Norwegian University of Life Sciences
Faculty of Biosciences
Department of Animal and Aquacultural Sciences

Philosophiae Doctor (PhD)
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Breeding for Milk Production in Sheep in Ethiopia

Avl for mjølkeproduksjon med sau i Etiopia

Haile Welearegay Gebreslase

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Hawassa, March 2021

Haile Welearegay Gebreslase

Dedication

This piece of work is dedicated to my beloved mother **Tsadkan Gebre-Giorgis**.

Table of Contents

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SUMMARY

The overall aim of this study was to investigate options to breed sheep for milk production and to find out the optimal proportion of Awassi in Local sheep breeds for milk production through the prevailing Community-Based Breeding Programs (CBBP) at Central Highlands of Ethiopia. The data was collected from Local (Menz, Wollo), Awassi-Local (AL) crossbred and pure Awassi ewes kept under farmers (FE) and breeding station (BE) environments, two production systems, in the 2015 to 2017 production years. A total of 1506 (466 from FE and 1040 from BE) test-day milk yield (TDMY) records from 326 (115 from FE and 211 from BE) lactating ewes (Local, AL, and pure Awassi) kept in either FE or BE were used, and univariate repeatability models with Legendre polynomials (LP) coefficients (up to 3^{rd} order) nested by genetic groups were used to model lactation curves from the TDMY data. The ewes were at different ages and different lactation stages.

Paper I aimed at estimating milk production performance using an approach that allows comparisons based on a limited number of data. Results revealed that the group of ewes with a high % Awassi produced consistently more milk than the Local breeds at the farmers' condition. Groups with 30-50% Awassi and >50% Awassi ewes produced significantly ($p < 0.05$) more than Local (0% Awassi) ewes over 120 Days in milk (DIM). Significant differences were also observed between <30% Awassi and >50% Awassi crossbred groups. The group of ewes with a high-level Awassi proportion (>50%) produced over 70% more milk than the Local ewes. This demonstrates the potential that exists in increasing milk production through the initiated crossbreeding program.

In Paper II variances and genetic parameters of TDMY in sheep recorded at two governmental breeding and multiplication centers (DB-R and AG-R) were estimated. Here it

was shown that the 100% Awassi ewes produced significantly ($p < 0.05$) more milk than the other studied ewe genetic groups (0%, 50%, and 75% Awassi) over the 120 DIM. The Local ewes produced significantly less TDMY than the other groups. The genetic advantage of the increased Awassi percentage was larger at the two centers than under farmers' conditions. Moreover, the advantage of Awassi increased when a comparison was done over more than 120 DIM. For TDMY, the estimate of heritability (h^2) was 0.10 ± 0.08 and of repeatability (r) 0.15 ± 0.03. The largest accuracy ($r_{\mathrm{a}_i,\hat{\mathrm{a}}_i}$) for breeding value prediction was found among the sires, due to sires being progeny tested. Accuracy could increase if actions could be taken to increase the size of the genetic parameters. If TDMY was recorded for all ewes at the two centers, preferably with increased heritability and repeatability values, there is potential to increase selection accuracy and genetic gain produced by the dissemination program.

In Paper III data from the farmers' field (reported in Paper I) and from the two breeding and multiplication centers (reported in Paper II) were utilized to evaluate genotype by environment interaction (G x E) for TDMY by estimates of contrasts between milk production estimates for the same proportions of Awassi and comparable stages of lactation in the two environments (BE vs. FE). No significant G x E interaction was found for any of the genetic groups across 120 days in milk. This implies that genetic superiority at breeding centers will in large be realized in the farmers' environment. However, the fitted graphs modelled indicate significantly ($p < 0.05$) less TDMY in FE compared to BE for the early stage of lactation for 0% Awassi (Local), 30% Awassi, and >30 - 50% Awassi ewes, but not for the >50% Awassi.

In conclusion: even with the limited number of ewes and records from the farmers' field as well as from the breeding centers, this study shows the potential that exists for increasing milk production of ewes through the initiated crossbreeding program in the central highlands of Ethiopia. The genetic variance found for TDMY is exploitable, though more data from ewes at breeding centers is preferable. Selection can be performed at the breeding centers and the genetic superiority at breeding centers will be realized in the farmers' environment. Further evaluation of the genetic parameters including other important traits with more data is required.

SAMANDRAG

Hovudmålet med denne studien var å undersøkja måtar å avla for mjølkeproduksjon og å finna optimalt innslag av Awassi i lokale sauerasar for mjølkeproduksjon basert på det etablerte Community-Based Breeding Programs (CBBP) i Central Highlands of Ethiopia. Data frå 2015-2017 blei samla frå sau som var av Lokale rasar (Menz, Wollo), kryssingar mellom Lokale rasar og Awassi (AL), og reine Awassi; enten hos bønder (FE) eller på avlsstasjonar (BE) – to ulike produksjonssystem. Til saman 1506 (466 frå FE og 1040 frå BE) testdagsregistreringar av mjølkeavdrått (TDMY) frå 326 (115 frå FE og 211 frå BE) mjølkande søyer (Lokale, AL, og reine Awassi) haldne enten i FE- eller BE-miljø blei analyserte med univariate gjentaksgradsmodellar der koeffisientar (opp til 3. grad) av Legendre-polynom (LP) innan genetiske grupper modellerte laktasjonskurvene. Søyene hadde ulike aldrar og laktasjonsstadiar.

Artikkel I prøvde å estimera mjølkeproduksjon med ein metode som tillet samanlikning med begrensa data tilgjengeleg. Det blei vist at søyer med ein høg % Awassi ga meir mjølk enn Lokale søyer under vilkår hos bønder. Grupper med kryssingar med 30-50% Awassi og >50% Awassi ga signifikant ($p < 0,05$) meir mjølk stipulert for ein 120 dagars laktasjon (DIM) enn Lokale (0% Awassi) søyer. Signifikante skilnadar blei òg funne mellom <30% og >50% kryssingsgrupper. Gruppa med høg Awassi-andel (>50%) ga over 70% meir mjølk enn Lokale søyer. Dette viser at det starta kryssingsprogrammet gir potensiale for å auka mjølkeproduksjon.

I artikkel II estimerte ein variansar og genetiske parameter for TDMY frå søyer på to statlege avls- og oppformerings-senter (DB-R og AG-R). Her blei det vist at 100% Awassi søyer ga

signifikant ($p < 0,05$) meir mjølk enn dei andre genetiske gruppene ein samanlikna med (0%, 50% og 75% Awassi) over 120 DIM. Lokale søyer ga signifikant mindre TDMY enn andre grupper. Fordelen med auka Awassi-prosent var større på dei to sentera enn hos bønder. Elles auka fordelen med Awassi når ein samanlikna over meir enn 120 DIM. For TDMY var estimat av arvegrad (h^2) 0.10 ± 0.08 og for gjentaksgrad (r) 0.15 ± 0.03. Høgast sikkerhet for avlsverdiprediksjon ($r_{a_i,\hat{a}_i}$) fann ein blant fedrar fordi dei var avkomsgranska. Sikkerheten kunne auka viss ein sette inn tiltak for å auka dei genetiske parametrane. Med TDMY registrert på alle søyer på dei to sentra, helst med høgare arvegrad og gjentaksgrad, kunne ein ha auka seleksjons-nøyaktigheten og dermed avlsframgangen som kjem av CBBP.

I artikkel III brukte ein data frå bøndene (som i artikkel I) og frå dei to avls- og oppformeringssentra (som i artikkel II) for å evaluera genotype-miljø samspel (G x E) for TDMY ved å estimera kontrastar mellom BE og FE for same andelar av Awassi og samanliknbare stadiar i laktasjonen. For 120 DIM viste ingen av dei genetiske gruppene (basert på % Awassi) signifikante kontrastar. Ein fann ikkje signifikant G x E samspel for nokon av gruppene basert på 120 DIM. Dette betyr at genetiske fortrinn på avlssentra i stor grad vil bli realisert òg hos bøndene. Men dei tilpassa grafane viste signifikant ($p < 0,05$) mindre TDMY i FE samanlikna med BE i tidleg laktasjon for 0% Awassi (Lokal), 30% Awassi og >30 - 50% Awassi søyer, men ikkje for >50% Awassi.

Som konklusjon kan ein seia at til og med med begrensa tal søyer og målingar frå bønder og avlssenter viser studien potensialet for å auka mjølkeproduksjon frå søyer gjennom det kryssingsprogrammet som er starta i det sentrale høglandsområdet i Etiopia. Den genetiske variansen som ein fann for TDMY er høg nok til å nyttast, sjølv om meir data frå søyene på avlssentera er å foretrekkja. Avlsdyrutval kan gjerast på sentera og deira genetiske potensiale koma til nytte i miljøet hos bøndene. Vidare evaluering av genetiske parameter òg for andre viktige eigenskapar der ein tar med meir data trengst.

ABBREVIATIONS

AG-R	Amed-Guya Sheep Breed Selection and Multiplication Center
AL	Awassi - Local crossbred
ANRSBoARD	Amhara National Regional State Bureau of Agriculture and Rural Development
BE	Breeding station environment
BED	Breeding, evaluation, and distribution sites
BHS	Black Head Somali sheep breed
BLUP	Best Linear Unbiased Prediction
BoARD	The Bureau of Agriculture and Rural Development
CSA	Central Statistics Authority
CBBP	Community-Based Breeding Program
DAGRIS	Domestic Animal Genetic Resource Information System
DBARC	Debre-Berhan Agricultural Research Center
DB-R	Debre-Berhan Sheep Breed Selection and Multiplication Center
DIM	Days in milk
EBV	Estimated Breeding Value
EIAR	Ethiopian Institute of Agriculture Research
ESGPIP	Ethiopian Sheep and Goat productivity Improvement Program
FAO	Food and agricultural organization of the united nations
FE	Farmers' environment
G x E	Genotype by Environment Interaction
GS	Genomic Selection
ICAR	International Committee for Animal Recording
ICT	Information and Communication Technology
Kg	Kilogram
Km	Kilometre
LDMPS	Livestock Development Master Plan Study

LP	Legendre polynomials
LSM	Estimated Least Square Means
m.a.s.l.	Meter above sea level
Mm	Millimetre
MY	Milk Yield
OIE	World organization for Animal Health
REML	Residual Maximum Likelihood Estimation
SARC	Sirinka Agricultural Research center
SWOC	Strengths, Weaknesses, Opportunities, and Challenges
TD	Test-day
TDMY	Test day milk yield

LIST OF PAPERS

This thesis is based on the following manuscripts/papers, which will be referred to in the text by their roman numbers.

