variance components.

Correlation of Blup EBV and phenotypic EBV

For estimation of the correlation between phenotypic based selection and estimated breeding value (EBV) across the years, a new data set of sires was created for each year separately, and only SMWT trait was taken into consideration. The phenotypic EBV was calculated following this equation: EBV_{ph} = (Animal's weight at the age of six months – Average six months weight of Peers) x Heritability. The BLUP EBV was taken from wombat output file (sum estimates). To determine the correlation between these two results we used spearman rank correlation method (SAS, 2012).

The genetic trends were estimated by the weighted regression of the average breeding value of the animals on the year of birth. Inbreeding coefficients were derived from WOMBAT outputs.

To study the effect of selection based on six months weight on other traits, the genetic trend for every trait was estimated by the weighted regression of the average breeding value of the animals on the year of birth. Inbreeding coefficients were derived from WOMBAT outputs.

Genetic data

Quality control

Out of 229 sampled animals, only a total of 189 animals (44 Menz control, 56 Menz improved, 117 Bonga improved from two villages) were genotyped with a call rate of 0.997. The genotype data were assessed for quality with PLINK v1.90 (Chang et al., 2015). Variants with large hardy-Weinberg equilibrium (HWE) deviations (P value < 1x10-6) and minor allele frequency (MAF) <0.001, missingness genotype rate per individual > 0.05, missing rate per SNP >0.05 were excluded from the final data set. Following the quality filtering, 514,624 variants and 182 individuals were retained for analysis. Bonga control samples (n=12) were not used for comparisons because of the poor quality of genotyping.

Genetic diversity

Observed hetrozygosity (Ho), expected heterozygosity (He), the inbreeding coefficient (FIS) were calculated using PLINK to estimate within population genetic diversity.

Genetic relationship and population structure

Pairwise genetic differentiation estimates measured as fixation index (FST) (Weir and Cockerham, 1984) were calculated among the 3 sheep populations using Arlequin v.3.5 (Excoffier and Lischer, 2010).

A multidimensional scaling analysis (MDS) based on pairwise identical-by-state (IBS) distances and Principal Component Analysis (PCA) were performed with PLINK v1.90 and visualized with the R software.

Genetic structure and admixture among breeds were analyzed using model-based clustering algorithm implemented in the software ADMIXTURE v. 1.2.3 (Alexander et al., 2009) for the same data sets used in PCA. Prior population information was ignored. The most probable number of populations in the data set (K) was estimated using the default cross validation procedure by which prediction errors are obtained for each K values (Alexander and Lange, 2011). The K value that minimizes this estimated prediction error is then assumed to be the most suitable. Individual coefficient of ancestry proportion produced by ADMIXTURE software were graphically visualized using R software (R Development Core Team, 2013).

Signatures of selection

FST between each locus was calculated using VCF tools software (Kunzhe et al. 2020) used to detect signatures of selection. Then, the genome wide FST was used to explore selection signatures between improved sheep under CBBP and non-selected sheep populations. Candidate regions were identified by different approaches and were used to annotate genes that were either entirely or partially included within each selected region, using the NCBI Genome Data Viewer. Gene Ontology (GO) enrichment analysis was also performed for the candidate genes revealed in pairwise comparisons between the studied groups

Results and discussion

Growth performance

Birth weight (BWT), weaning weight (WWT), six months weight (SMWT) and yearling weight (YWT) of Bonga sheep were 3.1, 14.5, 19.9 and 35.7 kg, respectively and 2.7, 8.0, 13.7, and 18.8 kg for Menz sheep, respectively (Table 14).

The birth weight of Bonga sheep under the current study (3.1 kg) is higher than those reported for the same breed in other studies (2.86 kg by Belete (2006); 2.8 kg by Eyoub et al. (2017). Weaning weight, SMWT and YWT found in this study were also higher than values reported in other studies. In this respect, Getahun (2010) reported an average of 12.23 kg for WWT, whereas Belete (2006) reported 11.6 kg for the same trait for Bonga breed. This variation could be explained by the number of observations and year variation; in the other cited studies the number of observations was much smaller than in our study.

The birth weight of Menz reported in current study was 2.7 kg which is higher than other findings like in the study by Tibbo et al. (2004; 2.1 kg) and very close to what has been reported by Haile et al. (2020; 2.75 kg).

Effect of fixed effect on body weight at different ages and reproductive performance

The results pertaining to effect of fixed factors on body weight are presented in Table 14. Growth performance of Menz and Bonga and reproductive performance of Bonga sheep were affected ($P < 0.05$) by all the fixed factors fitted except for birth/lambing year on LI, and sex and parity on YWT ($P > 0.05$).

The ram lambs were heavier than their female counter parts from birth throughout to one year of age. The variation in birth weight between the two sexes found in the present study agrees with those reported by Yilmaz et al. (2006). The superiority of male lambs over female lambs is about 0.1 to 0.3 kg for Menz sheep. For Bonga sheep, the ram weight wasn't always superior to the weight of the ewe. For yearling weight, the ewe weight was superior by 3.5 kg. In fact, this may be caused by unbalances in the number of animals aged 1 year; more females were available in the database as male rams are sold at younger ages.

Single born lambs were heavier than their multiple counterparts ($P < 0.001$). A similar result was reported by Momoh et al. (2013) for pigs in Nigeria and Berhanu et al. (2009) for Ethiopian sheep. This could be because of the finite capacity of the maternal uterus space to gestate offspring. As reported by Mousa (2013), the higher weights at birth of single litters may be caused by intrauterine competition of the multiple born lambs both for space and nutrients. Body weight at later ages was also significantly affected by litter size. Single born lambs had significantly higher weaning weight (at 90 days) than multiples ($P < 0.001$). The significant effect of birth type on the body weight at weaning was because of competition among the multiples than singles for limited amount of milk of the dams. Our results are in agreement with results reported in other studies (Mousa et al., 2013; Mestafe et al., 2015) where it was shown that singles were heavier at six months of age and they maintained their superiority until they were 1-year-old. The difference was from 2 to 4 kg between single and multiple lambs for SMWT. These differences in weight between litters were also significant in Menz ($P<0.05$) and single born lambs were heavier than the ones born as twins at BWT, SMWT and YWT. For the weaning weight, both the single and the multiple born lambs weighted 8 kg.

Season of birth had an important effect on BWT and WWT of Bonga sheep ($P<0.001$), where higher weights were observed in wet/rainy season. On the contrary, lambs born in the dry season (from October to May) had lower weights. Higher birth weight in rainy season could be due to the better body condition and body reserves of the pregnant dams during the rainy season. Pregnant ewes especially during the last 6 weeks of pregnancy grazing lush vegetation during the wet season would have heavier lambs at parturition.

Season effect was also significant on body weights in Menz. The highest birth weight was reported in the heavy rain and the harvest seasons, 2.7 and 2.8 kg, respectively. The SMWT was also highest during the heavy rain season and this is most likely the consequence of important improvement of the quality and quantity of forages and grass in the pastures during the rainy seasin. The lowest reported weights were recorded during the dry season which is characterized by scarcity of feed and low crop production due to extreme low temperatures and drought during this season.

The effect of parity was found to be significant on growth performances for both Menz and Bonga sheep. Lower BWT was observed at first parity and the highest BWT was observed at fifth parity for Menz and the 4th parity for Bonga. There was a declining trend in birth weight starting from 4th – 5th parity onwards and this may have some management applications for the farmers who may consider keeping dams until parity 6 before proceeding with culling. Lower BWT at early parity is due to younger ewes that are still growing; there is a competition between the fetus and the dam for nutrients, which has negative influence on BWT (Gbangboche et al., 2006) and the milk production of the younger ewes has not yet reached its peak. Heavier birth weights at later parities are due to heavier dam weight and larger body size (Awgichew 2000) as well as a uterine capacity that may facilitate relatively greater foetal growth in the subsequent pregnancies. Weaning weight of lambs was also significantly affected by ewes' parity. As parity of ewes increased, so did the weaning weight which is in line with previous findings of Surafel et al. (2012) who found that parity had significantly influenced WWT and dams with higher parity produced heavier lambs at weaning. Variation in WWT due to parity earlier reported by Momoh et al. (2013) is also in consensus with the current result. This could be a reflection of enhanced mothering ability of ewes as age increases and failure of young ewes to provide sufficient nourishment for the growth of fetuses (Baneh et al., 2009)

For Bonga breed, average lambing interval (LI) was 251.5 days which is lower than 267 days reported by Zewdu (2008) for Bonga sheep. Season, parity and birth type significantly affected LI ($P<0.05$). It can be also observed that LI is four days lower in wet season than in the dry one. This is in agreement with findings of Mengiste (2008) who reported shorter LI for Ethiopian ewes lambing in wet season than those with a parturition during the dry season of the year. The same author found that as parity increased, the LI showed a decreasing trend. The highest LI was recorded for the 2nd and 3rd parities, but it was evident that the interval became shorter with less variability after the 4th parity.

Average litter size of sheep under the current study, 1.56 lambs per ewe is within the range of tropical sheep breeds; Girma (2008) reported a range between 1.08 and 1.75. The finding of the current study is higher than 1.36 that was reported for Bonga sheep (Edea et al., 2012). In a report related to the community-based breeding program (CBBP) of Bonga breed, Haile et al. (2020) reported an average of 1.54 ± 0.006 for litter size for a total of 10,814 observations under village conditions which is comparable with our current findings. Depending on management system and other environmental factors, there could be variation in litter size between sites and breeds. However, the increase since the reports by Edea et al. (2012) may be attributed to the improvement CBBP brought.

Table 14. Least squares mean (±SE) for effects of sex, birth type, and season on different growth traits

Area	**Menz**				**Bonga**					
Fixed effects and level	**BWT**	**WWT**	**SMWT**	**YWT**	**BWT**	**WWT**	**SMWT**	**YWT**	**LI**	**LS**
Overall	2.7±0.09	8.0±0.27	13.7±0.30	18.8±0.24	3.1±0.10	14.5±0.51	19.9±0.89	35.7±2.40	251.5±7.8	1.56±0.01
CV %	11.32	10.51	10.23	40.09	25.60	43.84	31.21	22.54	44.62	11.53
Sex	**	*	*	*	*	**	**	NS	_	_
Male	2.80±0.09	8.1±0.28	13.0±0.03	18.9±0.24	3.2±0.10	14.8±0.51	20.6±0.89	34.0±0.82	_	_
Female	2.69±0.09	7.7±0.28	13.6±0.03	18.6±0.24	3.1±0.10	14.1±0.52	19.3±0.90	37.5±0.40	_	_
Birth type	*	*	*	**	**	***	***	*	*	_
1	2.8±0.08	8.0±0.04	14.0±0.06	19.4±0.07	3.6±0.05	16.0±0.10^{a}	23.4±0.09^{a}	37.7±2.40	250.3±2.90	_
2	2.6±0.11	7.8±0.06	13.39±0.04	18.1±0.46	3.2±0.05	14.1±0.10^{bd}	20.9±0.1^{b}	35.7±2.41	243.0±4.14	_
3	-	-	-	-	2.8±0.07	12.9±0.26^{c}	19.6±0.45^{c}	33.9±3.02	261.1±22.5	_
Parity	**	*	*	*	*	**	**	NS	*	*
1	2.5±0.04^{ac}	7.9±0.05^{a}	13.5±0.19^{a}	18.8±0.27^{a}	2.9±0.10^{a}	13.7±0.52^{a}	19.4±0.90^{a}	35.0±2.50^{a}	233.2±12.55	1.42±0.041
2	2.7±0.04^{b}	7.9±0.05^{a}	13.9±0.18^{b}	18.6±0.27 ^{a}	3.1±0.10^{b}	14.5±0.51^{b}	19.7±0.90^{a}	34.9±2.50^{a}	261.3±8.60	1.44±0.038
3	2.7±0.04^{b}	8.2±0.04^{b}	13.8±0.18^{b}	18.6±0.26 ^{a}	3.1±0.11^{b}	14.7±0.52^{b}	20.0±0.90^{bc}	36.3±2.61^{a}	260.1±8.56	1.55±0.029
4	2.8±0.04^{b}	8.1±0.04^{b}	13.7±0.18^{b}	18.9±0.26 ^{a}	3.2±0.12^{bc}	14.8±0.52^{b}	20.2±0.90^{bc}	36.6±2.40^{a}	251.2±9.13	1.57±0.040
5	2.8±0.05^{b}	8.2±0.05^{b}	14.0±0.19^{b}	18.8±0.27 ^{a}	3.2±0.11^{bc}	14.6±0.52^{b}	20.4±0.90^{b}	35.9±2.55^{a}	251.1±9.22	1.58±0.024
6	2.8±0.05^{c}	8.3±0.02^{b}	13.6±0.18^{b}	18.8±0.27 ^{a}	3.2±0.12^{c}	14.5±0.51^{b}	19.9±0.91^{c}	35.7±2.50^{a}	251.8±8.30	1.59±0.020
Season	*	**	*	**	*	***	**	*	*	**
1	2.7±0.09^{a}	8.2±0.01^{a}	13.9±0.30^{a}	17.0±0.26^{a}	3.1±0.1	17.8±0.51	20.35±0.89	36.1±2.40	249.9±8.06	1.61±0.019
2	2.8±0.09^{b}	8.0±0.09^{b}	13.6±0.30^{a}	18.9±0.25^{b}	3.4±0.1	14.2±0.510	19.62±0.9	35.4±2.49	253.0±8.12	1.58±0.020
3	2.7±0.09^{a}	7.8±0.09^{c}	13.4±0.30^{b}	19.5±0.24^{c}	-	-	-	-	-	-
4	2.6±0.09^{a}	8.2±0.09^{a}	13.5±0.31^{b}	18.8±0.27^{bd}	-	-	-	-	-	-

BWT: birth weight, WWT: weaning weight, SMWT: six months weight, YWT: yearling weight, LI: lambing interval, LS: litter size Means with different letter in column within fixed effects are significantly different, (P<0.05): *P<0.05, **P<0.01 and ***P<0.001, NS = non-significant. **Bonga has only two seasons while Menz has four.**

Estimation of genetic parameters

The estimates of (co)variance components and genetic parameter estimates for growth and reproductive traits along with estimated maximum likelihood and Akaike's Information Criterion (AIC) for six models for each body weight are depicted in Table 15.

Model comparison

Importance of inclusion of both or one of each of additive maternal genetic or dam permanent environment effect on direct animal genetic effect was tested using likelihood ratio test (LRT) and AIC to determine the most appropriate model fitting the dataset (Table 15).

Birth weight

Estimates of the direct heritability of birth weight (Table 15) depended on the model used and the breed, ranging from 0.02 to 0.10. For this trait, ignoring maternal effects (Model 1), yielded substantially higher estimates of σ^2_a and h_a^2 than other models for both Bonga and Menz breeds. Fitting a permanent environmental maternal effect (models 4, 5 and 6) slightly increased the log likelihood over that of model 1 (Table 15). Fitting a maternal genetic (model 2) rather than permanent environmental effect also resulted in an increase in log L over model 1 with an estimate of the maternal heritability of 0.03 for Menz and 0.2 for Bonga. In model 3, the estimate of direct-maternal genetic covariance (σ_{am}) was positive (0.004) and the direct maternal genetic correlation (r_{am}) was 0.39 for Menz sheep while for Bonga, the covariance was -0.15 and r_{am} was also negative -0.95. Based on the logarithm of the likelihood function, fitting both genetic and environmental components of the dam (Model 15) resulted in a significantly better fit as compared to other models. The inclusion of both genetic and environmental components due to dam effect (m^2, c^2) increased the estimate of c^2 to 0.02. After adding am in model 6, the estimate of (σ_{am}) was 0.001 with a corresponding estimate of r_{am} of 0.075. Besides, the likelihood value increased compared to a model ignoring additive maternal correlation (Model 15). The most appropriate model for birth weight included a maternal genetic as well as permanent environmental effects and their covariance am (Model 6). The direct heritability estimate (0.04) of Bonga breed in the present study was in agreement with the finding of Rashidi et al. (2008) for Kermani sheep (0.04) and Mandal et al. (2008) for Muzaffarnagari sheep (0.08). However, higher estimates were reported by Vatankhah and Talebi (2008) for Lori-Bakhtiari sheep (0.31), Lobo et al. (2009) for a Brazilian multi-breed meat sheep population (0.35), and Shokrollahi and Baneh (2012) for Arabi sheep (0.42). The low values in our study may be explained by the high contribution of maternal effects to this trait. Several maternal factors such as the amount of milk production, milk composition, udder conditions, metabolic disorders, sexual transmitted diseases significantly influence the BTW. Therefore, BTW is mainly controlled by diverse non-genetic factors resulting in low estimates of the heritability. The maternal heritability estimates for birth weight (0.03) obtained in this study was lower than the findings of Aguirre et al. (2016) in Santa Ines sheep (0.14). Similar results are also reported by Mohammadi et al. (2013) in Lori sheep as well as Tamioso et al. (2013) in Suffolk sheep (0.17). The estimate of permanent environmental maternal effect (c^2) for birth weight (0.07) in our study was in agreement with the findings of Zishiri et al. (2014), Gholizadeh and Ghafouri-Kesbi (2015), Abderrahmane et al. (2015) who reported figures between 0.05 and 0.09. The permanent environmental effect (c^2) due to the dam can be ascribed to uterine environmental effects and the feeding level in late gestation of the ewe (Maria et al., 1993; Snyman et al., 1995).

Weaning weight

Depending on the model used and the breed, estimates of direct additive variances ranged from 0.63 to 3.28. Addition of a permanent environmental maternal effect (model 3) led to a reduction in additive direct heritability compared to model 1. Model 2, which included only direct and maternal additive effects yielded an estimate of m^2 that explained only 20% of phenotypic variance for Menz and 42.1% for Bonga. Fitting a non-zero covariance (σ_{am}) along with a maternal genetic effect (model 3) resulted in a large positive direct maternal covariance (3.49) along with a negative direct maternal genetic correlation (r_{am}) of -0.99. Model 5 attempted independent estimation of the genetic and environmental components of the effect of dam, but the estimate of m^2 was reduced to 5%, indicating low additive maternal variance for weaning weights in these data. Adding σ_{am} in model 6 led to an estimate of additive maternal correlation of 0.93 with a corresponding estimate of r_{am} of -0.99, but inclusion of the covariance component improved goodness of fit when compared to model 5. According to likelihood, model 1 was the preferred model for description of weaning weight for both Bonga and Menz breeds and was used to estimate breeding value for weaning weight of Bonga and Menz sheep. The estimate of the direct heritability of weaning weight in the present study for Menz (0.18) was similar to the findings of Snyman et al. (1995), Abegaz et al. (2002), Matika et al. (2003), and Ozcan et al. (2005) for different breeds of sheep under different production systems. However, the direct heritability of weaning weight for Bonga (0.28) was also in accordance to studies reported by other workers in various sheep breeds (Snyman et al., 1995; Notter 1998; El Fadili et al., 2000; Assan et al., 2002; Gizaw et al., 2007), and lower heritabilities for this trait were reported by Notter (1998) in Polypay sheep (0.07) and Ekiz et al. (2004) in Turkish Merino sheep (0.06). The estimate of total heritability (h_t^2) for weaning weight in Menz breed was moderate in magnitude (0.16), indicating a possible phenotypic response to selection for this trait. Estimates of h_t^2 reported by Notter (1998) in Suffolk sheep and Yazdi et al. (1997) in Baluchi sheep were in agreement with those from this study. However, both lower (El Fadili et al. 2000; Ekiz et al. 2004; Ozcan et al. 2005) and higher (Snyman et al. 1995; Assan et al. 2002) estimates for h_t^2 for this trait have been reported in other studies involving different breeds of sheep.

Six months weight

For SMWT trait, Model 2 was the best fit for Menz sheep while for Bonga, model 1 was considered the best suitable one. In model 1, where the maternal effect was not considered, heritability was high for both Menz and Bonga (0.39, 0.32). Introducing a maternal effect (Model 2) explained 17% of the total phenotypic variance for 6 months weight of Bonga sheep. However, for Menz breed, the maternal effect did not contribute to the phenotypic variance. Fitting a non-zero covariance ($\boldsymbol{\sigma_{am}}$) along with a maternal genetic effect (Model 3) provided a large negative direct maternal covariance. Model 4, which includes permanent environmental maternal effects, also identified an environmental effect contributing 17% of total variation for this trait. In model 5, the genetic and environmental components of the effect of dam are pulled apart and resulted in a substantial reduction in the estimate of the maternal genetic effect for 6-months weight. Allowing for a direct-maternal covariance ($\boldsymbol{\sigma_{am}}$) yielded a positive direct maternal covariance (Model 6), 0.66 for Bonga sheep with a negative estimate of r_{am}, (-0.19). The low maternal effect on 6-months weight for Menz breed indicated that the maternal effect had less effect on selection response for this trait. The c^2 effect for post-weaning weights of Bonga lambs contributed 5% of the total phenotypic variance. These results were also in accordance with those published in literature by several authors (Matika et al. 2003; Safari et al. 2005; Mokhtari et al. 2008). The c^2 effect increased from birth to weaning weight and thereafter declined. However, Tosh and Kemp (1994) observed that the permanent environmental effect decreased in importance as lambs became increasingly independent of their dams. These analyses suggest that after weaning, maternal permanent environmental effects were still a source of variation up to yearling age. Similar trends were reported by Maria et al. (1993), Tosh and Kemp (1994), and Miraei-Ashtiani et al. (2007). This decrease in maternal permanent environmental effects at later ages presumably reflects an increasing impact on body weight of the animal's own genotype at more advanced ages. Total heritability estimates for 6-months weights of Bonga and Menz were high in magnitude, ranging from 0.33 to 0.41, and were similar to direct heritability estimates. The high estimates of total heritability indicate the scope for some selection progress for these traits. These estimates of h_t^2 for 6-months weights were comparable with the findings of other researchers (Abegaz et al. (2002); Ozcan et al. (2005); Safari et al. (2005)) but lower than the estimates of Snyman et al. (1995) and Yazdi et al. (1997) in other sheep breeds.

Table 15. Estimates of (co)variance components and genetic parameters for body weight traits from univariate analyses