I. W. G. Haile, S. Banerjee, A. Ayele, T. Mestawet, G. Klemetsdal, and T. Ådnøy. 2020. **Finding best exotic breed proportion in crossbred lactating sheep kept under farmers' conditions in Ethiopia determined by use of nested Legendre polynomials with limited data**

(Acta Agri Scand. A Animal Sci. 68(4):174-180)

II. W. G. Haile, G. Klemetsdal, S. Banerjee, A. Ayele, T. Mestawet, and T. Ådnøy. 2020. **Genetic analysis of test-day milk yield in sheep recorded at two governmental breeding and multiplication centers in Ethiopia**

(Submitted to Journal: Acta Agri Scand. A Animal Sci.)

III. W. G. Haile, G. Klemetsdal, S. Banerjee, A. Ayele, T. Mestawet, and T. Ådnøy. 2020. **Genotype by environment interaction for test-day milk yield in sheep recorded in farmers' field and at breeding stations in Ethiopia, by stage of lactation and various proportions of Awassi**

(Submitted to Journal: Frontiers in Genetics)

1. GENERAL INTRODUCTION

1.1 Background

In Ethiopia, sheep and goat production accounts for 40% of the cash income earned by farm households, 19% of the total value of subsistence food derived from all livestock production, and 25% of the total domestic meat consumption (Hirpa and Abebe, 2008). Sheep are kept in five broad production systems; namely, Sub-alpine Sheep-barley, Highland Cereal-livestock, Highland Perennial Crop-livestock, Lowland Crop-livestock Pastoral, and Agro-pastoral Systems (Gizaw *et al*., 2011). Ethiopia has a 31.3 million sheep population (CSA, 2018). Although sheep are found in all agro-ecologies of the country, 75% of the sheep population is concentrated in the highlands (i.e., in Sub-alpine Sheep-barley, Highland Cereal-livestock, Highland Perennial Crop-livestock Systems) of the country (Tibbo, 2006), where most settled agriculturalists practice mixed crop-livestock agriculture and own sheep in small flock sizes. Because in the Sub-alpine Sheep-barley and the Lowland Crop-livestock Pastoral and Agro-pastoral Systems the crop production is unreliable, sheep are the major livestock species in these areas and are kept by farmers in relatively large flock sizes (LDMPS, 2007; Gizaw and Getachew, 2009). The sheep production is based on local breeds, except for less than 1% of exotic sheep (Getachew *et al*., 2016; Ayele *et al*., 2015).

Smallholder sheep production is a major source of food security, but serving a diverse function, including cash income, meat, milk, and wool, for the smallholder farmers (FAO, 2009; Abebe *et al*., 2013; Asresu *et al*., 2013; Legesse *et al*., 2008; Nigussie *et al*., 2013). Thus, they contribute to the livelihood of many small and marginal farmers (Beneberu and Jabarin, 2006; Hiwot *et al*., 2020). Though the country has a large population of sheep, the contribution of the sub-sector to the national economy is below its potential (EIAR, 2018). Sheep production and productivity in the country are challenged by feed shortages, diseases, poor infrastructure, lack of market information and technical capacity, and an absence of planned breeding programs and breeding policies (Gizaw *et al*., 2013b). Sheep production in Ethiopia, particularly in the Sub-alpine Sheep-barley Production System has proved to be a major source of food security (Gizaw *et al*., 2013a). Sheep breeds in these areas are low producers. Thus, crossbreeding of the local sheep with exotic sire breeds has been adopted as a major breeding strategy to improve the productivity of the local sheep.

In recent decades, due to less land held by smallholder farmers and the shortage of feed resources, sheep and goats have increased importance in food production in Ethiopia (Leta and Mesele, 2014). Sheep milking may potentially play a notable role in the nutrition, economy, and environment of the farmers because of lower capital investment and production costs, rapid generation turnover, and lower space and feed requirement than for cattle (Nuru, 1985; Tibbo *et al*., 2006; EAIR, 2017). There is an increasing demand in Ethiopia for milk and milk products due to population increment and urbanization. As a result of this, farmers have shown increasing interest in producing milk from sheep. Sheep are primarily reared as a milk source for household use in the Pastoral and Agro-pastoral farming systems. Likewise, Local and different degrees of crosses of Awassi ewes are milked for household use in other parts of the country (Lemma *et al*., 1998; Legesse *et al*., 2008; Getachew *et al*., 2016; Mekasha *et al*., 2016a). There is a need to explore and genetically improve Local and crossbred sheep breeds for milk production. This is an untapped sector. Information pertaining to the milk production potential of sheep breeds and strategies to breed sheep for milk in Ethiopia is limited. Besides being a local contribution (to small input farming in

Africa), the importance of the information developed in this thesis could contribute to the expanding sheep milking industry globally. This work is new in its kind by focusing on milk and possible options to breed sheep for that in Ethiopia. Thus, this project could give practical knowledge of the less explored sheep milking. The current Ph.D. project, therefore, aimed at investigating options to breed sheep for milk production and to find out the optimal proportion of Awassi in Local sheep breeds for milk production. The prevailing Community-Based Breeding Programs (CBBP) at Central Highlands of Ethiopia was taken as a case study. The possibility to use TDMY records from farmers' field, and from these breeding and multiplication centers for evaluating sheep milking ability and genetic evaluations was chosen for this study, but the findings can be adopted and scaled up elsewhere in the country or in the region.

1.2 Sheep Breeding Practices in Ethiopia

The fourteen sheep breeds in Ethiopia (Figure 1) may be categorized into four groups (Sub-alpine Short-fat-tailed, Highland Long-fat-tailed, Lowland Fat-rumped, Lowland Thin-tailed) based on their ecological distribution, geographic proximity, tail types, and tail form/shape (Gizaw *et al*., 2013b). There is high morphological and ecological diversity among the major sheep breeds. There is also a strong relationship between sheep breeds, ethnic groups, and production systems. In the past, there have been a few attempts and successes in the genetic improvement of sheep resources in Ethiopia. Several efforts have been made to this end since the early 1960s (Tibbo 2006). Selective pure breeding is not practiced or largely neglected. An approach that has been adapted to and implemented for Afar, BHS, Horro, and Menz sheep breeds is to generate an improved ram in closed nucleus flocks and then disseminate it to village flock (Gizaw *et al*., 2013a). Selection projects in the closed nucleus flocks of Black head Somali (BHS) and Afar sheep exist but have not been documented, while in Horro sheep no appreciable genetic progress has been achieved even if farmers have been involved in the planning, as reported by Abegaz and Duguma (2000). According to Gizaw *et al*. (2013a), appreciable genetic improvement has been achieved in the Menz sheep breed. Body weights at birth, 3, and 6 months of age increased by 0.42, 2.29, and 2.46 kg, respectively, in the third generation over those in the base generation. Most of the crossbreeding and selective pure breeding sheep breeding programs have been hierarchically structured (Gizaw *et al*., 2008a; Amare, 2018). Following the failure of these conventional hierarchical breeding schemes, participatory community-based breeding schemes have been suggested as viable options in low-input, smallholder production systems (Sölkner *et al*., 1998; Kosgey and Okeyo, 2007; Gizaw and Getachew, 2009). Breeding objectives and description of the production system are the basis for designing tailor-made management and breeding interventions (Kosgey, 2004; Getachew *et al*., 2020). The CBBPs utilize crossbreeding, involving imported exotic breeds (Lemma *et al*., 1989; Gizaw, 2002) and distribution of crossbreed rams from stations, including some selective breeding in the central nucleus schemes of the community-based breeding programs (Aynalem *et al*., 2019).

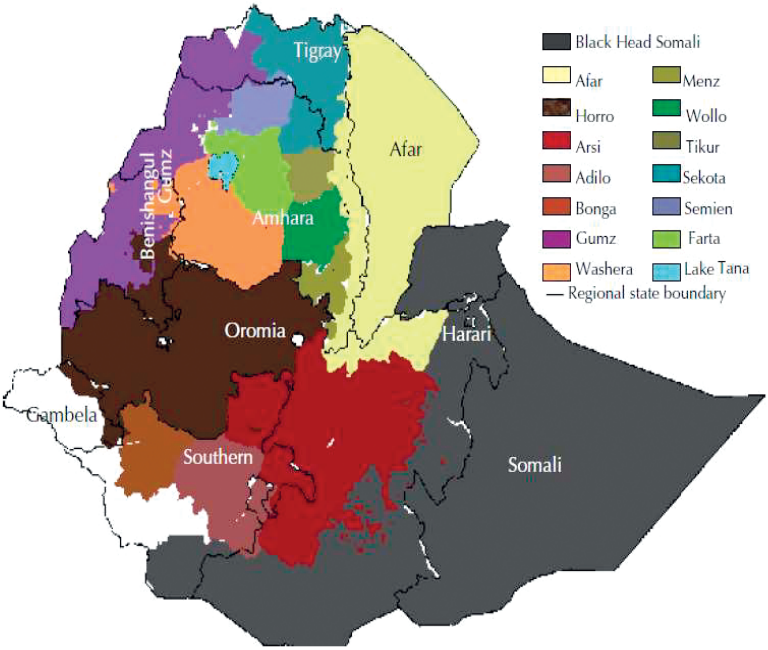

Figure 1. Geographic distribution of sheep types (breeds) by Gizaw *et al*. (2008a).

A CBBP refers to village-based breeding activities planned, designed, and implemented by smallholder farmers, individually or cooperatively, to effect genetic improvement in their flocks and conserve indigenous genetic resources (Gizaw *et al*., 2013b). In CBBP, the farmers and pastoralists are both breeders and producers (Baker and Gray, 2004). CBBP have been initiated in Ethiopia by research institutes (Gizaw *et al*., 2013b). Presently a variety of village-based cooperative breeding programs exist, namely, in four indigenous sheep farming communities located in Lowland Crop-livestock Pastoral (Amibara), Sub-alpine Sheep-barley (Menz), Highland Perennial Crop-livestock (Bonga), and Highland Cereal-livestock (Horro) production systems. Breeding objectives are shown in Table 1.

1.3 Breeding Goal Traits for Sheep

1.3.1 Breeding Goal Traits for Sheep in Developing Countries

In other developing countries, sheep production is also becoming steadily more important (Skapetas and Kalaitzidou, 2017), playing a significant role in human nutrition and for income (Kosgey, 2004; Tibbo *et al*., 2006; Mohapatra *et al*., 2019). Smallholder farmers depend on non-specialized multipurpose breeds and extensive production systems, and no selective breeding is usually carried out. Existing breeds in these countries have been adapted to variable environmental situations which are often characterized by feed scarcity, disease challenges, small flock-size, and communally shared grazing land; uncontrolled mating, and the absence of pedigree and performance recording is also common (Gizaw *et al*., 2008a; Mirkena *et al*., 2011). Thus, the implementation of effective genetic improvement programs is a challenge. Unlike the commercial farmers, smallholders in these regions tend to keep animals for family needs and farming is livelihood oriented (Kosgey *et al*., 2004). Farmers expect their animals also to fulfil many traditional functions (e.g. savings, insurance, culture, and prestige) (Wilson, 1985; Ayalew *et al*., 2003).