Area	Trait	Model	σ^2_a	σ^2_m	σ^2_e	σ^2_c	σ^2_p	σ_{am}	h^2_a	h^2_m	c^2	h^2_t	r_{am}	log L	AIC
Menz	**BWT**	1	0.03	-	0.38	-	0.41	-	0.08±0.02	-	-	0.07	-	-323.369	-325.369
		2	0.02	0.008	0.37	-	0.42	-	0.06±0.02	0.02±0.01	-	0.06	-	-322.136	-325.136
		3	0.02	0.005	0.38	-	0.41	0.004	0.06±0.02	0.01±0.01	-	0.07	0.39	-322.033	-326.033
		4	0.03	-	0.37	0.005	0.41	-	0.07±0.02	-	0.01±0.01	0.07	-	-322.878	-325.878
		5	0.02	0.01	0.38	0.001	0.42	-	0.06±0.02	0.03±0.03	0.02±0.02	0.06	-	-323.513	-327.513
		6	**0.02**	**0.02**	**0.40**	**0.004**	**0.54**	**0.001**	**0.04±0.02**	**0.03±0.07**	**0.07±0.04**	**0.06**	**0.075**	**-330.692**	**-336.692**
	WWT	**1**	**0.71**	-	**3.22**	-	**3.94**	-	**0.18±0.03**	-	-	**0.18**	-	**-4737.248**	**-4739.248**
		2	0.65	0.04	3.24	-	3.94	-	0.16±0.03	0.01±0.01	-	0.17	-	-4603.773	-4606.773
		3	1.07	0.32	3.00	-	3.99	-0.40	0.26±0.06	0.08±0.04	-	0.16	-0.68	-4601.483	-4605.483
		4	0.63	-	3.23	0.07	3.94	-	0.16±0.03	-	0.01±0.01	0.16	-	-4603.217	-4606.217
		5	0.63	0.001	3.24	0.07	3.95	-	0.16±0.03	0.00±0.03	0.01±0.03	0.16	-	-4603.232	-4607.232
		6	1.02	0.13	2.99	0.15	4.07	-0.33	0.25±0.07	0.03±0.06	0.03±0.03	0.14	-0.89	-4600.985	-4600.985
	SMWT	1	2.48	-	3.86	-	6.32	-	0.39±0.03	-	-	0.39	-	-4681.127	-4683.127
		2	**2.49**	**0.001**	**3.84**	-	**6.34**	-	**0.39±0.03**	**0.10±0.02**	-	**0.39**	-	**-4681.146**	**-4684.146**
		3	5.64	1.79	2.05	-	6.46	-3.02	0.47±0.06	0.27±0.04	-	0.31	-0.95	-4631.327	-4635.327
		4	2.48	-	3.82	0.02	6.33	-	0.39±0.03	-	0.003±0.01	0.39	-	-4681.110	-4684.110
		5	2.49	0.001	3.82	0.02	6.34	-	0.39±0.04	0.00±0.04	0.005±0.03	0.39	-	-4681.136	-4685.136
		6	3.80	0.75	3.79	0.02	6.94	-0.90	0.54±0.01	0.10±0.01	0.004±0.01	0.41	-0.90	-4653.501	-4659.501
Bonga	**BWT**	1	0.10	-	0.26	-	0.37	-	0.28+0.02	-	-	0.27	-	150.409	148.409
		2	0.06	0.03	0.27	-	0.36	-	0.16+0.02	0.10+0.01	-	0.21	-	182.344	179.344
		3	0.10	0.16	0.22	-	0.48	-0.15	0.20+0.01	0.34+0.01	-	-0.09	-0.99	194.079	189.079
		4	0.08	-	0.28	0.04	0.48	-	0.18+0.01	-	0.10+0.01	0.02	-	174.821	168.821
		5	0.06	0.01	0.26	0.04	0.37	-	0.17+0.02	0.03+0.03	0.11+0.03	0.18	-	194.877	190.877
		6	**0.06**	**0.10**	**0.26**	**0.04**	**0.36**	**-0.08**	**0.17+0.02**	**0.20+0.02**	**0.11+0.01**	**0.17**	**-0.99**	**195.632**	**192.632**
	WWT	**1**	**3.28**	-	**4.49**	-	**7.78**	-	**0.42±0.02**	-	-	**0.42**	-	**-12568.42**	**-12570.42**
		2	2.37	1.34	4.21	-	7.92	-	0.29±0.02	0.17±0.01	-	0.38	-	-12296.08	-12299.08
		3	4.34	3.49	3.08	-	8.01	-2.89	0.54±0.04	0.43±0.03	-	0.22	-0.74	-12247.21	-12251.21
		4	2.48	-	4.07	1.35	7.91	-	0.31±0.02	-	0.17±0.01	0.31	-	-12287.25	-12290.25
		5	2.48	0.56	4.07	1.30	7.92	-	0.31±0.02	0.007±0.03	0.16±0.03	0.35	-	-12287.19	-12291.19
		6	1.21	0.72	5.17	0.50	5.37	0.93	0.14±0.22	0.08±0.04	0.01±0.01	0.55	0.99	-12364.67	-12370.67
	SMWT	**1**	**5.13**	-	**7.30**	-	**12.44**	-	**0.32+0.01**	-	-	**0.41**	-	**-7815.363**	**-7817.363**
		2	4.12	2.21	6.33	-	12.67	-	0.32±0.03	0.17±0.23	-	0.41	-	-7783.898	-7786.898
		3	8.99	8.08	3.57	-	12.97	-7.69	0.39±0.05	0.62±0.05	-	0.12	-0.90	-7723.938	-7727.938
		4	4.16	-	6.11	2.37	12.65	-	0.32±0.03	-	0.08±0.02	0.33	-	-7775.478	-7778.478
		5	4.16	0.01	6.11	2.37	12.65	-	0.23±0.03	0.00±0.06	0.08±0.06	0.33	-	-7775.480	-7779.480
		6	3.50	3.19	5.41	1.09	18.50	0.66	0.18±0.01	0.17±0.01	0.05±0.01	0.33	-0.19	-7784.184	-7790.184

BWT: birth weight, WWT: weaning weight, SMWT: six months weight. σ^2_a, σ^2_m, σ^2_e, σ^2_c, σ^2_p: variance of direct, maternal, residual, maternal permanent environment and phenotypic respectively; σ_{am} covariance between direct and maternal; h^2_a, h^2_m, h^2_t: heritability of direct, maternal and total respectively; c^2: ratio of maternal permanent environmental variance to phenotypic variance; r_{am}: genetic correlation between direct and maternal; log L: maximum log likelihood AIC: Akakie information criteria.

Correlation estimates

Multivariate estimates of genetic correlations between body weights at different ages are presented in Table 16. The genetic correlations between body weights at different ages were moderate to high and positive for Menz, ranging from 0.31 (WWT-YWT) to 0.90 (WWT-SMWT). Moderate to high genetic correlations in the range of 0·59 to 0·96 among different body weights were also reported by Yazdi et al. (1997), Ozcan et al. (2005), and Bahreini-Behzadi et al. (2007) for different breeds of sheep. The high genetic correlations between body weights of lambs indicate that selection based on any of these traits could lead to considerable genetical improvement of the other correlated traits because similar sets of genes appear to be responsible for body weights at various ages. The large genetic correlation (0.90) between WWT and SMWT of lambs in the present study confirms that early age selection at weaning age would result in a substantial correlated genetic response in SMWT weight. This decision is helpful for farmers who are interested to sell at early age for their immediate cash needs.

Similarly, positive and medium to high (ranging from 0.33 to 0.74) phenotypic correlations were observed between all body weights in Menz. The estimates of phenotypic and residual correlations among investigated traits were generally lower than the genetic correlations (Table 16). Birth weight and yearling weight had the low to moderate phenotypic correlation with the other traits, ranging from 0.31 to 0.68, whereas the remaining weights had moderate to high correlations, ranging from 0.47 to 0.90. In general, the phenotypic correlations between traits at different ages decreased as the time between measurements of the traits increased. Our estimates for phenotypic correlations were comparable with those reported in the literature (Bahreini-Behzadi et al., 2007; Miraei-Ashtiani et al., 2007; Rashidi et al., 2008; Mokhtari et al., 2008).

Table 16. Estimated genetic (above diagonal) and phenotypic (below diagonal) correlations (Menz)

Trait	BWT	WWT	SMWT	YWT
BWT	--	0.88*	0.79*	0.39
WWT	0.33	--	0.90*	0.31
SMWT	0.68*	0.71*	--	0.53
YWT	0.65*	0.47	0.75	--

BWT: birth weight, WWT: weaning weight, SMWT: six months weight YWT: yearling weight. *: (P<0.05).

Genetic correlations estimated for Bonga showed that this parameter decreases when the time interval between traits increases (similar to what we mentioned above for phenotypic correlations of Menz breed). Favorable positive correlations were consistently estimated among the same group of traits (growth traits or reproductive traits) (Table 17). Phenotypic correlations were generally slightly lower than the corresponding genetic correlations. As reported by Boujenane & Hazzab (2008), genetic and phenotypic correlations were higher in adjacent weights than in non-adjacent ones. Many authors have already reported the same patterns on genetic correlations in other sheep populations. For instance, Miraei-Ashtiani et al. (2007) reported estimate of 0.4 for genetic correlations of BW-6MW versus 0.946 for WW-6MW in Sangsari lambs. In addition, similar values have been reported by Ozcan et al. (2005) in Turkish Merino sheep. The estimated genetic correlation of BWT-SMWT was 0.57 and is in accordance with those reported by Miraei-Ashtiani et al. (2007) in Sangsari sheep (0.50) and Mokhtari et al. (2008) in Kermani sheep (0.53). The positive and high estimate for the genetic correlation between WWT and SMWT (0.97) in current study is in agreement with those reported by Vatankhah and Talebi (2008) in Lori-Bakhtiari sheep (0.90) and Gizaw et al. (2007) in Menz sheep (0.98). Relatively high and positive estimates of genetic correlations indicate that selection for any one of the studied body weight traits could result in genetic progress for the other traits. Also, an estimate of the phenotypic correlation between BWT and WWT (0.24) from the current study was close to the value of 0.25 reported by Mokhtari et al. (2008) who also reported an estimate of 0.59 for phenotypic correlation between WWT and SMWT in Kermani sheep. The high genetic correlation between WWT and SMWT weight indicates that sires could be selected at an earlier age in a selection program with emphasis on meat and body size.

Table 17. Estimated genetic (above diagonal) and phenotypic (below diagonal) correlations (Bonga)

Trait	BWT	WWT	SMWT	YWT	LI	LS
BWT	--	0.48*	0.57*	-0.53	0.37*	0.35
WWT	0.24*	--	0.97*	0.70*	-0.53	0.43
SMWT	0.43*	0.73*	--	0.78	-0.52	0.42*
YWT	-0.81	0.27*	0.32	--	-0.12	0.02
LI	0.11	0.06	-0.54	-0.21	--	-0.98
LS	0.63*	0.28	0.26*	-0.84	0.01	--

BWT: birth weight, WWT: weaning weight, SMWT: six months weight YWT: yearling weight, LI: lambing interval, LS: litter size *: (P<0.05)

The phenotypic correlations between litter size and BWT, WWT and SMWT were 0.63, 0.28 and 0.26, respectively. Genetic correlations were higher than phenotypic correlations (0.43 and 0.42 for WWT and SMWT, respectively). Rosati et al. (2002) reported estimates of genetic correlation between number of lambs born alive and weaning weight to be 0.51 which is considered moderate and is comparable to the 0.43 correlation found in current study. In a review by Fogarty (1995), there were six values on genetic and phenotypic correlations between number of lambs and weaning weights with averages of 0.83 and 0.88. Hansen & Shrestha (1999) reported genetic correlations of 0.19 for litter size at birth and lamb weight at weaning (91 days) with corresponding phenotypic correlations of 0.48. Hanford et al. (2002) reported an estimate of genetic correlations ranging from 0.00 between litter size and birth weight to 0.33 between litter size and weaning weight while Bromley et al. (2000) reported a negative correlation -0.37 for the Columbia breed. It appears that there is a large between-breed variation with respect to genetic correlations between litter size and weaning weight and at times, standard error estimates are very high. This suggests that correlation between litter size and live weight can be used as a selection criterion for indirect improvement in productivity.

The negative genetic correlations of LI with WWT, SMWT and YWT imply that different genetic mechanisms are involved in expressing these traits at different stages of growth. Only few studies present genetic correlations between LI and live weight traits.

Correlation between phenotypic based selection and EBV-BLUP

Accuracy of EBV is based on the amount of performance information available on the animal and its close relatives - particularly the number of progenies analyzed. Accuracy is also based on the heritability of the trait and the genetic relationships (correlations) with other recorded traits. Since pedigree data was unavailable at the beginning of the CBBP, farmers were practicing selection based on phenotype; the sire with the highest SMWT was ranked first and selected. Table 18 shows the correlation between the phenotype BV and the BLUP EBV. Generally, the correlation in both Menz and Bonga is high during all the years ranging from 0.77 to 0.92. There was a trend for the correlation values to be higher in the early years and this may be explained by the fact that BLUP EBV was based on limited information and the weight of SMWT in estimating BLUP EBV was high. As more information became available allowing the data to be corrected for fixed effects and also as a result of incorporating the pedigree information, the value of the correlation slightly decreased meaning that a deviation between phenotype BV and BLUP EBV is taking place. Ultimately, at the foundation of the CBBP, the phenotype-based selection helped creating a good basis, but for more informed and reliable selection decisions, and more genetic progress to be achieved, pedigree data is crucial. This could justify the use of phenotypic values (duly adjusted for non-genetic factors) as an approximation to breeding values and to estimate responses to selection in village-based breeding programs when data recordings were unavailable.

Table 18. Correlation between phenotypic based selection and EBV-Blup

Year	**Six months weight correlation**	
	Bonga	Menz
2010	0.86	0.79
2011	0.91	0.77
2012	0.90	0.80
2013	0.84	0.92
2014	0.87	0.84
2015	0.84	0.80
2016	0.83	0.81
2017	0.85	0.83

Impact of selection of SMWT on other traits and genetic trends

Following participatory discussion with communities to define the breeding objectives in both Menz and Bonga CBBPs, six months weight was found to be a trait of high economic importance like in other meat-producing Ethiopian sheep (Gizaw et al, 2018). The SMWT trait was set as a main selection criterion since the kickoff of CBBP. In current CBBPs, lambs are weighed at six months of age before farmers make selection decisions and sell surplus lambs for slaughter or castrate and fatten them. There was an important genetic response that led to an increased SMWT in CBBPs flocks (Haile et al., 2020). The genetic response for the selective breeding program of CBBP wasn't limited to SMWT only, it has also affected other growth traits such as YWT, BWT and WWT.

For both sites, 6-months weight, the major selection trait in CBBPs, increased (P < 0.05) over the years (Figures 7 and 8). The average increase was 0.12 ± 0.011 kg/year and 0.042 ± 0.003 kg/year for Bonga and Menz, respectively. The increases were more pronounced in the larger Bonga breed compared to the smaller Menz sheep. Our results are backed by many previous reports that confirmed the genetic progress in SMWT. Mueller et al. (2019), reported an increase of 0.11 kg/year for Menz breed. Results from Haile et al. (2019) has revealed a significant increase of SMWT (P<0.05) in CBBP flocks. Indeed, in Bonga, the average increase was 0.21 ± 0.018 kg/year, while it was 0.11 ± 0.003 kg/year for Menz. Similar trends were reported for estimates of genetic change per year for SMWT and were positive in the case of Ossimi and Rahmani sheep (Shaat et al., 2004). Mokhtari and Rashidi (2010) also reported positive and significant genetic trends in Kermani Sheep. Differences in terms of genetic gain between our results and those available in the literature for Bonga and Menz breeds can be explained by the fact that in the current study, we used much larger datasets resulting from including all available data since the start of the CBBP's. Different sites are at various stages of implementation of the breeding program and there are also important differences in management and in the prevalence of environmental factors.

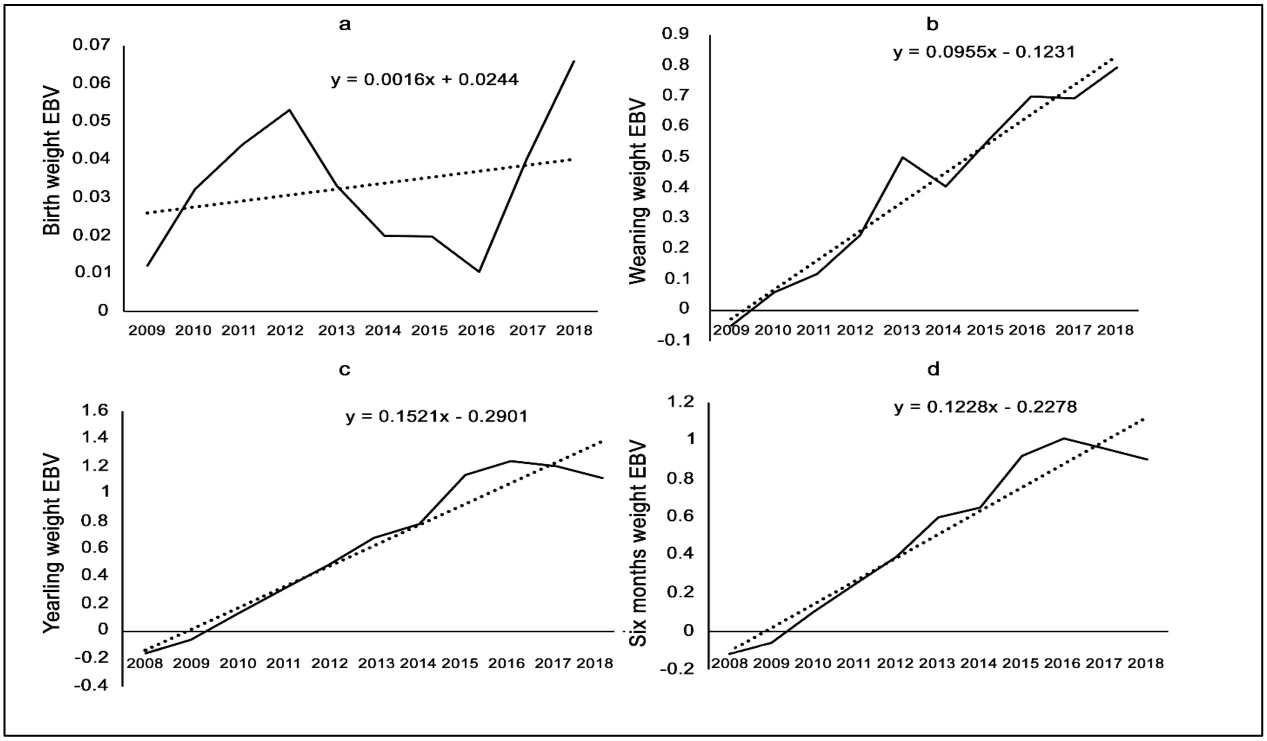

Figure 7. Genetic trend of estimated breeding values (EBV) for body weight at birth (a), weaning weight (b) Six months weight (c) and yearling weight (d) in Menz sheep.

The genetic trend of weaning weight in figure 7 and 8 shows a significant increase ($P < 0.05$) of 0.10 and 0.03 kg/year for Bonga and Menz, respectively. Considering that there was no direct selection on weaning weight in CBBP flocks, the estimated increases in Menz and Bonga are due to a positive correlated response with SMWT- based selection. This is consistent with previous findings by Haile et al. (2019) who also reported a lack of increase in birth weight in Bonga and Horro and it was argued that this is advantageous because improvement in this trait beyond a threshold level may be associated with dystocia and loss of productivity (particularly in young females).

In Menz, positive and significant annual genetic progress was recorded for WWT, SMWT and YWT traits. Birth weight was slightly improved during the study period (+0.0016 kg/year), therefore, if improvement in birth weight is desired, then selection trait has to be adjusted and not only focused on SMWT. However, improvement in BWT is not recommended in the case of Menz because of increased frequency of lambing disorders because of the low adult weight of females.

The yearling weight has increased slightly over the years with 0.008kg/year. The low but significant genetic gain is due to the fluctuations of the genetic trend and especially the big drop that happened in 2016. In 2015, a relatively sharp drop by 0.05kg/year is observed in weaning weight, and then the drop was 3 folds in yearling weight (Figure 8). It is difficult to explain such a drop without going back and scrutinizing the database to understand what could have happened. One among the reasons could be an influx of animals from outside the CBBP. Contrary to Menz, yearling weight with Bonga sheep was characterized by a significant ($p<0.05$) increase in its genetic trend by 0.15 kg/year. The increasing direct genetic trend value of body weight at advanced ages may be attributed to the relatively higher additive genetic variation. As reported by Shaat et al. (2004), high genetic trend may be explained by the high additive genetic variation.

The genetic trend for LI and LS for Bonga breed over the years is significant ($P<0.01$; Figure 8). While the trend is positive for LS, there is a decreasing trend for LI. The estimated breeding values (EBV) for LS is increasing over the years although the pattern is not regular. The trend is showing sharp increase from 2008 to 2011 followed by a decreasing trend till 2014. Starting from 2014 the trend has increased again and then plateaued in 2016 and 2017. Litter size is one of the selection traits in Bonga. The results indicate that positive trends in reproductive traits, despite their low heritability, could be achieved. With a structured selection program backed by improvement in management practices, substantial impact in sheep production could be expected (Haile et al., 2020). Atkins (1986) has reported a high correlation between body weight and litter size (0.66); he also reported that indirect selection on body weight alone would result in greater response in litter size than direct selection on dam's litter size performance. The proportional change in body weight would be of the same magnitude as the proportional change in litter size. This comparison of direct and indirect selection responses in litter size is only applicable to post weaning body weight (Oliver et al. 2001). Physiologically, faster growing ewe lambs are reported to display earlier sexual maturity than slow growing females and heavier weights of females at mating times have been shown to be correlated with increased ovulation rate and litter size. This is supported by observations in Australian Merino ewes.

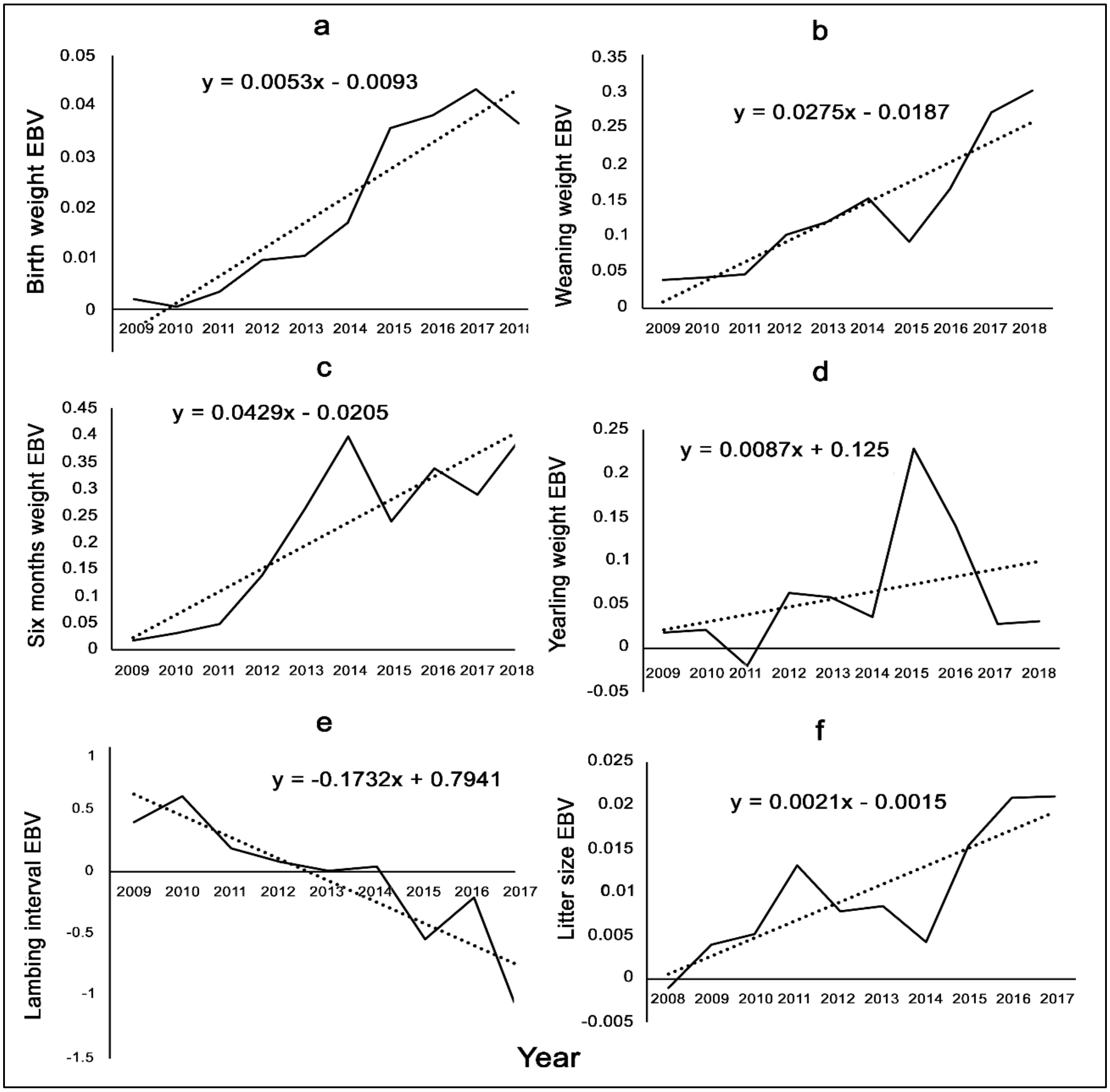

Figure 8. Genetic trend of estimated breeding values (EBV) for body weight at birth (a), weaning weight (b), yearling weight (c), six months weight (d), lambing interval (e) and litter size (f) in Bonga sheep

In contrast to litter size, the genetic trend for LI has shown decreasing trends over the years with a fairly irregular pattern. The irregular patterns were mainly reflected in years 2009 to 2011 and 2014 to 2016. A significant and negative trend in LI confirms that the sheep have reached their sexual maturity at younger ages along with a relatively shorter interval between successive lambing as a result of selection resulting in heavier females entering mating and hence general improvement in the flock performance. Genetic responses in selective breeding experiments have been reported in many studies. For example, in an experiment set up to evaluate the response of Menz sheep to selection for yearling live weight, a substantial response was evident on lambing interval (Gizaw et al., 2007). Positive changes have also been reported for purebred Tsigai and improved Valachian and Lacaune sheep in the Slovak Republic (Oravcová and Peškovičová, 2008), for Lohi sheep of Pakistan (Javed et al., 2013) and for Malpura sheep of India (Arora et al., 2010). However, these reports all referred to on-station performance and there are no reports from on-farm, community-managed flocks.