Survival of animals to many stresses (heat, disease, parasite, poor nutrition) is one of the most important traits but is given less emphasis than the growth rate. However, on the contrary, comprehensive breeding goals are mostly complex and include traits that represent components of production and reproduction (Sölkner *et al*., 1998). Another challenge under the smallholder and pastoral conditions, as reported by Kosgey (2004), is that recording such traits, and individual animal identification, in many cases are difficult. When selecting the most desirable breed or selecting within the breed, one needs to start with defining the breeding objectives (Kosgey *et al*., 2004). Kosgey *et al*. (2006) reported that smallholder sheep producers' traits of interest were body size, growth performance, body conformation, temperament, colour, and horns, ranked in that order of importance.

1.3.2 Breeding Goal Traits for Sheep in Ethiopia

The local sheep in village flocks in Ethiopia are year-round breeders and the mating is not controlled (Tibbo, 2006; Gizaw *et al*., 2016). In many studies (Gizaw *et al*., 2008a; Asresu *et al*., 2013; Amare, 2018) in Ethiopia on local sheep breeds (Menz, Bonga, Horro, Wollo, and Afar sheep) body size or any size explanatory trait are considered the most preferred traits (Table 1). Regular cash income and financing/insurance benefits derived from sheep production were identified as the main functions of sheep in both Sheep-barley and Pastoral production systems (Gizaw *et al*., 2008a). Sheep production contributes more to the diet of pastoralists (in the form of milk) than to the diet of farmers in the Sheep-barley system. The main breeding goal of farmers in the Sub-alpine Sheep-barley system for Menz sheep breed is to improve their market value through increased meat production (i.e., improved growth rates and conformation). The same is true for farmers in the Perennial Crop-livestock Production System, for the Bonga breed and for farmers in the Highland Cereal-livestock Production System, and for the Horro breed (Gizaw *et al*., 2013b). However, Afar pastoralists prioritize milk yield before meat production.

Lambing interval, mothering ability, and milk yield in both crop-livestock and pastoral systems were also important traits in the choice of breeding ewes (Getachew *et al*., 2010). Yet again, Mirkena *et al.* (2011) and Getachew *et al*. (2010) reported that milk yield, temperament, and pedigree were important attributes in pastoralists' systems (Afar area) when ranking sheep breeding goals. Farmers' traditional breeding practices are characterized by a lack of genetic progress in productivity due to diverse selection criteria including those that do not confer to productivity, communal uncontrolled breeding practices, and negative selection practices through the sale of the best-performing animals (Gizaw *et al*., 2012).

Table 1. The community breeding objective traits for some sheep breeds reared by smallholder farmers and pastoralists in Ethiopia.

Traits	Rank indexes of breeding objective traits			
	Menz*	Bonga**	Horro**	Afar*
Breeding rams				
Appearance/conformation & Size	0.290	0.349	0.412	0.350
Colour	0.200	0.282	0.216	0.150
Horn	0.030	0.009	0.007	0.006
Ear	0.020			0.005
Growth rate	0.240	0.052	0.014	0.170
Fleece yield	0.004			
Mating ability	0.040	0.027	0.002	0.110
Tail size and shape	0.180	0.273	0.280	0.210
Temperament		0.005	0.002	
Breeding ewes				
Appearance/size	0.080	0.279	0.403	0.150
Coat colour	0.120	0.238	0.233	0.100
Mothering ability	0.220	0.075	0.046	0.160
Age at first lambing	0.030	0.020	0.101	0.030
Lambing interval	0.310	0.076	0.006	0.120
Twining	0.160	0.124	0.024	0.090
Tail size and type	0.050	0.137	0.089	0.090
Milk yield for family				0.220
Ear size	0.010			0.000
Longevity	0.020	0.003	0.00	0.040

Index = [(3 × number of households ranking as first + 2 × number of households ranking as second + 1× number of households ranking as third) for each selection criteria]/[(3 × number of households ranking as first + 2 × number of households ranking as second + 1 × number of households ranking as third) for all selection criteria for a production system].

Adapted from *Getachew (2008) and **Edea (2008)

1.3.3 Milk as A Breeding Objective

Sheep's milk in tropical countries is mainly for home consumption and could be an important item of diet (Welham, 1976). Sheep and goats are considered as dairy animals of the poor due to their rapid generation turnover, short pregnancies, and supply milk in quantities that are suitable for immediate use (FAO, 2007). Furthermore, by-products can be developed that can create income for smallholder farmers. A study by Tulicha (2013) showed that small ruminants withstand drought on low-value feeds and can be an important milk and meat source also for children when cattle are unable to provide milk. In Ethiopia, though, the use of ewes as milk sources has rarely been reported. However, the practice of keeping and selecting sheep for milk production in the country is increasing. The good milking and long-legged BHS sheep are, for example, suited to the nutrition and nomadic tradition of the pastoral community (Nigussie *et al*., 2013; Gizaw *et al*., 2013b).

1.4 Pure Breeding Programs of Sheep

1.4.1 Pure Breeding of Sheep in Developing Countries

Within breed selection (i.e. pure breeding) is a sustainable and viable option also in developing countries (Kosgey *et al*., 2006; Tibbo *et al*., 2006). Thus far, high within-breed genetic variation in the indigenous livestock populations are reported by many studies (Lauvergne *et al*., 2000; Gizaw *et al*., 2007; Gizaw *et al*., 2011). This indicates that a high response to selection may be anticipated. Most conventional breeding programs in developing countries have failed due to the lack of continuous supply of improved genotypes to farmers' flocks and inappropriate sets of selection objectives (Kosgey, 2004). A good example of this is the case of D'man sheep breed improvement program to increase ewes' prolificacy and increase lamb growth observed in Morocco (Turner, 1978). Likewise, insufficient involvement of farmers and the shortage of financial and logistical resources for sustaining sheep breeding program (eg. Peul and Djallonké breed in Senegal) are additional reasons for the lack of success (Fall, 2000). Some pure breed genetic improvement programs have been implemented for indigenous sheep breeds in developing countries particularly in Africa. Quite a few reports indicated that breeding programs had been initiated to increase meat production and improve trypano-tolerant traits in Ivory Coast, Gambia, and North Togo for Djallonké sheep breed (Yapi-Gnoare, 2000; Dempfle and Jaitner, 2000; Bennison *et al*., 1997; Van Vlaenderen 1985; FAO, 1988). Another sheep breed improvement program reported in humid sub-humid part of east Africa was focused on Red Maasai (Baker *et al*., 1999) and Blackhead Persian sheep breed (Baker, 1995) to improve trypano-tolerant and resistance to parasites.

1.4.2 Pure Breeding of Sheep in Ethiopia

Several studies have been conducted to design suitable breeding schemes for implementing selective breeding in smallholder farming systems in Ethiopia (Gizaw and Getachew, 2009, Duguma, 2010; Aynalem *et al.,* 2011; Mirkena *et al*., 2011). In the 1980's, a few sheep selective breeding programs were initiated by the Ethiopia Institute of Agricultural Research (EIAR), including Afar and Horro sheep breeding programs, that were limited to the formation of elite nucleus flocks, but the programs have since been ended (Gizaw *et al*., 2013b). One problem was no distribution scheme in place for the improved genotypes from the nucleus centers. Selective breeding as a genetic improvement strategy is gaining momentum (Gizaw *et al*., 2013b): there are now breeding programs underway for Menz, Horro, Bonga, Washera, Doyogena, Atsbi, and Afar sheep.

1.5 Crossbreeding Programs of Sheep

Crossbreeding is considered an attractive breed improvement method due to its promise of quick benefit as the result of breed complementarity and heterosis effects (Goddard and Hayes, 2009; Leroy *et al*., 2016). In developing countries, initiatives have been undertaken since the beginning of the 20th century to replace or introduce new breeds. Much of the sheep crossbreeding in these regions have been criticized as incompatible with the conservation of indigenous adapted breeds (Kosgey, 2004). However, there is a belief that indigenous breeds are less productive and unlikely to continue sustaining the fast-growing demand for food (Gizaw *et al*., 2008b). Hence, many African countries still favor the development of crossbreds (FAO, 2007). Lack of adaptation of the crossbreds to harsh production environments and low complementary socio-economic support has elevated uncertainties about the sustainability of crossbreeding in some regions or for some breeding systems. On the other hand, when local conditions allow its proper implementation, crossbreeding has induced substantial increases in animal performance, as well as farmers income (Roschinsky *et al*., 2015). In the past, the government of Ethiopia has placed much emphasis on importing exotic genetics and crossbreeding with local stock as a strategy for genetic improvement (Tibbo, 2006). However, crossbreeding programs based on exotic and local sheep populations in Ethiopia remain few, indicating that the effort of sheep crossbreeding in Ethiopia did not deliver the expected benefit to smallholder farmers so far. It has not led to a significant productivity improvement and many of the programs have been unsustainable (Aynalem *et al*., 2020b; Gizaw *et al*., 2013b). Getachew *et al*. (2016) indicated that there is still a growing interest of the government and of farmers in sheep crossbreeding.

1.5.1 Crossbreeding of Sheep in Developing Counties

In developing regions, particularly in Africa, reports on structured sheep crossbreeding programs are limited (Kosgey *et al.*, 2006). Most of the breeding programs were managed by governments with little participation by farmers (Aynalem *et al*., 2011). In South Africa, many crosses were made between various European wool breeds and indigenous hair type sheep breeds to combine their mutual advantages. For instance, the Dorper Sheep breed was formed by crossing Dorset Horn x Blackhead Persian in 1950. Dorper has been used to improve sheep in other parts of Southern and Eastern Africa as well. In Kenya, crossbreeding between Dorper and Red Maasai sheep has been used by most farmers in the Kajiado district and is playing an important role in the livelihood of the people (Liljestrand, 2012; Zonabend *et al*., 2014). However, there is no structured breeding program available to enable sustainable utilization of Red Maasai together with Dorper (Zonabend *et al*., 2017). Another much introduced sheep breed into developing countries is Merinos, a breed with fine wool (Razali *et al*., 2005). Several developing countries (e.g. South Africa, Mexico, India, Kenya, Zimbabwe, and Egypt) have used Merino to improve the wool production of their indigenous sheep breeds (Acharya, 1982). However, in West Africa Merino crossing programs have not been successful in many areas (to mention some: West Africa, Chad, Nigeria) (Burns, 1967). Alongside the Merino sheep breed, in Egypt, a crossbreeding program was initiated in 1974 to improve the productivity of two native sheep breeds (Ossimi and Rahmani) through crossing with the known prolific Finn sheep breed (Elshennawy, 1995; Marai *et al*., 2009).