From the results it is evident that selection on the major trait, SMWT, has positively affected all the growth and reproduction traits, except birth weight. Therefore, where positive correlation exists, and under small holder farmers' condition where performance and pedigree recording are difficult, breeding programs could focus on a few carefully selected traits, but the benefits would be evident through correlated responses. Very interesting are the correlations between growth and reproductive traits in Bonga where these two types of traits are economically important and our work did not show any indication of antagonism.

Sire genetic trends

In CBBP, selection is done on males only, that's why all males are considered improvers compared to their contemporaries. The Sire trend was calculated as deviations of average EBV of selected sires from the average EBV of their population. The genetic trends obtained in the study indicated that significant and sustained genetic progress in the desired direction has been achieved in SMWT in Bonga and Menz breeds.

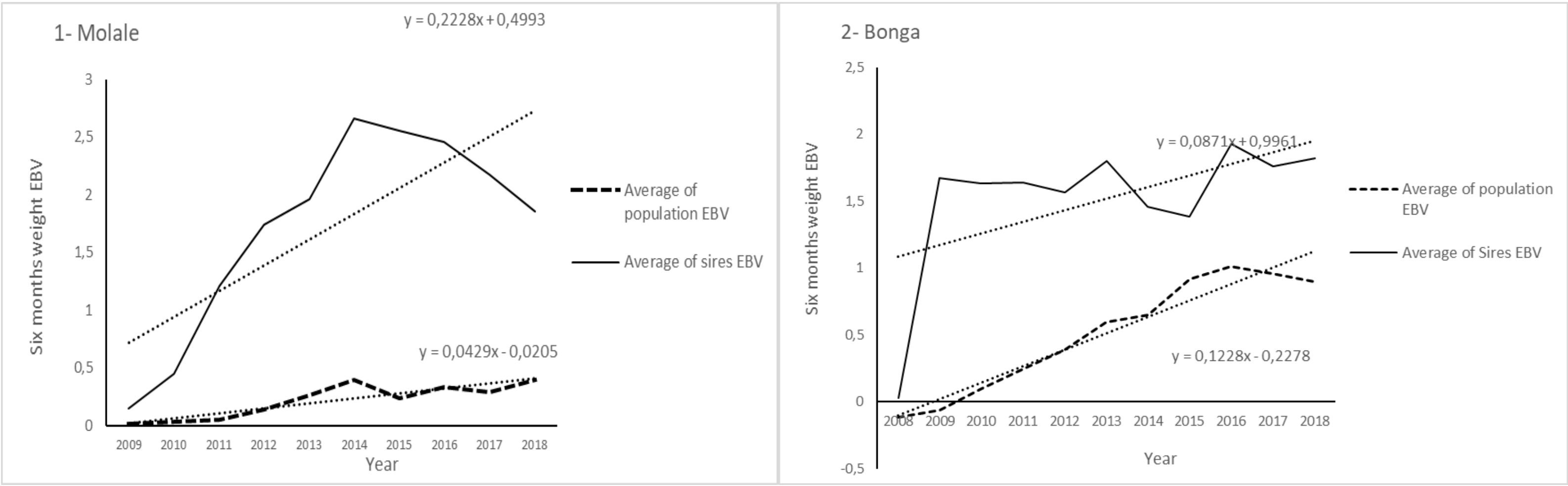

Figure 9. Genetic trend of sires and population in Menz (1) and Bonga (2)

The sire lambs had a genetic superiority of 2.40 kg over the base generation lambs in 6-month weight in 2014. The genetic progress in the 6-month weight in the selected sires was five times faster than the progress in the base flock from 2010 to 2016 for Menz breed (Figure 9). In the population trend, average breeding values of lambs increased by 0.042 kg over the base generation. The corresponding values for the sires' group were 0.22 kg.

The evaluation of genetic trend gives an indication of breed direction as well as the rate of genetic improvement due to the application of breeding program (Bosso et al., 2007). In this study, sire genetic trend estimates showed that there was a significant and positive genetic improvement in SMWT trait and provided evidence that selection for improvement of body weight traits in sheep

CBBP's in Ethiopia is effective. There were some irregular fluctuations in the trend of SMWT for Bonga sheep (Figure 10) like the abrupt increase in the first year of selection which may be explained by the rapid genetic gain that can be realized when the first cohort of improved sires are selected within the base population. The decrease in the mean predicted breeding values of Bonga sires in 2013 was probably due to selection of sires with low breeding values. This low selection response could indicate that introduction of sires was based solely on phenotypic characteristics (Mokhtari and Rashidi, 2010).

Mueller et al. (2018) reported that, the genetic mean of SMWT of base Menz lambs' lags about two generations (seven years) of improvement behind the selected sires. More intense use of some rams in a CBBP through artificial insemination (AI) allows the reduction of number of rams required and an increase in their selection differential. He also reported a genetic improvement of 0.14 kg/year for Bonga which is in accordance with the figure of 0.12 kg/year recorded in current study.

Genetic diversity

In this study, we present findings of analysis of genome diversity, structure and dynamics comparing between breeds: Menz *vs.* Bonga and within breed: Menz improved (CBBP members) and Menz control (animals outside CBBP). Because of the lack of data on control animals from Bonga, the comparison within this breed is limited to flocks recruited under CBBP in two sites, namely Boqa and Shuta.

Observed heterozygosity H_O, which is the proportion of heterozygotes observed in a population, and expected heterozygosity H_E, that refers to the percentage of loci heterozygous per individual or the number of individuals heterozygous per locus (Ojango et al., 2011) are the most widely used parameters to measure genetic diversity in a population (Toro et al., 2009). Literatures suggest that estimates having greater than 0.5 heterozygosity values are believed to be appropriate for genetic diversity studies (Davila et al., 2009; Dorji et al. 2012). However, the H_O in the current study of Menz control, Menz improved and Bonga (Table 19) were below 0.5. Bonga showed a H_O of 0.30 which is in accordance to Abulgasim et al. (2019) findings (0.29) for Bonga breed. Bonga's expected heterozygosity (0.3) was lower than 0.66 reported by Gizaw et al. (2008).

A low heterozygosity estimates may be because of the effect of small population size and minimal or null immigration of new genetic materials into the population (Canon et al., 2006). The observed heterozygosity estimates in Menz improved and control were 0.31 and 0.32, respectively. The slight difference between both can be explained by the fact that improved Menz sheep are undergoing selection through the CBBP. Getachew et al. (2019) reported a higher H_O for Menz, 0.34. The small difference between this estimation and the current one can be due to number of observation (34<56). Edea et al. (2017) reported a 0.33 H_O and 0.32 H_E for Menz. Most of the observed heterozygosity values are generally closer to, but lower than, the expected heterozygosity in most of the breeds indicating no overall loss in heterozygosity (allele fixation) (Araujo et al., 2006) and the populations are at Hardy-Weinberg equilibrium (HWE). Nigussie et al. (2018) reported higher level of genetic diversity H_O and H_E in three other Ethiopian breeds, Afar, Blackhead Somali and Hararghe Highland, that ranged from 0.57 to 0.75. Lower heterozygosity is expected in the improved breeds as a result of intensive selection in order to improve growth weight.

Table 19. The observed and expected heterozygosity of the studied population and their inbreeding coefficient

Population	**H_O**	**H_E**	**F_{IS}**
Bonga_improved	0.306	0.308	0.0044
Menz_control	0.326	0.328	0.0046
Menz_Improved	0.319	0.324	0.0141

H_O = Observed heterozygosity, H_E = expected heterozygosity, F_{IS} = inbreeding coefficient.

The inbreeding coefficient (F_{IS}) is estimated for populations which show significant deviation from the HWE (Ojango et al., 2011). A high positive F_{IS} indicates a high degree of homozygosity and vice versa while negative values indicate low level of inbreeding (Dorji et al., 2012).

The F_{IS} varied between 0.014 in Menz improved sheep and 0.004 in Bonga improved sheep. The low inbreeding values in the CBBP population would imply that the measures taken (ram rotation) have generated desirable results. Moderate to high inbreeding levels were reported by various scholars for different sheep populations. The inbreeding coefficient for three populations in Ethiopia, were 0.02, 0.03 and 0.01 for Afar, Blackhead Somali, and Hararghe Highland respectively (Table 19), reported by Nigussie et al., (2015). Other inbreeding coefficient such as Vembur (F_{IS}=0.29) reported by Pramod et al. (2011) ,Magra (F_{IS} =0.159) (Arora and Bhatia 2006) and Kheri (F_{IS} =0.128) (Arora and Bhatia 2006), these were sheep breeds of India, some Merino derived sheep breeds of Italy (F_{IS}=0.048-0.118) (Ceccobelli et al. 2010), some Turkish sheep breeds (F_{IS} =0.09-0.16) (Evren 2004) eight local sheep breeds of China (F_{IS} =0.404) (Zeng et al. 2010), fifteen sheep populations of Kenya (F_{IS} =0.109) (Mukhongo et al., 2014) and Nigerian indigenous sheep (F_{IS} =0.34) (Agaviezor et al., 2012).

The reported values of inbreeding in this study are considered ** might be because of the small sheep population size, closed breeding system and very limited number of breeding rams used for many consecutive years. However, tolerable mean values of F_{IS} (0.087) for Ganjam (Arora et al., 2010), (0.0525) for Kail (Ahmed et al., 2014) and (0.0786) for Tamil Nadu (Kavitha et al., 2010) sheep breeds of India and F_{IS} (0.07) for Turkish breeds (Yilmaz et al., 2015) were reported by scholars. These moderate levels of inbreeding may be a result of moderate levels of mating between closely related individuals under field conditions and may be the uncontrolled and unplanned mating that caused high levels of inbreeding (Mekuriaw et al., 2016). On the contrary, F_{IS} (-0.19) (Hatami et al., 2014) and F_{IS} (-0.197) (Nanekarani et al., 2011) depicting low levels of inbreeding and an excess of heterozygotes was reported for three Iranian sheep breeds and Karakul sheep breed of Iran, respectively.

Principal Component Analysis (PCA)

To illustrate relationships within individuals and among Ethiopian sheep populations, PCA was performed using 514,624 SNPs. The first two components accounted for 14.47% (PC1) and 1.70% (PC2) of the variation, and clustered the Ethiopian sheep population according to their region and breed development. The first component clearly separates the Menz breed from the Bonga breed (Figure 10). These clustering patterns corresponded with their geographic distribution. Bonga sheep formed a tight cluster, whereas outliers were detected in the Menz population. The second component permited the separation within the breed. The Menz control showed higher degree of within population variation whereas the improved were more clustered together. Separation of Improved Menz from control Menz attributed to results of selection for improvement of production traits. Boqa and Shuta, the two sites where CBBP was undergoing for Bonga breed, were clustered together. This shows that the management and the selection procedures in both sites are the same, leading to homogenous population. It’s also important to mention the overlapped clusters of Menz control and improved Menz. This can be explained by the fact that some farmers are using the improved rams of CBBP for their flocks.

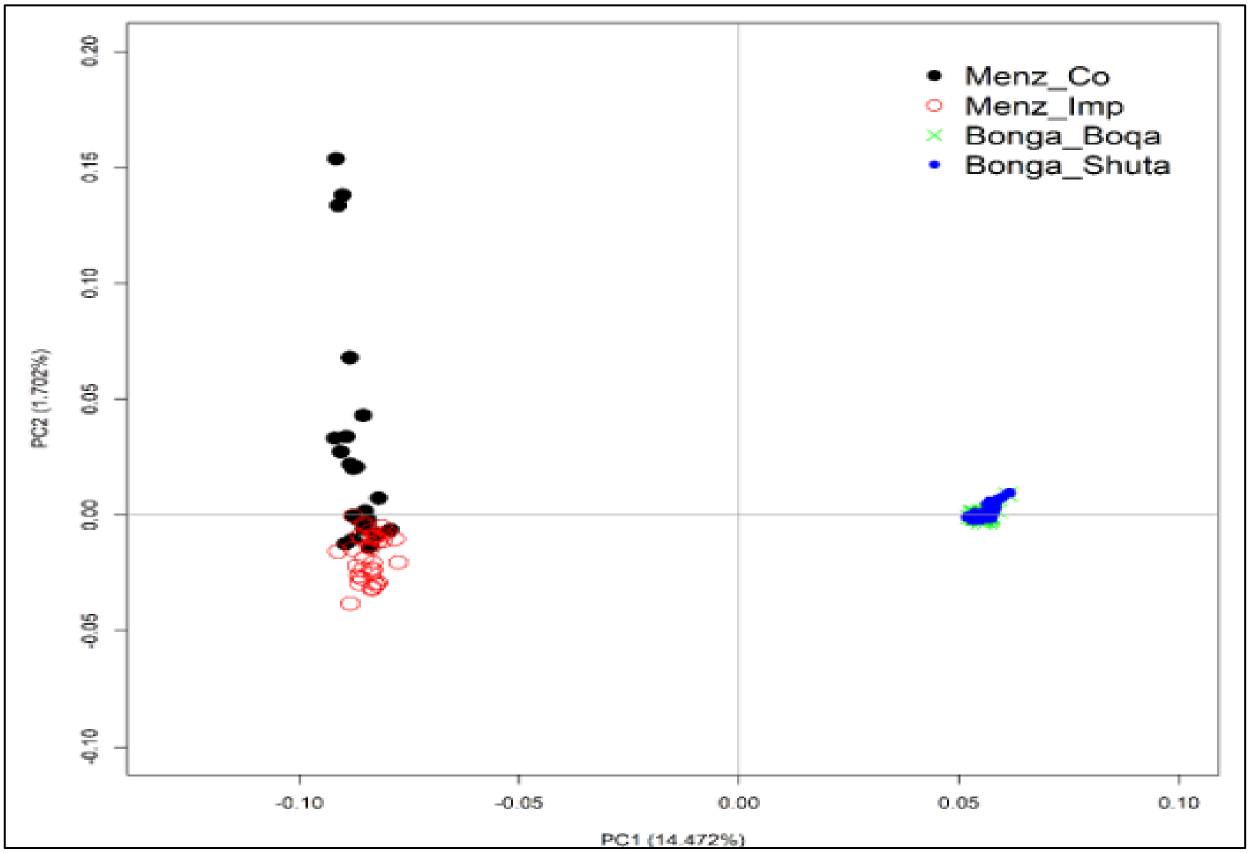

Figure 10. Principal component analysis (PCA) results of Menz and Bonga breeds

Admixture analysis

Differences between breed groups and within breed is visualized by the admixture analysis results. Results from admixture analysis at k=2 for Menz control and improved was consistent with the PCA results (Figure 11). The Menz control population formed a single group while the improved Menz formed an independent cluster with some admixture from the control one

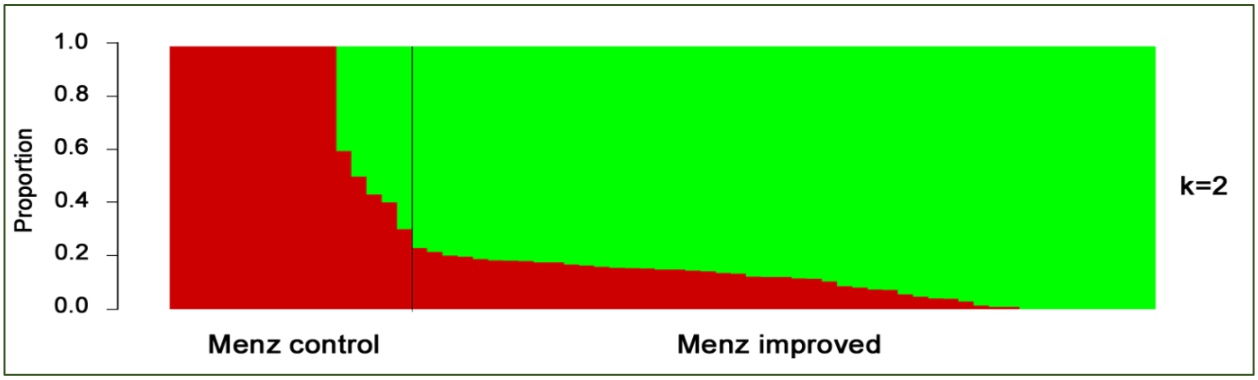

Figure 11. Model based structure analysis of Menz sheep breeds considering the probable number of ancestral population (K) = 2 in the data set. Breeds are separated by black lines. Each individual represented by a vertical bar and partitioned in to colored segments representing the proportion of each ancestors.

In figure 12, at the *K* = 2 plot, Admixture clustering managed to successfully detect a clear phylogeographic pattern within the breeds genotyped. At the breed level, clear genetic division was detected separating Menz from Bonga breed.

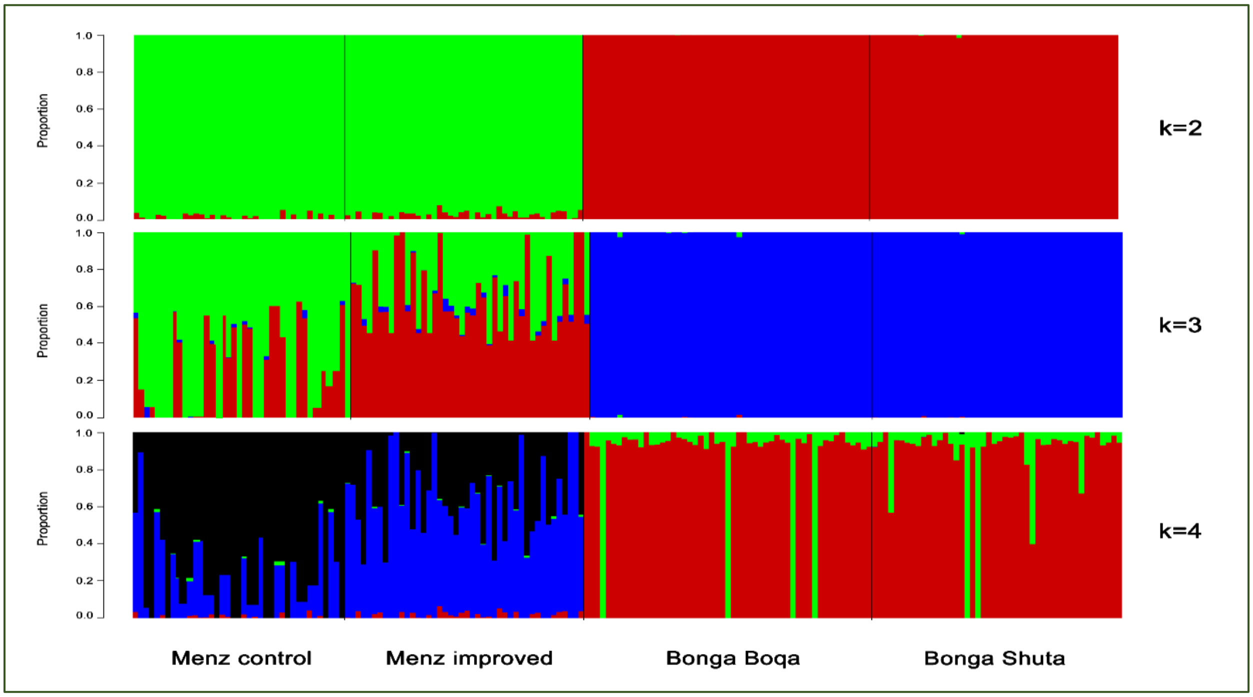

Figure 12. Model based structure analysis of Ethiopian Menz and Bonga sheep breeds considering the probable number of ancestral population (K) = 2 to 4 in the data set. Breeds are separated by black lines. Each individual represented by a vertical bar and partitioned in to colored segments representing the proportion of each ancestors.

At k=3, both manmade selection and geographic location are responsible for differentiation of sheep population. The separate clustering between breeds at k=2 was maintained, whereas within the breed level, isolated populations in Menz were identified. The Menz control exhibited little admixture with improved Menz which is expected since it's the same breed. The differences in allele frequencies within Menz population is due to selection exerted in the framework of CBBP.

Clusters were reproducible up to K=4 and grouped individuals according to their geographic location in the same way as for PCA, further confirming the genetic uniformity of Bonga breed at both sites. As indicated by the genetic distance, PCA and Admixture results, the Bonga sheep showed greater genetic differentiation and clearly separated from the rest of the populations due to the ecological adaptation, differences in migration histories and geographical isolation. The role of selection on shaping the genome architecture of the current indigenous East African cattle was also documented (Mbole-Kariuki et al., 2014). The clear genetic divergence between the indigenous Improved Menz and Menz control is attributed to the strong selection for improvement of production traits. This was also reflected in the higher level of genomic inbreeding previously reported.

The relationships between the studied sheep breeds were assessed by calculating a pairwise F_{ST} matrix (Table 20). The F_{ST}, which is directly related to variance (s) in allele frequency, is the most commonly used method to detect selection signatures. Approaches such as F_{ST} detect better long-term selection because they are dependent on the accumulation of mutations around the causative variant. Their resolving power, however, declines if the selection advantage is small, as it takes longer for the frequency of the favored allele to increase to the point of detection. In general, values between 0 and 0.05 are categorized as 'little to no differentiation,' values between 0.05 and 0.15 as 'moderate differentiation', values between 0.15 and 0.25 as 'great differentiation', and values above 0.25 as 'very great differentiation' between populations tested (Weir & Cockerham 1984; Frankham et al., 2002). The overall F_{ST} value among the four populations was low (0.056) but significant ($P < 0.0001$). FST for all pairs of populations also differed significantly from zero ($P < 0.001$) and ranged from 0.0003 to 0.08.

Table 20. Pairwise FST index for Ethiopian breeds

	Menz_improved	**Menz_Control**	**Bonga_Boqa**	**Bonga_Shuta**
Menz_improved	--			
Menz_Control	0.0078	--		
Bonga_Boqa	0.0792	0.0874	--	
Bonga_Shuta	0.0788	0.0874	0.00039	--

F_{ST} between Bonga (Shuta and Boqa) and Menz (improved and control) is ~ 0.08. This F_{ST} value indicates a moderate differentiation between the two breeds due to genetic structure. The average F_{ST} among Ethiopian sheep populations was higher than the values reported for Ethiopian cattle (0.01) and goats (0.0245) (Edea et al., 2013; Mekuriaw, 2016), and also higher to the mean value of 0.046 obtained using microsatellite markers for Ethiopian sheep (Gizaw et al., 2007). Many studies have reported FST values for the sheep breeds like the Moroccan breeds 3.6% (Gaouar et al., 2016), Algerian 3.8% (Gaouar et al., 2015), and Tunisian 3% (Sassi-Zaidy et al., 2014). These differences may be due to several reasons. Despite the number of breeds or the microsatellite *loci* studied, sampling strategy might be the main factor underlying discrepancies between results among studies.

Considering within the breed pairwise analysis, the F_{ST} between Boqa and Shuta sites of Bonga breeds was very low: 0.0003. Whereas in Menz, the pairwise F_{ST} value was 0.008. Both values are considered low, but the Bonga value is 26% higher than the Menz pairwise value. This difference is certainly attributed to the selection exerted by the CBBP in Menz.

Signatures of selection — F_{ST}

In this study, we calculated the genome-wide distribution of the F_{ST} values, to explore the selection signatures between the groups of Menz breeds (Menz improved & Menz Control). Several genomic regions with high F_{ST} values were detected (Figure 13). The average F_{ST} across the genomes was 0.0078, indicating low genetic differentiation according to Wright's classification.

The F_{ST} values were transformed to Z-scores using the formula: $Z(F_{ST}) = (F_{ST} - \mu F_{ST})/\sigma F_{ST}$;

Where μF_{ST}: overall average value of F_{ST} and σF_{ST} is the standard deviation derived from all the windows tested. The value of $Z(F_{ST}) \geq 5$ was the threshold used to identify selection signatures.In total, 104 outlier windows and 19 genomic regions under selection were detected across the 26 autosomes. Candidate regions identified by different approaches were used to annotate genes that were either entirely or partially included within each selected region, using the NCBI Genome Data Viewer. Gene Ontology (GO) enrichment analysis was performed for the candidate genes revealed in pairwise comparisons between the studied groups. Finally, the biological functions of each annotated gene within the selection signatures was investigated via a comprehensive search of literature. The strongest candidate regions were located on chromosomes (OAR1, OAR2, OAR3, OAR7, OAR, OAR11, OAR24 and OAX, which spanned multiples genes, for instance, CREBZF, DKK3, ADCY10, KHDRBS1 and (Table 21 & Annex 2). The top three most significant GO terms were associated with regulation of cell growth, metabolism, and immunity.