A little work has been done on the crossing to locally adapted breeds to exploit either hybrid vigour or complementarity. In Libya, the Barbary has been improved in size, weight, and fleece weight, by crossing with the white Karaman from Turkey. In Tunisia, farmers are crossing the local Barbarin (a fat-tailed breed) with thin tailed breeds, Algerian Ouled Djellel and Black Thibar. This happens because the fat tail is known as an adaptation to harsh conditions and fat-tailed animals are preferred for religious practices (Bedhiaf-Romdhani *et al*., 2008). Crossbreeding programs done to develop sheep for milk production are rare or undocumented in the developing countries. In Northern Tunisia, milk sheep (referred to as Sardinian) are developed by the interbreeding of imported Sardinian and Sicilian milk sheep in specialty milk production (DAGRIS, 2005).

1.5.2 Crossbreeding of Sheep in Ethiopia

Several efforts have been made to this end since the early 1960s (Tibbo, 2006). These have included importing various exotic breeds (Bleu du Maine, Merino, Rambouillet, Romney, Hampshire, Corriedale, Awassi, and recently Dorper) aimed at improving growth and wool yield (Tibbo *et al*., 2006; Getachew *et al*., 2016; Ayele *et al*., 2015; Awgichew and Gipson, 2009). Since the downfall of the monarchy (in 1974), crossbreeding efforts by DB-R and AG-R have been oriented to produce and disseminate crossbred rams of different breeds (Awassi, Corriedale, and Hampshire) to smallholder farmers (Getachew *et al*., 2016) at a subsidized price (DB-R, 2007 as cited by Getachew *et al*., 2016). Corriedale and Hampshire breeds were initially used, but these breeds were gradually replaced by Awasssi following the introduction of Awassi in 1980 (Getachew *et al*., 2016; Gizaw and Getachew, 2009). The target has been on the dissemination of rams with 75% Awassi inheritance to farmers for crossbreeding with their local ewes (DB-R, 2007 as cited by Getachew *et al*., 2016). Specifically, Awassi crossbred rams have been distributed in the Highlands of Ethiopia to increase the body size of the indigenous fat-tailed sheep breeds through crossbreeding (Gizaw and Getachew, 2009). The indigenous are Menz (in North Shewa) and Wollo sheep (in South Wollo) breeds. They are predominant to the Menz and South-Wollo areas and are characterized by being short-fat-tailed traditional sheep breeds, with coarse wool and small body-size (Gizaw *et al.*, 2012). The indigenous sheep breeds are highly adapted to a low input system and have evolved largely through natural selection for survival under sub-optimal and disease-ridden environments (Tibbo, 2006; Gizaw *et al*., 2011).

The community-based breeding programs (CBBP) in Ethiopia were initiated at the end of 1980, facilitated by outsiders: Development agents, researchers, experts, governmental and non-governmental organizations (Gizaw and Getachew, 2009). Awassi is also a fat-tailed, long coarse wooled, sheep breed, most common in the Near East region. Although considered as a dairy breed, these sheep are used for both milk and meat production. The breed is said to be hardy and adapts to a wide range of environmental conditions from the steppe to highly intensive systems (Epstein, 1982).

In the Awassi - Menz/Wollo crossbreeding program, breeding rams from three governmental farms: DBARC, DB-R1, and AG-R2 have been allocated to local cooperatives. Each breeding ram is assigned a mating group of 20 - 35 ewes. After three years of use, rams are culled and replaced with other rams from the governmental farms. Ewes are first mated at around 12 months of age. A local breeding cooperative is organized in groups of 6 - 12 (more in some cases) households based on neighborhood and use of common grazing area. The Bureau of Agriculture and Rural Development (BoARD) of Amhara regional state is responsible for the dissemination of the selected Local x Awassi crossbred rams to villages. One 75% (¾ Awassi × ¼ Menz) crossbred ram, and rarely one 50% (½ Awassi × ½ Menz), is given for free to each group. The group of farmers is responsible for the use and care of the breeding ram. Breeding rams are rotated both within the group, among groups of farmers and across the villages, to avoid mating between relatives and to widen the gene pool (Gizaw and Getachew, 2009).

Similar initiatives have been taken place to cross Awassi with another local breed (Tikur sheep) in two villages of North-Wollo by Sirinka Agricultural Research center (SARC) starting in 2007 (Getachew *et al*., 2016). Lately, the Dorper-indigenous breed crossbreeding program implemented by Ethiopian Sheep and Goat Productivity Improvement Program (ESGPIP) project in collaboration between local Universities and research centers at 2 nuclei and 10 breeding, evaluation, and distribution (BED) sites, have been established in different parts of the country since 2007. The ESGPIP imported this sheep breed and began a crossbreeding program at different BED sites of the country (Ayichew, 2019). Some crossbreeding among indigenous breeds has also been practiced at 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, 2004). In 2005, a village based Farta × Washera sheep crossbreeding program was started (Mekuriaw *et al*., 2013) with the aim to increase productivity of medium sized indigenous Farta (Gizaw *et al*., 2008a) by crossing or introducing males and females of indigenous Washera sheep. Another example of crossbreeding of indigenous sheep with selected Bonga rams is taking place in peri-urban areas of Arbegona district of Sidama area of southern Ethiopia that have access to markets (Mekasha *et al*., 2016b). In this program, cross-bred males are being sold to the market directly when they reach market age/weight or after value addition through fattening.

1.6 SWOC Analysis for Forming Synthetic Breed

In Ethiopia, there are a few available studies that describe the development of synthetic breeds (Tibbo, 2006; Gizaw *et al*., 2010). Designing a sustainable breeding scheme considering long-term genetic consequences for the within-flock genetic diversity and improving its genetic merits (for instance its milking or meat production ability) for the Awassi-Menz crossbreeding program has been explained by Gizaw *et al*. (2010). The formation of a composite breed based on the crossbred ewes which suit the subsistence nature of agriculture in the country is among the top identified thematic areas for research (EIAR, 2018). The experience to be gained from other developing countries with emphasis on the selection within or between sheep crossbred for milk or related trait is limited. The need to determine the optimum proportion of Local and Awassi inheritance to establish and select within the synthetic breed is important. Tibbo (2006) suggested the development of a synthetic breed and Gizaw *et al*., (2010) also further showed the possibilities of developing a stable and self-replacing synthetic breed in the existing breeding program. By carrying out breeding value estimation with a model containing a genetic group of animals, a synthetic population could be established, converging towards the Awassi percentage that would be favorable in the FE. Crossing could continue until the foundation animals have the suggested admixture of breeds and then the foundation animals are mated amongst themselves. Selection in crossbreeding programs could also be introduced to enable to stabilize the synthetic population and further improve its genetic merit as reported by Gizaw *et al.* (2010). And the stable and self-replacing synthetic breed from the Awassi-Menz/Wollo sheep could be an alternative crossbreeding program.to the existing design. A summary of SWOC **(**Strengths, Weaknesses, Opportunities, and Challenges**)** is given in Table 2 based on the available literature (Tibbo, 2006; Gizaw *et* *al*., 2010; EIAR, 2018) for station-based breeding (present Awassi–Menz/Wollo crossbreeding program) and synthetic breeding (as alternative breeding program) based on information from farmers .

Table 2. SWOC analysis of the existing station-based breeding vs. forming synthetic breeding as alternative breeding program in Ethiopia.

SWOC	Station-based breeding	Synthetic breeding
Strength	• Cooperating and motivated farmers • Presence of infrastructure	• Enable farmers to produce high grade crosses right away without the need for replacement rams from the government farms. • Useful in combining merits of parental breeds into self-replacing straight breeding flocks. • Can speed up multiplication of crossbred rams (50 and 75%) to villages. • Allow using adapted genes.
Weaknesses	• Insufficient finance and logistics to support the program, • Farmers lack skill on recording (performance, pedigree, etc), • Needs centralized flocks (government ranches), which also requires extra costs of maintenance of the purebred exotic flock. • Dissemination and maintaining the desired exotic blood level at village level • The complicated procedure of other crossbreeding systems such as upgrading • Operationally very difficult	• Insufficient finance resource to support the program, • Farmers lacks skill on recording • Several generations required to get stable genetic composition • No heterosis use

Opportunities	• The required structure and facilities are available including by law and institutions • Good support from the government, i.e., Government has accepted the approach as the strategy of choice for genetic improvement	• There is possibility of developing a stable and self-replacing synthetic breed from crosses of Awassi-Menz sheep that are tested at DBARC (albeit a very small Awassi-Menz population). This can be replicated in stations (DB-R and AG-R) to build up population size. • Can be implemented alongside the on-going crossbreeding design to disseminate the improved genetic material of the synthetic breed.
Challenges	• Genetic dilution of Local breeds, • Requires strong research and development support • Long and complicated bureaucracy • AI is not practiced	• Requires stabilizing the crossbred population into a straight-breeding population. • May cause loss of heterozygosity • Long and complicated bureaucracy • AI is not practiced

1.7 Evaluation of Test-Day Milk Yield

Some traits like milk yield can be observed repeatedly throughout the lactation (Mrode, 2014). The observations are made either at specific or at random intervals and the number of observations can vary from animal to animal. There exists an earliest test-day (*t*min) and then a latest test-day (*t*max), beyond which no more observations are made. Orthogonal polynomials have been suggested to be used with longitudinal data to model the shape of the lactation curve (Prakash *et al*., 2016). A possible feature of the analysis of such repeatedly measured traits is modelling the correlation between observations, e.g. through the permanent environmental effect (Szyda and Liu, 1999; Schaeffer, 2004), or in other ways. A flexible type of orthogonal polynomials are Legendre polynomials (LP), dating back to 1797. To use LP or other kinds of orthogonal polynomials, the time values may be rescaled into ranges from -1 to +1. The first four normalized LP functions of scaled units of time (x) are the following: $\phi_0 = 0.7071$, $\phi_1 = 1.2247x$, $\phi_2 = -0.7906 + 2.3717x^2$, and $\phi_3 = -2.8062x + 4.6771x^3$, where x is the time value (Schaeffer, 2016). Plotting the response variable against linear models where the LP functions of the time values are multiplied to parameters to be estimated gives a shape that is called the trajectory. A goal can be to find a trajectory that fits the data as closely as possible and to study the amount of animal variation around the trajectory, for example the additive and permanent environmental variance.

Genetic evaluation of milk yield in many dairy animals has now turned to the use of test-day records (Anang *et al*., 2019). The test-day models may reduce the cost of milk recording by requiring fewer milking measurements and less frequent and stringent collection of milk samples (Prakash *et al*., 2016). Repeated measurements per animal can be modelled with a test-day model requiring less computational effort and less parameters than a multiple trait model where milk production at different stages of lactation are taken as different traits (Mrode, 2014). In a test-day model, the orthogonal polynomials are often used to model the average lactation curve but can also be used to model individual deviation from the curve through random regressions (Schaeffer and Dekkers, 1994). One simpler model is a repeatability model that contains only the 0^{th} order random regression for the permanent environmental effect, but which also can contain orthogonal polynomials of higher order for the additive genetic effect. Many studies have used LP as they make no assumption about the shape of the curve and are easy to apply (Mrode, 2014). Using LP allows accounting for other fixed effects, e.g. of test day, and so allows for better utilization of the inherent information contained in the experiment (field) data relative to that in the cumulative lactation yield (Szyda and Liu, 1999). In developing countries where data on milk production is generally scarce, effective use of all available information is of importance (Prakash *et al*., 2016).