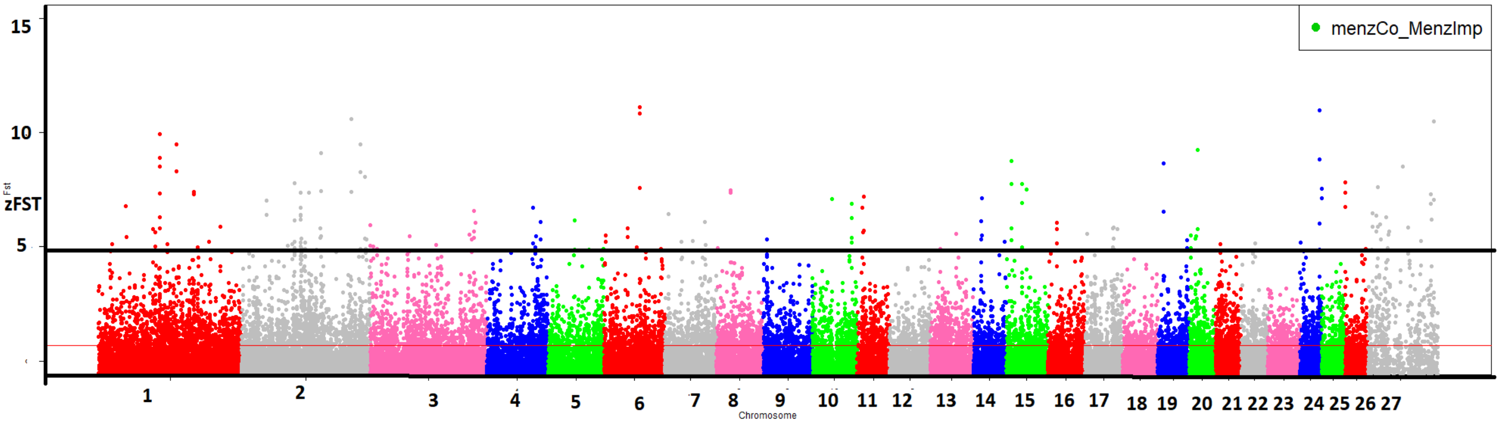

Figure 13. Manhattan plots of genome-wide autosomal zF_{ST} analyses for the comparison within Menz breed

PPP1R1C, which belongs to a group of PP1 inhibitory subunits that are themselves regulated by phosphorylation, is identified on OAR2. This gene is involved in heat stress response and the heat shock family of genes (Shi and Manley, 2007). The presence of multiple genes associated with heat stress would seem to suggest that the trait is under selection especially in tropical breed. DNAJC10 involved in recognizing and degrading misfolded proteins and also in regulation of stress induction of heat shock protein (hsp40) in Bos Taurus (Roy and Collier, 2012). They play an important role in responding to and regulating heat shock/stress and its negative effect on protein activity. Both genes have been found in numerous studies to be among genes that are differentially expressed in heat stressed animals of different species including bovines (Castellote et al., 2015; Ortega et al., 2016), sheep (Du et al., 2016) and goats (Parida et al., 2019). These genes can therefore be strong candidates for selection to involve in the regulation and response to heat stress tolerance. Another gene found to be related to environment adaptation is P2RX7 which regulates downstream kinases in response to environmental stress, and play a role in regulating the actin cytoskeleton

Genes involved in regulating innate and adaptive immunity in mammals were identified; for example, CREBZF, MYD88 and CYBB genes that were reported to regulate innate and acquired immune responses. These results would suggest that immunity genes are hotspots for CBBP selection in Menz sheep breed in response to high burden of pathogen/parasite challenge in the local environment (Thumbi et al., 2014; Bahbahani and Hanotte, 2015). We hypothesize that the variation within the breeds may be due to the genes indirect selection on resistance traits. MYD88 gene is related to innate immune response system and encodes a cytosolic adapter protein that plays a central role in the innate and adaptive immune response.

Furthermore, four genes clustered on the candidate region on OAR3, OAR1, OAR6 and OAR2 (PEF1, DCAF6 and FBXO11). Among these, Ubiquitin protein ligase domain (PC00234), LNX1 containing E3 ubiquitin protein ligase on the region OAR6 which has various role in innate and acquired immune response mechanism, and encodes a membrane-bound protein that is involved in signal transduction and protein interactions. This gene has been reported to play an important role to resist the most important diseases affecting the small ruminant industry (Gastrointestinal infection) (Estrada-Reyes et al., 2019)

Table 21. Candidate genes in the genomic regions based on the F_{ST} approach

OAR	Gene	Gene Name	Function	Domain
2	DNAJC10	DnaJ heat shock protein family (Hsp40) member C10	Involved in recognizing and degrading misfolded proteins	Cell redox homeostasis
2	PTP4A2	Pre-T Cell antigen receptor alpha	The pre-T-cell receptor complex (composed of PTCRA, TCRB and the CD3 complex) regulates early T-cell development	Immunity
6	LNX1	ligand of numb-protein X 1	The encoded product is an E3 ubiquitin-protein ligase	Ubiquitin-protein transferase activity
7	PAK6	ligand-gated ion channel (PC00141)	ATP-dependent lysis of macrophages through the formation of membrane pores permeable to large molecules	Stress-activated protein kinase signaling cascade

15	DKK3	dickkopf WNT signaling pathway inhibitor 3	Involved in embryonic development through its interactions with the Wnt signaling pathway	Reproduction
19	MYD88	scaffold/adaptor protein (PC00226)	Innate immune encodes a cytosolic adapter protein that plays a central role in the innate and adaptive immune response.	Immunity

Reproduction is a critically important trait in livestock breeding and in the sheep industry particularly. It appears to be controlled by multiple genes and factors, impacting on pathways of ovarian follicular development, embryogenesis, oocyte maturation, ovulation, fertilization, and uterine receptivity. Related genes were identified like DKK3, ADCY10, PMS2, and CAPZA3. They encode proteins that influence male fertility, embryonic development and spermatogenesis, and may indirectly influence traits such as growth (Arvand et al., 2019). PTP4A2 regulates early T-cell development.

The candidate regions spanned genes that have been associated with regulation metabolic processes. For instance, stromal interaction molecule 2 (STIM2) is an integral membrane protein responsible for store-operated calcium entry. LMTK2 also plays a critical role in endosomal membrane trafficking, while CASQ1 plays an important role in regulation of skeletal muscle contraction by regulating the release of Calcium ion. These processes are essential for osmoregulation and the transport of a variety of organic and inorganic molecules. COPA gene has reportedly been involved in metabolism and function as a structural molecule and hormone activity. Caudal type homeobox 4 (CDX4) is a gene which plays roles in development of limbs, hematopoiesis (Ahbara et al., 2019) and is vital for embryo development.

Conclusion

The current study, as well as other studies have proved that CBBP is a successful approach for achieving genetic and husbandry improvements in Ethiopia. The aim of this study was to contribute to an understanding of the results of CBBP practices for two breeds (Bonga and Menz) of Ethiopian sheep.

- ✓ Animal ranking based on phenotype measurement and BLUP EBV was in a high correlation in the Menz and Bonga sheep flocks. This could justify the use of phenotypic values (duly adjusted for non-genetic factors) as an approximation to breeding values and to estimate responses to selection in village-based breeding programs when pedigree recordings were unavailable. The conclusion obtained from the first objective is, even though the correlation between the phenotypic values and BLUP- EBV was high, pedigree data is important for higher accuracy at the selection process. In case of difficulty to obtain these recordings, phenotypic selection remains a reliable option.

- ✓ Results from the current study have demonstrated a significant increase in WWT for both Bonga and Menz due to a positive correlated response with SMWT- based selection. The positive and significant correlations among different growth traits suggest high predictability among the different traits. This finding is helpful for farmers, since they can start selection at early age. Early selection is desirable in intensive production systems because it allows producers to cull unwanted animals earlier and to distribute the maintenance costs of the flock over a larger number of lambs. SMWT-based selection was also positively correlated with a positive improvement of LS and a shorter lambing interval with Bonga sheep. These results are highly valuable since the heritability for reproductive traits is always low. Thus, selection based on SMWT can be introduced as selection criteria to indirectly improve and increase the genetic merit of reproductive traits in Bonga sheep. The outputs of the study could also be utilized to develop optimum alternative improvement and dissemination schemes (breeding structures) for Menz and Bonga sheep and a model scheme for other sheep breeds in the country.

- ✓ The genetic trends obtained in the study indicated that significant and sustained genetic progress in the desired direction has been achieved in SMWT growth traits in Bonga and Menz. The genetic trends provided evidence that selection for improvement of body weight traits in sheep CBBP's in Ethiopia is effective and that it can lead to further significant genetic improvement. This result confirms the success of CBBP in Ethiopia.
- ✓ Selection for body weight improvement in CBBP have definitely shaped Menz sheep genomes. The identification of candidate regions as being under selection can help researchers understand the molecular mechanisms involved in adaptation and may also be useful in identifying regions associated with important traits that are under selection. The genetic diversity test has showed a lower genetic diversity of the improved flocks compared to the control one, and also a higher inbreeding value. The principle component analysis and Admixture showed a clear clustering of the improved Menz flock which proves the selection pressure on genome. Selection signature analysis identified various candidate genomic regions spanning genes related to skeletal structure and morphology, body temperature regulation, disease resistance, reproduction, and possibly adaptation to local environments. Our findings will provide valuable information to support genomic improvement of these local sheep breeds through CBBP for an increased performance.

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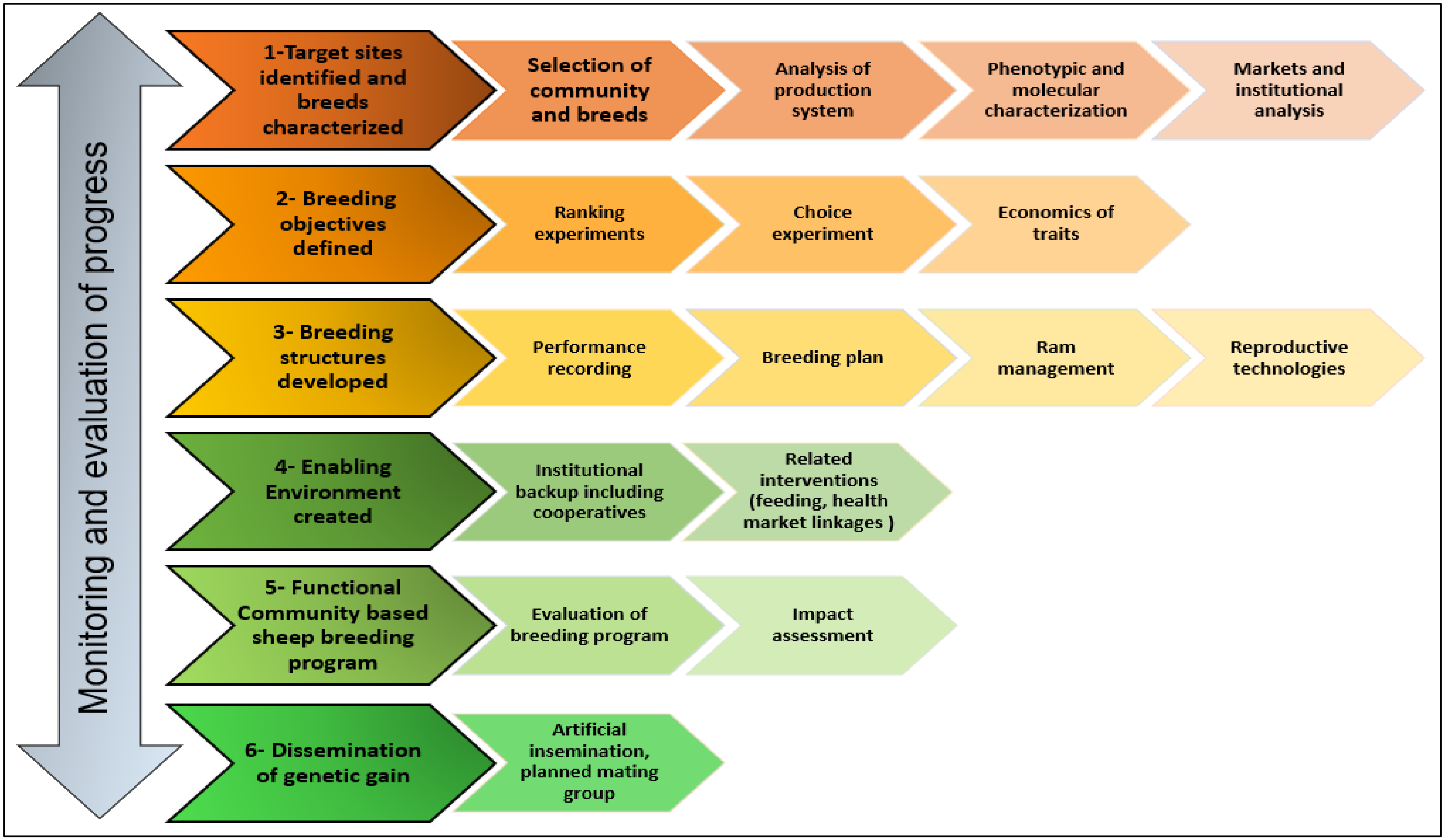
Annexes/Appendices