1.8 Selection Method and Response

In Ethiopia, there are limited genetic responses in selective sheep breeding experiments reported from on-station performance. Gizaw *et al*. (2007) and Tibbo (2006) have shown the use of selection on EBV for body weight traits of Local and crossbred sheep in the cool central highlands of Ethiopia. When Gizaw *et al*. (2007) in an experiment set up to evaluate the response of Menz sheep to selection for yearling live weight, a sizable response was observed, for instance. Aynalem *et al*. (2020a) reported genetic parameter estimates from the on-farm evaluation under the community managed flocks, which resulted in substantial genetic gains for birth weight, 6 months' weight, and litter size for Bonga, Horro, and Menz flocks. Proper selection of parents will give a positive response in the next generation and create progress in breeding goal traits. Conventionally, the selection index method combined phenotypes precorrected for fixed effects of relevant traits recorded on the breeding candidate and their relatives (Toghiani, 2012; Ellen *et al*., 2007). Today, the preferred method over the selection index to predict breeding values (EBV) is called Best Linear Unbiased Prediction (BLUP) (Robinson, 1991; Urioste *et al*, 2003) due to its possibilities for simultaneous estimation of the fixed effects. Intense selection may increase the rate of inbreeding (Khaw *et al*., 2014). To maintain inbreeding at an acceptable rate, appropriate selection algorithms that maximize the selection response for a given rate of inbreeding, denoted optimal contribution selection (OCS) have been developed (Meuwissen, 1997). Genomic selection (GS) will play a role also in sheep breeding programs (e.g. Lillehammer *et al*., 2020; Sutera *et al*., 2019; Meyermans *et al*., 2019; Dodds *et al*., 2014; Moioli *et al*., 2013) largely by reducing generation intervals and by giving larger opportunities for example for maternal traits (Lillehammer *et al*., 2020). However, it should be noted that this method requires extensive genotyping of individuals and will thus be costly to apply. So far in Ethiopia, genotyping has been limited to few experimental animals and for a few breeds (Asrat *et al*., 2019; Ahbara *et al*., 2019).

1.9 Hypothesis of the Study

This thesis is mainly focused on the TDMY data collected from Local (Menz/Wollo), pure Awassi and their available crossbreed ewes under the Awassi-Local crossbreeding program. In the Central Highlands of Ethiopia Selection of breeding rams is done at the two multiplications and breeding center stations based on their merit for meat and wool production. The gene flow is from the multiplication and breeding centers (DB-R and AG-R) to the member farmers organized in groups. In this study, it is assumed that the best Awassi percentage at the stations (DB-R and AG-R) is also best under the farmers' conditions.

Additionally, the TDMY trait at the stations is heritable. The genetic superiority of ewes for TDMY is spread-out across the farmers' herd and in this study, it is assumed to be realized at large in the CBBP member farmers due to no G x E exists for milk yield between BE and FE. We chose to study TDMY of ewes at different degrees of Awassi percentage. Therefore, how the TDMY is registered and used current ewe’s performance and genetic evaluation is further explained in the following.

2. AIM AND OUTLINE

The main objective of the current Ph.D. project was to investigate the optimal proportion of Awassi in Local ewes for milk production in the existing CBBP of Ethiopian Central Highlands, and how to breed them for milk production.

The following goals were investigated in three scientific articles:

- To estimate milk production performance utilizing test-day milk yield records and fitting lactation curves of Awassi crosses relative to that of Local sheep breeds (Menz and Wollo) reared under the farmer's environment in the central highlands of Ethiopia.
- To estimate variances and genetic parameters for test day milk yield as well as lactation curves in ewes with different level of Awassi percentage (when crossed with Local) at the two governmental (DB-R and AG-R) owned breeding and multiplication centers, using a repeatability animal model, and
- To estimate genotype by environment interaction for test day milk yield utilizing available crosses of Awassi with Local breeds, kept either by smallholder farmers or at breeding stations (DB-R and AG-R).

3. DATA MATERIAL

The TDMY records included in the first paper were obtained from two villages of smallholder farmers (Faji and Chiro) involved in the Awassi - Menz/Wollo Community-Based breeding program in the Amhara Regional State of Ethiopia. The TDMY data set used for the second paper was collected from the two sheep breeding and multiplication centers in the same program. In the third paper, both the data from the farmers and the two governmental (DB-R and AG-R) owned breeding and multiplication centers were used to understand if there is any G x E interaction of the environments for the TDMY. The number of observations and animals (ewes) with data used in the three papers are given in Table 3.

Table 3. Total number of observations and number of ewes recorded for TDMY included in Papers I - III.

	Paper I	**Paper II**	**Paper III**
Source of data	Farmers	Breeding and Multiplication Centers	Farmers and Breeding and Multiplication Centers
Number of observations	466	1040	1506
Number of ewes	115	211	326

4. GENERAL DISCUSSION

The first paper estimated milk production performance of studied genotypes based on available TDMY under farmers' conditions and presents an approach that allows comparisons using a limited number of data. The group of ewes with a high % Awassi produced consistently more milk than the Local breeds at the farmers' condition. These results demonstrate the potential that exists in increasing milk production through the initiated crossbreeding program. The results from the second paper indicated that the 100% Awassi ewes produced significantly more milk than the other studied ewe groups at the centers. The estimated genetic variance for TDMY could give genetic gains in the dissemination program if all ewes at the centers are measured and the heritability may be increased by reducing the environmental error. The accuracy of predicted breeding values may be increased by more relatives and better design (not confounding sire and environment, like having offspring or descendants of same sires in more than one farm and environment). The largest accuracy was found among the sires due to sires having progeny tested. However, accuracy could become increased if actions could be taken to increase the size of the heritability. In the third paper, no significant G x E interaction was found for BE compared to FE over 120 days in milk. This implies that the selection can be performed at the breeding centers and genetic superiority can largely be realized in the farmers' environment. The main outputs (Papers I - III) are briefly discussed under the following sub-titles.

4.1 Breeding for Milk Production

To include a trait in a breeding goal requires knowing that the trait is important, shows genetic variation, and can be measured with sufficient accuracy for selection (Toghiani, 2012). The importance of milk to the smallholder farmers' nutrition, income, environment, and better growth rate of lambs is evaluated in different studies (e.g., Legesse *et al*., 2008; Getachew *et al*., 2016; Mekasha *et al*., 2016a). In the southern part of Ethiopia, in the Sidama area, there exist markets for sheep milk as well as when mixed with cow milk (Mekasha *et al*., 2016a). In the lowland part of Ethiopia (Afar and Somali pastoralists) milk yield is part of their breeding goal trait (Nigussie *et al*., 2013; Mirkena *et al*., 2011; Gizaw *et al*., 2013b). Results from Paper I indicated that the best genotype of the studied % Awassi (30 - 50%) crosses can produce a significantly higher yield than the 0% Awassi ewes in TDMY in the farmers' environment. Results from Paper II showed an exploitable amount of genetic variation among individuals for TDMY. In Paper II, results indicated that even with limited data for a part of the population for the estimated variances, it was possible to achieve moderate reliability of selection accuracy for observed ewes (55%) and sires of observed ewes (52%). Genetic progress of the trait will depend on both male and female selection accuracy, although since selection intensity is higher for males, their accuracy has the highest impact on genetic gain.

Currently, rams are selected for the field based on mass selection for their own weight. Selection can be done by looking at the possible genetic correlation between traits. To improve milk production a realistic alternative would be to select these rams directly on their breeding values for milk yield coming from related daughters etc. Afolayan *et al*. (2009) reported moderate positive genetic correlations between milk production and growth traits of ewes, which means there is little conflict between selection for growth traits and milk yield. Similarly, positive correlated responses in milk production of ewes following selection for the early growth of their lambs (or vice versa) are reported by some authors (Pattie, 1965; Morgan *et al*., 2007; Snyman *et al*., 2016). The absence of antagonism among the traits suggests the joint selection for both objectives will be efficient, so one may consider improving milk traits without large sacrifices in meat production (Brito *et al*., 2020). When two or more traits constitute the goal of a breeding program (e.g., to select animals with an adequate genetic balance for milk and meat production traits), a selection index should be established for ram evaluation. An economic weight for TDMY in areas where there is a market for milk and consumers should be computed. Both body weight and milk should be included, but also other traits should make up the breeding goal.

4.2 Genotype by Environment Interaction

Sheep production takes place in a wide range of environments or production systems, and thus G x E might be expected. When the production environments vary widely, decisions on breed choices need due attention to possible G x E. Our estimate showed that none of the genetic groups had significant G x E when compared over the defined whole lactation (120 DIM) under the two management systems (Paper III). This implies that the selection can be performed at the breeding stations, and the genetic superiority multiplied will in large be realized in the farmers' field. Selection can be done in the stations and genetic gain can still be achieved under farmers' conditions since the G x E interaction is low. However, at early lactation and for the Local, a significant TDMY increase was found in the stations' environments, but this did not exist for the group with >50 - 75% Awassi. This G x E interaction implies that it is the high % Awassi (>50 - 75%) ewes that appear to be robust to environmental changes when it comes to milk production. The interaction observed can be important because a high rate of lamb mortality has been reported in the area, with a phenotypic relation to milk production of the mother (Snowder and Glimp, 1991; Tibbo, 2006; Getachew, 2015). Differences in growth and reproduction performances of sheep have been reported that may be regarded as G x E (Demeke *et al*., 1995; Getachew, 2015). Moreover, estimation of genetic group-specific residual and permanent environmental variances in either of the two environments could have been obtained with more data and would have added information about the environmental sensitivity of the genetic groups at the micro and macro level, in analogy with Bytyqi *et al*. (2007) and Steinheim *et al*. (2008).

4.3 Genetic Parameters of TDMY in Sheep

Knowledge of genetic and phenotypic parameters is required for planning efficient breeding programs (Roman *et al.,* 2000). Genetic variation between or within breeds is essential for long-term genetic improvement (Biscarini *et al.*, 2015). In the two station farms, variance components for TDMY were estimated in Paper II. However, both the additive genetic and the permanent environmental variances were estimated with large standard errors due to missing pedigree data, data not recorded for all animals, and the fact that test-day effects could not be accounted for. From these variances, the heritability (h^2) and repeatability (r) of TDMY were estimated. We used the estimates to exemplify the use of these parameters in the prediction of breeding values and their accuracy. Suggestions from an earlier study on meat (Tibbo, 2006) also used in this thesis, was to carry out a genetic evaluation at the nucleus flock level, where the gene flow is started. Up to now, no genetic analysis has been conducted on sheep milk in the study area for comparison. With predicted (BLUP) breeding values, the current phenotypic selection could be replaced and made more efficient. Our genetic parameter estimates for TDMY in sheep were considerably smaller in size than comparable estimates of repeatability and heritability, e.g. the 0.39 and 0.28 obtained by Bauer *et al*. (2012); and 0.40 and 0.15 reported by Othmane *et al.* (2002). So possibly genetic gain by selection could be higher than we envisaged.

Today, prediction of breeding values (EBVs) is commonly carried out by BLUP techniques, either using pedigree or genomic relationship. For the ewes' in the 100% Awassi group, the EBV had the largest individual range and mean accuracy (Paper II). The largest individual accuracy was found among the sires due to sires being progeny tested. This group contributes the most through the 50 and 75% Awassi ewes in the breeding stations. The ram lambs with the same Awassi percentages are disseminated to the CBBP member farmers. Currently, rams are selected for the field based on their own weight. These rams could also be selected based on breeding values for milk yield, the information coming from female relatives in the nucleus. Hence, sheep milk traits could be included in breeding schemes. Selection within the purebred groups in the centers (with more than 3000 sheep in each of the two), both 100% Awassi and Local, could be based on the same TDMY information. This would require recording the milk yield on all ewes in the centers and include the young ram selection candidates in an expanded relationship matrix (**A**). With the manpower and facilities available in the breeding stations, it is possible to record 5 times per ewe per lactation in the station which amounts to 5000 observations per year. This gives a more representative performance level of the breeds/genotypes. Pedigree based performance evaluations have dominated national livestock programs in developing regions including Ethiopia. The present accuracy of EBV is based on the rams of the observed ewes. In the future, the cost of genotyping might become very cheap, and possibly we will know the genomic relationship of all individuals. If we have the genomic data, we could be able to increase the accuracy of EBV (Paper II) up to 50 or 60%.

4.4 Transfer of Genetic Gain for Milk

Over 120 DIM and in BE in Paper III, the LSM estimates were close to those obtained in Paper II, while the corresponding estimates in FE for 0% Awassi and <30% Awassi were considerably higher than those estimated in Paper I. Thus, the transfer of genetic gain or production advantage of the 30 - 50% Awassi group found in farmers field (Paper I) or more in the better environment became less clear. In Paper III modelling of the trajectory of DIM was done across the trajectory of the Awassi percentages of ewes, while in Paper I the trajectories of DIM was done within predefined genetic groups, classified beforehand according to % of Awassi, which might be high or low within the classes. This continuum as well as the product of the coefficients for the two trajectories are considered as reasons for the somewhat changed LSM estimates, especially for FE with the least data (Paper I vs Paper III). Note that the form of the Legendre fit for % of Awassi will also be affected by TDMY values outside the genetic group studied.

Although farmers select for several traits (body size, growth performance, type, conformation, color, and horn; Kosgey *et al*., 2006) based on own performance of indigenous and crossbred sheep, milk traits are often ignored. Locally, milk as a selection criterion is currently only carried out in Afar (Mirkena *et al*., 2011). Similar phenotypic records so far are limited to experimental farms and research stations. In addition to contributing to increased weight gain, Awassi is also a good milk producer (Rummel *et al*., 2005). A few studies have examined milk yield in Local and crossbred sheep under variable environments, for example for Afar breed (0.224 kg day^{-1}) by Mirkena *et al*. (2011); for Menz breed (0.21 kg day^{-1}) by Mekoya *et al*. (2009). In this PhD study, TDMY of Local ewes were predicted with LP and compared to

Awassi crossbred ewes using a limited number of animals and observations recorded over 120 DIM under farmers' environment (Paper I) and breeding station environments in Ethiopia (Paper II). The approach with modelling of lactation curves with LP within genetic group had power enough to give some clear recommendations as to what breed percentages to be given emphasis with respect to milk yield in either of the two environments or production systems. The use of LP within the breed group for lactation curve combined with a model with effects of different parities allowed us to utilize data for all available animals and to estimate the trajectory of the lactation curves. For all genetic groups, these curves were continuously decreasing from the start of lactation. Moreover, the trajectory of the curves showed (Paper I and II) a shorter length of lactation for Local (0% Awassi) than the rest of the genetic groups. The comparison over 120 DIM favored the Local ewes by not including production beyond 120 days. Our findings showed (Paper I) that the 30 - 50% Awassi ewes produced best in farmers' environment. The available genetic groups were not the same in the two environments. In Paper II data from the two governmental farms were utilized and the results showed that Awassi (100%) ewes could produce more milk than any of the crossbred group and the Local ewes. Awassi is a widespread sheep breed and adapts to a wide range of environmental conditions particularly in tropics (Galal *et al*., 2008), however, maintaining a high blood level of the exotic breed in the farmers' environment is still a challenge due to disease, lack of feed and management (Tibbo, 2006) and a limited supply of the genetic material.

Daily milk intake is the most important factor in determining lamb growth rate, survival and potential growth of lambs depend on the lactation of the dam (Ünal *et al.,* 2007; Peniche *et al*., 2015). It is also noted that the Local ewes are low in yield but likely better in adaptation to the local environment while the disease resistance of the exotic sheep is poor. In the crossbreds both traits are combined. Our results showed that it is possible to determine the advantageous % Awassi in the cross based on their TDMY. It can be hypothesized that mortality, survivability, and growth rate of new-born could also be improved if we plan to improve milk production from them, but this remains to be further examined. Some ewes are genetically predisposed to have better maternal characteristics including greater mothering ability and milk production (Assan, 2020). Based on Getachew (2015), the best growth performing lambs had an average Awassi level of 37.1%. His finding was comparable with the current result presented in Paper I, that the group of ewes with 30-50% Awassi significantly outperformed the others for milk yield in the farmers' environment. However, in areas with a good supply of feed and better management, a higher percentage of Awassi in the cross (>50%) might be an alternative (Paper I and II).

4.5 Milk Recording Techniques

Recording systems are attracting worldwide interest across high, mid, and low-income countries (FAO, 2016). Implementing of a well-designed selection program requires an organized trait recording to be able to estimate parameters and do efficient selection. Poor recording system has often been reported as one of the limitations in genetic improvement programs (Philipsson *et al.*, 2011). Many guidelines have been developed to foster standardization of animal recording systems (FAO, 2016). However, the suitability of the recording systems for direct application in mid- and low-income countries, particularly in the small-scale production systems are debatable given the presence of large numbers of small-scale producers.

Selection would be more efficient and accurate if based on more data as much as possible. Among the smallholder farmers, there has been an effort to adopt easy and resource wise breeding records. There exists a recording system for growth traits. However, pedigree data and performance details of animals are kept only for research. Getting accesses to big data, efficient use, and measurement of phenotypic information at low cost in the farmers' environment is a challenge. Dairy related traits are new, and no simplified methods exist for recording of traits. Obtaining reliable milk yield data for use in this study was a challenge. The data used in this study (Paper I - III) was based on the ICAR method for ewes. In fact, the ICAR guidelines are primarily written by and for technicians who run highly developed state of the art animal identification and performance recording systems (FAO, 2016). In the future simplified and economical sheep recording methods that allow easy data registration (e.g. FAO, ICAR, or OIE versions developed for developing countries or small input systems) should be adapted to the farmers' environment. Besides the protocols, ICT can be used to collect and transmit recorded data by smallholder farmers' in the field. Nowadays, most farmers own smartphones. Therefore, developing mobile-based applications to measure milk traits in the field can be an option. In northern Kenya, farmers have achieved significant results using smartphones in tracking livestock disease outbreaks (Long'or *et al*., 2018). Similar experiences were reported using cell phone-based applications (e.g. iCow) giving information needed to improve dairy cattle for many farmers and scientists (Patel, 2019).

4.6 Further Recommendations

- This study was focusing only on limited areas of the country due to logistic and distance but could have been conducted in all the other remote areas where milk yield is involved in their breeding goal.

- The papers were based on limited data set and tried to use it efficiently to withdraw inferences to decide to what % Awassi is best and demonstrate methods for parameter estimates. However, more data are required to have a more robust and efficient genetic performance prediction of animals kept at farmers' and stations' environments.
- A future evaluation could be including other traits than milk to reach a more definite conclusion along with more data. A detailed comparison of the advantage of the traits could also be required.
- Research should be done by including more ewes/rams with deeper pedigree information or any other alternative at the genomic level.
- G x E for sheep needs to be studied using more data from sheep control at farmers environment and for more traits.

5. GENERAL CONCLUSIONS

- With a limited number of ewes and records from the field, modelling of the lactation curve within genetic groups can be used to draw an inference as to what breed percentage ewes should be given preference.

- The best performing ewes produced consistently more milk than Local breeds throughout the lactation.

- The results reported in this thesis show the potential that exists for increasing milk production of ewes through the Awassi – Local sheep crossbreeding program in Ethiopia.

-The advantage of Awassi would increase if the comparison was done over more than 120 DIM.

- An exploitable amount of the genetic variance was indicated for TDMY. If information were recorded for all ewes at the two centers included in this study, preferably with higher heritability and repeatability values than in the current study, there is potential to considerably increase selection accuracy and genetic gain produced by the dissemination program.

- No significant G x E interaction was found for any of the genetic groups across 120 days in milk. This implies that the selection can be performed at the breeding stations, and that the genetic superiority multiplied will in large be realized in the farmers' field.

- The significant G x E interaction for milk yield found in early lactation could be physiological and would be avoided for most animals with the current regime for dissemination of rams that are either 50% or 75% Awassi.

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PAPER I

Finding best exotic breed proportion in crossbred lactating sheep kept under farmers' conditions in Ethiopia determined by use of nested Legendre polynomials with limited data

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Finding best exotic breed proportion in crossbred lactating sheep kept under farmers' conditions in Ethiopia determined by use of nested Legendre polynomials with limited data

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ABSTRACT

The present study was conducted to estimate milk production performance and fit lactation curves for groups of ewes of Local and of Awassi crosses, with a variable blood level, reared under farmer's environment. The Weigh-Suckle-Weigh method plus hand milking was used to estimate milk yield for ewes. A total of 466 observations from 115 ewes were used. Estimated least-squares adjusted means for the milk production over 120 days were 0.56 kg day^{-1} (Local), 0.67 (<30% Awassi), 0.86 (30–50% Awassi), and 0.96 (>50% Awassi). Groups with 30–50% Awassi and >50% Awassi ewes produced significantly ($p < 0.05$) more milk than Local ewes. Significant differences were observed between <30% Awassi and >50% Awassi crossbred groups. The best crosses (>50% Awassi) produced over 70% more milk than the local ewes which demonstrates the potential that exists in increasing milk production through the initiated crossbreeding programme with sheep in Ethiopia.