Annex 1. Steps for setting up community-based breeding program for sheep



Annex 2. Candidate genes in the genomic regions

OAR	Gene	Gene name	Function	Domain
1	ADCY10	Adenylate Cyclase 10	Has a critical role in mammalian spermatogenesis by producing the cAMP which regulates cAMP-responsive nuclear factors indispensable for sperm maturation in the epididymis. Induces capacitation	Reproduction testicular soluble adenylyl cyclase
1	CASQ1	Calcium-binding protein (PC00060)	The skeletal muscle specific member of the calsequestrin protein family. Calsequestrin functions as a luminal sarcoplasmic reticulum calcium sensor in both cardiac and skeletal muscle cells.	Regulation of skeletal muscle contraction by regulation of release of sequestered calcium ion
1	COPA	Vesicle coat protein (PC00235)	Structural molecule activity and hormone activity	Metabolism
1	DCAF6	DDB1 And CUL4 Associated Factor 6	Enhance transcriptional activity of the nuclear receptors NR3C1 and AR. May function as a substrate receptor for CUL4-DDB1 E3 ubiquitin-protein ligase complex	Metabolism ubiquitin-protein ligase
1	DCDC2B	Doublecortin domain containing 2B	Enhance microtubule polymerization.	Microtubule organizing center
1	GPR161	G-protein coupled receptor (PC00021)	Metabolism	Integral component of membrane
2	ADGRB2	Adhesion G Protein-Coupled Receptor	Inhibitor of angiogenesis	G protein-coupled receptor activity

Annex 2. Cont'd

OAR	Gene	Gene name	Function	Domain
2	COL15A1	Extra-cellulaire matrix structural protein (PC00103)	Fibril-associated collagens with interrupted helices	Endothelial cell morphogenesis
2	COL16A1	Extra-cellular matrix structural protein (PC00103)	Associated with fibril-forming collagens such as type I and II, and serve to maintain the integrity of the extracellular matrix.	Extra-cellular matrix structural constituent
2	DNAJC10	DnaJ heat shock protein family (Hsp40) member C10	Involved in recognizing and degrading misfolded proteins	Cell redox homeostasis
2	EIF3I	Translation initiation factor (PC00224)	Initiates translation of a subset of mRNAs involved in cell proliferation, including cell cycling, differentiation and apoptosis	Programmed cell death involved in cell development
2	EXTL3	Glycosyltransferase (PC00111)	Metabolism	Golgi apparatus
2	FRZB	Transmembrane signal receptor (PC00197)	Involved in the regulation of bone development	Canonical Wnt signaling pathway
2	GALNT12	Glycosyltransferase (PC00111)	Metabolism	Golgi apparatus
2	HCRTR1	G-protein coupled receptor (PC00021)	The protein encoded by this gene is a G-protein coupled receptor involved in the regulation of feeding behavior.	G protein-coupled receptor activity
2	INTS9	Integrator complex subunit 9	Plays a role in small nuclear RNA processing.	Regulation of transcription, DNA-templated
2	KHDRBS1	RNA splicing factor (PC00148)	This gene encodes a member of the K homology domain-containing, RNA-binding, signal transduction-associated protein family	Poly(A) binding

Annex 2. Cont'd

OAR	Gene	Gene name	Function	Domain
2	KPNA6	Transporter (PC00227)	Functions in nuclear protein import as an adapter protein for nuclear receptor KPNB1	Nuclear localization sequence binding
2	PDE1A	Phosphodiesterase 1A	Regulation of gene transcription.	Signal transduction
2	PEF1	Penta-EF-hand domain containing 1	Cyclic nucleotide phosphodiesterase regulators of many important physiological processes	Ubiquitin ligase-substrate adaptor activity
2	PPP1R1C	Protein phosphatase 1 regulatory inhibitor subunit 1C	Essential for the assembly of the distal half of centrioles, required for centriole elongation.	Intracellular signal transduction
2	PTP4A2	Pre T cell antigen receptor alpha	The pre-T-cell receptor complex (composed of PTCRA, TCRB and the CD3 complex) regulates early T-cell development	Immunity
3	CAPZA3	Non-motor actin binding protein (PC00165)	Important in determining sperm architecture and male fertility	Reproduction
3	FBXO11	Ubiquitin-protein ligase (PC00234)	Function in phosphorylation-dependent ubiquitination.	Protein ubiquitination
3	NUP214	Transporter (PC00227)	The protein encoded by this gene is localized to the cytoplasmic face of the nuclear pore complex where it is required for proper cell cycle progression and nucleocytoplasmic transport.	Structural constituent of nuclear pore

Annex 2. Cont'd

OAR	Gene	Gene name	Function	Domain
3	PIK3C2G	Actin or actin-binding cytoskeletal protein (PC00041)	The encoded protein has been shown to form a heterodimer with the programmed cell death 6 gene product and may modulate its function in Ca^{2+} signaling.	Phosphatidylinositol kinase activity
3	PLCZ1	Phospholipase (PC00186)	Protein product is also an important regulator of platelet responses	Phosphatidylinositol-mediated signaling
4	CHCHD3	Coiled-coil-helix-coiled-coil-helix domain containing 3	Absence of the encoded protein affects the structural integrity of mitochondrial cristae and leads to reductions in ATP production, cell growth, and oxygen consumption	Inner mitochondrial membrane organization
5	ARHGAP26	GTPase-activating protein (PC00257)	Regulate the organization of the actin-cytoskeleton	GTPase activator activity
6	FIP1L1	Factor interacting with PAPOLA and CPSF1	FIP1L1 contributes to poly(A) site recognition and stimulates poly(A) addition	MRNA polyadenylation
6	LNX1	Ligand of numb-protein X 1	The encoded product is an E3 ubiquitin-protein ligase	ubiquitin-protein transferase activity
6	STIM2	Stromal interaction molecule 2	The protein is regulated by intracellular calcium ions and is found in both the plasma membrane and intracellular organellar membranes, where exchange of Na+ for Ca2+ occurs in an electrogenic manner	Store-operated calcium entry

Annex 2. Cont'd

OAR	Gene	Gene name	Function	Domain
7	BUB1B	Non-receptor serine/threonine protein kinase (PC00167)	Essential component of the mitotic checkpoint	Mitotic spindle assembly checkpoint
7	PAK6	Ligand-gated ion channel (PC00141)	ATP-dependent lysis of macrophages through the formation of membrane pores permeable to large molecules	Stress-activated protein kinase signaling cascade
7	PLCB2	Kinase (PC00137)	(PI3K) family. PI3-kinases play roles in signaling pathways involved in cell proliferation, oncogenic transformation, cell survival, cell migration, and intracellular protein trafficking	Phosphatidylinositol-mediated signaling
7	POC5	DNA binding protein (PC00009)	The mismatch repair system that functions to correct DNA mismatches and small insertions and deletions that can occur during DNA replication and homologous recombination.	Centrosomal protein
7	SLC8A3	Chromatin/chromatin-binding, or -regulatory protein (PC00077)	Be involved in regulating homeotic gene expression during development	Integral component of plasma membrane
7	SUSD6	Stromal interaction molecule 2	Plays a role in mediating store-operated Ca^{2+} entry	Molecular function and biological process
11	BRIP1	DNA helicase (PC00011)	Maintenance of chromosomal stability	Double-strand break repair involved in meiotic recombination

Annex 2. Cont'd

OAR	Gene	Gene name	Function	Domain
11	INTS2	Integrator complex subunit 2	Is a subunit of the Integrator complex, which associates with the C-terminal domain of RNA polymerase II	Integrator complex
11	MED13	Mediator complex subunit 13	This gene encodes a component of the mediator complex (also known as TRAP, SMCC, DRIP, or ARC), a transcriptional coactivator complex	Regulation of transcription by RNA polymerase II
14	ITFG1	Integrin alpha FG-GAP repeat containing 1	Modulator of T-cell function.	Immunity
15	DKK3	Dickkopf WNT signaling pathway inhibitor 3	Involved in embryonic development through its interactions with the Wnt signaling pathway	Reproduction
17	DYNLL1	Microtubule or microtubule-binding cytoskeletal protein (PC00157)	Regulate numerous biologic processes through its effects on nitric oxide synthase activity	Metabolism
17	P2RX7	Purinergic receptor P2X 7	It regulates downstream kinases in response to environmental stress, and may play a role in regulating the actin cytoskeleton	Adaptation to environment
19	MYD88	Scaffold/adaptor protein (PC00226)	Innate immune encodes a cytosolic adapter protein that plays a central role in the innate and adaptive immune response.	Immunity
19	OXSR1	Oxidative stress responsive kinase 1	Has some calmodulin-like activity with respect to enzyme activation and growth regulation	Cell Growth

Annex 2. Cont'd

OAR	Gene	Gene name	Function	Domain
20	BICRAL	Nteracting Chromatin Remodeling Complex Associated Protein Like	Changing chromatin structure by altering DNA-histone contacts within a nucleosome in an ATP-dependent manner.	Transcription coactivator activity
20	PTCRA	Phosphatase inhibitor (PC00183)	Increase cell susceptibility to TNF-induced apoptosis.	Apoptosis
21	CREBZF	CREB/ATF bZIP transcription factor	Suppresses the expression of HSV proteins in cells infected with the virus in a HCFC1-dependent manner	Immunity
22	MOCS1	Molybdenum cofactor synthesis 1	Molybdopterin cofactor synthesis protein a	Molecular function and biological process
24	CCZ1	CCZ1 homolog, vacuolar protein trafficking and biogenesis associated	Protein Trafficking And Biogenesis Associated	Intracellular membrane-bounded organelle
24	LMF1	Lipase Maturation Factor 1	Involved in the maturation of specific proteins in the endoplasmic reticulum. Required for maturation and transport of active lipoprotein lipase	Protein maturation
24	LMTK2	lemur tyrosine kinase 2	Plays a critical role in endosomal membrane trafficking	Positive regulation of kinase activity
24	OCM	Oncomodulin	Oncomodulin is an oncodevelopmental protein found in early embryonic cells in the placenta	Cell Growth

Annex 2. Cont'd

OAR	Gene	Gene name	Function	Domain
24	PMS2	Phospholipase (PC00186)	This protein localizes to the acrosome in spermatozoa and elicits Ca^{2+} oscillations and egg activation during fertilization that leads to early embryonic development	Reproduction
27	CDKL5	Non-receptor serine/threonine protein kinase (PC00167)	Encodes a phosphorylated protein with protein kinase activity.	Protein phosphorylation
27	CDX4	Homeodomain transcription factor (PC00119)	Regulate homeobox gene expression	Animal organ morphogenesis and embryo development
27	CHIC1	Cysteine rich hydrophobic domain 1	Protein-coding genes found near the X-inactivation center	Metabolism
27	CYBB	Oxidase (PC00175)	Primary component of the microbicidal oxidase system of phagocytes	Immunity
27	SCML2	Protein tyrosine phosphatase 4A2	The protein encoded by this gene belongs to a small class of the protein tyrosine phosphatase (PTP) family. PTPs are cell signaling molecules that play regulatory roles in a variety of cellular processes.	Metabolism