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Introduction

In Ethiopia, the major source of milk for human consumption comes from cattle, followed by camels (CSA, 2013). Small ruminants are mainly kept by smallholder farmers as a source of income from meat, milk and wool (Legesse et al., 2008; FAO, 2009; Abebe et al., 2013; Asresu et al., 2013). In the pastoral system of the Afar region to the north of Ethiopia, sheep are commonly used for milk in as well as for meat and skin (Getachew et al., 2010; Mirkena et al., 2011). The use of sheep milk has also been reported as important in southern Ethiopia (Legesse et al., 2008; Mekasha et al., 2016), and in South-Wollo (DBARC, 2011), in the central highlands of Ethiopia.

Over the years, there has been a fragmentation of land with less land per household, in the highlands and midlands of the country. In these situation farmers in the highlands seem to switch from cows to small ruminants, especially sheep, as they are easier to rear and have multipurpose roles (Abebe, 2012). Keeping sheep for milk production and promoting products developed from them will have advantages for smallholder farmers owning little land, and in food insecure areas. An increase in demand for milk and dairy products in rural and urban areas of Ethiopia is also observed (Mekasha et al., 2016); for direct consumption, for making butter, and to make the local drink 'hashara' (Getachew et al., 2010) by boiling sheep milk in water with roasted coffee hulls.

Due to the increasing demand for milk and milk products, there is an interest to increase milk production by genetic means. Genetically improved ewes would also improve the environment for the lambs resulting in higher pre-weaning growth (Ünal et al., 2007). Improved growth potential and subsequent survival of lambs also depends on the shape of the lactation curve of the ewe (Peniche et al., 2015).

To genetically improve production of sheep in Ethiopia a crossbreeding project has been implemented with various exotic meat and wool breeds, particularly Awassi. Awassi was imported from Israel and has been well accepted by producers. To date, most studies have focused on growth, wool and reproduction performances of native and crossbred sheep (Gizaw et al., 2007; Gizaw and Getachew, 2009; Getachew et al., 2013). However, when it comes to the milk production and the potential for genetic improvement through the current community-based sheep breeding programme (CBBP) in the central highlands of Ethiopia, there is a

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Table 1. Study area characteristics as well as number of herds and ewes observed in the two villages included in the study.

	Villages (Zone)	
Study areas characteristics	Faji (North Shoa)	Chiro (South Wollo)
Number of herds	16	18
Number of ewes	55	60
Distance from Addis-Ababa, km	120	501
Altitude, m.a.s.l.[a]	2770	1500–3700
Latitude and longitude	10°00N–39°00 E	11°00N–39°00 E
Rainfall, mm	920	700–1200
Rainy season, pattern	June–September, bi-modal	June–September, bi-modal
Temperature (annual), °C	14.4	13

[a]m.a.s.l. = meters above sea level.

knowledge gap. Especially, there is a need for detailed information pertaining to the milk production potential of crosses with various levels of exotic blood. In developing countries like Ethiopia where limited resources are available for data recording, getting information is a big challenge. For traits like test day milk yield which is measured repeatedly, Legendre polynomials; a mathematical approach to model the average lactation curve; are widely used (Mrode, 2014; Schaeffer, 2016). Therefore, the objective of the present study was to estimate milk production performance and fit lactation curves of Awassi crosses relative to native sheep breeds reared under farmer's environment in the central highlands of Ethiopia based on registered test-day milk yields using Legendre polynomials. Since gathering information under farmer's conditions is a challenge, efficient use of data is important, and we have presented an approach that allows comparisons of milk yield in different parts of the lactation given a limited number of ewes and observations per ewe.

Material and methods

Study area, genetic groups, and herd management

This study was carried out in two villages taking part in CBBP, in Faji (North Shoa zone) and Chiro (South-Wollo zone), of the Ethiopian central highlands (Table 1). Various genotypes involved in CBBP were included in this study. These were bred by smallholder farmers, locally organized as cooperative breeding groups. The local breeds were the Menz (http://eth.dagris.info/node/2448) and Wollo sheep breeds that are indigenous to the selected study areas, classified as short fat-tailed, dual purpose breeds used for meat and wool and reared in the subalpine and cold highlands agro-ecological zones of Ethiopia (Gizaw et al., 2007).

Awassi is a fat-tailed meat and milk producing breed in common use around the Mediterranean Sea, particularly in Israel (http://afs.okstate.edu/breeds/sheep/awassi/). In this study, the indigenous Menz ewes were considered as Local (0% Awassi) including the limited number of records of Wollo breed ewes. The Awassi crossbred ewes were categorized based on their Awassi blood percentage (<30% Awassi, 30–50% Awassi, >50% Awassi). Milk production from the various genotypes was measured on farm by trained local people and the first author. All animals were ear-tagged and housed in shaded open front barns. They were fed clover, straw and green fodder (maize and natural pasture) during the rainy seasons. Crop residues, hay, and often oat (*Avena Sativa*) straw and vetch (*Vicia sativa*) grass were commonly fed during the dry season. During crop harvesting, sheep had access to feed crop aftermath. Some farmers also gave supplementary feeds for the pregnant and nursing ewes.

Breeding rams

Breeding rams from three governmental farms: Debre-Berhan Agricultural Research Center (DBARC), Debre-Berhan Sheep Breeding and Multiplication Center (DB R1), and Amed-Guya Sheep Breeding and Multiplication Center (AG R2) had been allocated to local cooperatives. Each breeding ram was assigned a mating group of 20–35 ewes. After three years of use, rams were culled and replaced with other rams from one of the governmental farms. Ewes were first mated at around 12 months of age. In both study areas, natural mating was practised throughout the year.

A local breeding cooperative is organized in groups of 6–12 (more in some cases) households based on neighbourhood and use of common grazing area. The Bureau of Agriculture and Rural Development (http://www.amhboard.gov.et/) is responsible for the dissemination of the selected Local x Awassi crossbred rams to villages. One 75% (¾ Awassi × ¼ Menz) crossbred ram, and rarely one 50% (½ Awassi × ½ Menz), is given for free to each group. The group of farmers is responsible for use and care of the breeding ram. Breeding rams are rotated both within the group, among groups of farmers, and across the villages, to avoid mating between relatives (to minimize inbreeding) and to widen the gene pool (Gizaw and Getachew, 2009).

Data structure

Data used in this study were collected from Local (L) and all available Awassi x Local (AL) crossbred ewes kept under farmers' conditions for the production years 2015–2017 from the smallholder farms in the study areas. The ewes were at different ages. A total of 34 herds from the two villages were used for the study. A total of 466 records at different lactation stages or days in milk (DIM) were used from Local x Awassi crossbred ewes and Local breed ewes (Table 2).

Measuring milk yield

Milk measurement started from the 2nd (earlier for few) week after parturition. Most ewes were measured 4 times for milk yield during lactation. Lambs were separated from their mothers the evening before test day. In the morning, at least 12 h later, one half-udder was hand milked until it felt empty and the milk weighed. The other half udder was suckled by the lamb. The Weigh-Suckle-Weigh (WSW) method plus hand milking was used to estimate milk production as described by Benchohra et al. (2013). Test-day milk yield (TDMY) was then taken to be twice the sum of the hand milked yield and that consumed by lamb, following the methods suggested by ICAR (2002).

Statistical model and estimation

The analysis was performed mainly in two steps, first identification of the significant fixed effect for TDMY, Kg d^{-1} was done using GLM procedure of SAS® and followed by estimation of variance components from Proc mix and finally in R programming to test significances of genetic groups for TDMY and fit lactation curves.

Important fixed effects for TDMY were identified, using the GLM procedure of SAS®. In addition to the identified fixed effects, data were analysed with fixed Legendre polynomials to model lactation curves nested within 4 genetic groups. Individual animals were included as a random effect. Regression coefficients for Legendre polynomials (up to order 3) were fitted as suggested by Schaeffer (2016) by use of mixed model and R (R Core Team, 2018) was chosen due to its ease of computing, data managing, and graphic display. Test days (t) with t_{min} (3rd day), the earliest test day, and t_{max} (147th day), the latest test day, were transformed to a normalized scale using$x = -1 + 2(t - t_{\min})/(t_{\max} - t_{\min})$. The coefficients of the Legendre polynomial used were: $d0 = 0.7071$, $d1 = 1.2247x$, $d2 = -0.7906 + 2.3717x^2$, and $d3 = -2.8062 + 4.6771x^3$.

Predicted TDMY of observed ewes were fitted and tested for significance where graphs are above zero.

In matrix notation, the model was:

$$y = Xb + Zu + e$$

where **y** is the vector of observations for daily milk yield in kg (TDMY); ***b*** is a vector of main fixed effects of: 2 villages (Faji, Chiro); 3 parities (first, second, later); 3 year-seasons of lambing (long rainy season, dry season, short rainy season); and 16 fixed regression coefficients for test days fitting lactation curves with the $d0$, $d1$, $d2$, $d3$ within the four genetic groups ($i = 1$, 2, 3, and 4): 0% Awassi (Local), <30% Awassi, 30–50% Awassi, and >50% Awassi; **X** is a design matrix assigning the fixed effects to the observations, including information on village, parity, year-season of lambing, genetic group, and transformed stage of lactation through the Legendre polynomial coefficients within genetic group; ***u*** is a vector of random effects of the 115 individual ewes (ID) included in the study, taken as independently distributed with same variance; **Z** is a matrix assigning the random effect of ewe (u) to its observations in y; and ***e*** is the vector of random independent residual effects.

The model assumptions were:

$$Cov(y, y') = V = ZGZ' + R,$$

$Cov(\mathbf{u}, \mathbf{u}') = \mathbf{G} = \sigma^2_{ID} I$, where $I$is a 115*115 identity matrix, and $\sigma^2_{ID}$is the variance component for ewes, and $Cov(\mathbf{e}, \mathbf{e}') = \mathbf{R} = \sigma^2_e I$, where $I$is a 466*466 identity matrix.

The variance components (σ^2_{ID} and σ^2_e) of **G** and **R** were estimated using the Proc Mixed procedure of SAS® with the model above. σ^2_{ID} was estimated to be 0.08 kg^2, and σ^2_e to be 0.04 kg^2. This approach was chosen due to the limited data available and incomplete pedigree of local ewes needed to run a random regression model. Given the estimated variance components, the **G, R,** and **V** were calculated as above and used in further calculations.

R software was used to estimate fixed effects of the model and carry out statistical testing. The b were

Table 2. Number ewes with records in each genetic group.

			Parity		
Genetic group	Number of ewe	Number of records	1	2	≥3
0% Awassi	46	196	39	66	94
<30% Awassi	19	85	11	32	43
30–50% Awassi	19	77	5	27	41
>50% Awassi	31	108	24	24	60
Total	115	466	79	149	238

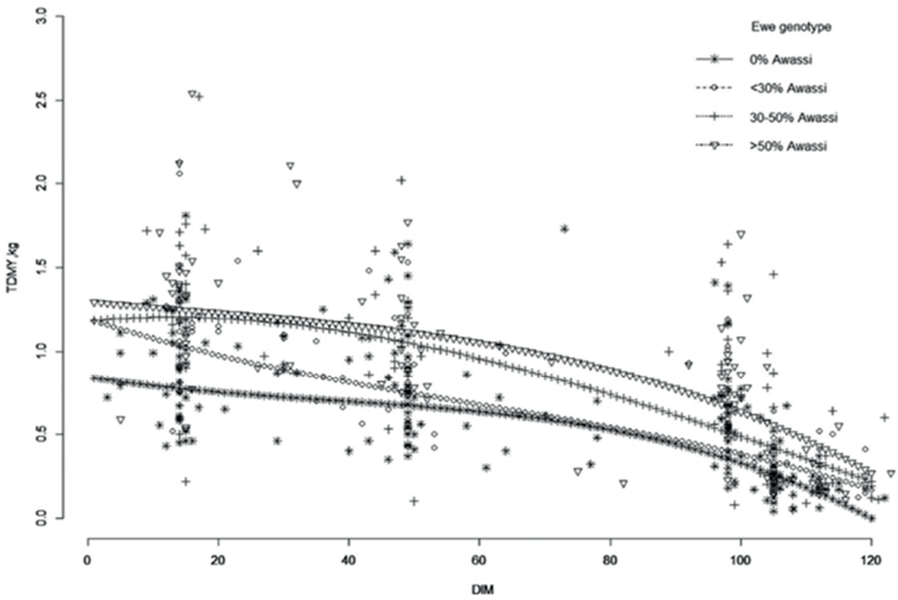

Figure 1. Observed test-day milk yield (TDMY, kg) against days in milk (DIM), and fitted lactation curves for each genetic group.

estimated with Generalized Least Squares means: $\hat{\boldsymbol{b}}$= $\mathbf{(X'V^{-1}X)^{-1}X'\ V^{-1}y}$, where $\hat{\boldsymbol{b}}$ is a 21*1 vector including 5 estimated fixed effects of: village, parity and year-season of lambing, in addition to the 4*4 = 16 $\hat{\boldsymbol{b}}$-s to establish the form of the lactation curves for the different genotypes for test day milk yield. Variance of this estimator is: $\mathbf{var}\ (\hat{\boldsymbol{b}}) = \mathbf{(X'V^{-1}X)^{-1}}$.

Calculation of lactation curves and averages

For ewes of each genetic group i = 1, 2, 3, and 4, the least-squares mean (LSM) yields for all lactation days t = 1, 2, …, 120, making up the lactation curve was computed with: $\tilde{y}ii = Li\,\widehat{\boldsymbol{b}}$, where $\mathbf{L}i$ is a 120*21 matrix with $d0$, $d1$, $d2$, $d3$ for each of the 120 days in the genetic group i's positions of the matrix $\mathbf{X}$; and averaged over the main effects of village, parity, and year-season of lambing(i.e. the $\tilde{y}i$ is a vector with 120 estimated TDMY values for group i).

The LSM daily milk yield for an ewe in genetic group i over the 120 first days of lactation was calculated as follows:

$$\bar{\bar{y}}i = \frac{1}{120}\sum_{t=1}^{120}\tilde{y}i(t) = k'\ Li\ \hat{\boldsymbol{b}}$$

where $\mathbf{k}$ is a vector with 120 equal elements: $\mathbf{k'} = \left[\frac{1}{120}, \frac{1}{120}, \ldots, \frac{1}{120}\right]$.

Comparison of daily TDMY and sub period yields of lactation

The three ranges of 5 test days (11–15, 46–50, 101–105 DIM; Figure 1.) with most observations were used for the calculation of LSM yields of three sub-periods of lactation per genetic group. These average yields for different lactation periods were calculated as follows:

$$\bar{\bar{y}}i_{\text{early}} = \frac{1}{5}\sum_{t=11}^{15}\tilde{y}i(t) = \boldsymbol{k}'_{\text{early}}\ Li\ \hat{\boldsymbol{b}}$$

with$\boldsymbol{k}_{\text{early}}$ being: $\boldsymbol{k}'_{\text{early}} = \left[0, 0, \ldots, 0, \frac{1}{5}, \frac{1}{5}, \frac{1}{5}, \frac{1}{5}, \frac{1}{5}, 0, 0, \ldots, 0\right]$, with the $\frac{1}{5}$ – elements in position 11–15 of the vector with a total of 150 elements, the rest of the elements being 0.

Similarly:

$$\bar{\bar{y}}i_{\text{mid}} = \frac{1}{5}\sum_{t=46}^{50}\tilde{y}i(t) = k'_{\text{mid}}\ Li\ \hat{\boldsymbol{b}}$$

and,

$$\bar{\bar{y}}i_{\text{late}} = \frac{1}{5}\sum_{t=101}^{105}\tilde{y}i(t) = k'_{\text{late}}\ Li\ \hat{\boldsymbol{b}}$$

with $\boldsymbol{k}_{\text{mid}}$ and $\boldsymbol{k}_{\text{late}}$ defined according to range of test days.

Table 3. Estimated least-square means (LSM) of test-day milk yield (kg) over 120 days in milk for 4 genetic groups and estimated contrasts between groups.

		LSM contrasts ± SE		
Genetic group	LSM ± SE	< 30% Awassi	30–50% Awassi	>50% Awassi
0% Awassi	0.56 ± 0.08	0.11 ± 0.07	0.31 ± 0.09*	0.40 ± 0.08*
<30% Awassi	0.67 ± 0.09		0.19 ± 0.10	0.28 ± 0.09*
30–50% Awassi	0.87 ± 0.07			0.09 ± 0.08
>50% Awassi	0.96 ± 0.07			

*$p < 0.05$.

Testing of differences between group of ewes

LSM differences between genetic groups (1 vs. 2, for example) of ewes over the whole lactation were found as:

$$\mathrm{L}\,\hat{b}_{12} = \bar{\bar{y}}1 - \bar{\bar{y}}2 = \boldsymbol{k}'L1\,\hat{\boldsymbol{b}} - \boldsymbol{k}'L2\,\hat{\boldsymbol{b}} = \boldsymbol{k}'(\boldsymbol{L}1 - \boldsymbol{L}2)\hat{\boldsymbol{b}}$$

and correspondingly for selected sub-period and genetic groups (1 vs. 2 shown):

$$\bar{\bar{y}}1_{\text{early}} - \bar{\bar{y}}i2_{\text{early}} = \frac{1}{5}\sum_{t=11}^{15}\tilde{y}1(t) - \frac{1}{5}\sum_{t=11}^{15}\tilde{y}1(t) = k'_{\text{early}}(L1 - L2)\hat{\boldsymbol{b}}$$

The variance of the differences between the average daily milk yield for genetic groups 1 and 2 in the first 150 days was calculated as:

$$\mathrm{var}(\bar{\bar{y}}1 - \bar{\bar{y}}2) = \mathrm{var}(\mathrm{L}\,\hat{b}_{12}) = k'(L1 - L2)\,\mathrm{var}(\hat{\boldsymbol{b}})(L1 - L2)'\,k = SE^2_{12}$$

and similarly for other groups and time periods. SE is the standard error of the estimated difference. A 95% confidence interval for the difference was calculated using a t-distribution with the number of ewes as degrees of freedom:

$$\mathrm{L}\,\hat{b}_{12} \pm 1.987 * \sqrt{}\mathrm{SE}_{12}$$

Similar confidence intervals were calculated for all presented estimated differences, replacing SE_{12} with the relevant standard errors in each case. LSM differences between genetic groups are taken as non-significant (NS) at a 5% level if their confidence interval includes 0.

Results

Observed TDMY and fitted lactation curves for the genetic groups are shown in Figure 1. The LSM of test-day milk yield from 120 days adjusted was 0.56, 0.67, 0.87, and 0.96 kg day^{-1} for groups with 0% Awassi, <30% Awassi, 30–50% Awassi, and >50% Awassi, respectively (Table 3). The estimated contrasts between the four studied genetic groups over the entire lactation and their standard errors are given in Table 3. The groups >50% Awassi and 30–50% Awassi produced significantly ($p < 0.05$) more than the Local (0% Awassi) group, while there were no significant differences between Local and groups with < 30% Awassi ewes. Significant differences were also observed between <30% Awassi and >50% Awassi cross bred groups.

Contrasts between the genetic groups were also calculated in the periods with most observations (11–15, 46–50, and 101–105 DIM, Figure 1). At days 11–15, the estimated milk yield tended to increase with Awassi blood percentage of ewes (Table 4). The >50% Awassi group had LSM test-day milk yield of 1.25 kg day^{-1}, followed by the 30–50% Awassi groups of ewes. In this period, the 0% Awassi group (Local) produced significantly ($p < 0.05$) less test-day milk than the three studied genetic groups of ewes (<30%, 30–50%, and >50% Awassi), while no significant differences were found between groups with <30%, 30–50% and >50% Awassi.

At 46–50 days after lambing, the LSM of groups with 30–50% Awassi and >50% Awassi produced significantly

Table 4. Estimated least-square means (LSM) and standard errors (±SE) of test-day milk yield (kg) over 3 sub-periods of lactation (DIM) for 4 genetic groups and estimated contrasts between groups per period.

		LSM contrasts 11–15 DIM ± SE		
Genetic group	LSM ± SE	<30% Awassi	30–50% Awassi	>50% Awassi
0% Awassi	0.78 ± 0.09	0.27 ± 0.10*	0.43 ± 0.11*	0.48 ± 0.11*
<30% Awassi	1.05 ± 0.11		0.16 ± 0.12	0.21 ± 0.12
30–50% Awassi	1.20 ± 0.08			0.05 ± 0.11
>50% Awassi	1.25 ± 0.09			
			LSM contrasts 46–50 DIM ± SE	
0% Awassi	0.67 ± 0.09	0.08 ± 0.09	0.38 ± 0.10*	0.45 ± 0.11*
<30% Awassi	0.76 ± 0.11		0.30 ± 0.12*	0.36 ± 0.12*
30–50% Awassi	1.06 ± 0.08			0.06 ± 0.11
>50% Awassi	1.12 ± 0.09			
			LSM contrasts 101–105 DIM ± SE	
0% Awassi	0.29 ± 0.09	0.07 ± 0.08	0.16 ± 0.10	0.30 ± 0.09*
<30% Awassi	0.35 ± 0.11		0.09 ± 0.11	0.23 ± 0.10*
30–50% Awassi	0.45 ± 0.08			0.14 ± 0.09
>50% Awassi	0.59 ± 0.09			

*$p < 0.05$.

($p < 0.05$) more than the two groups with either 0% Awassi or < 30% Awassi (Table 3). Likewise, after mid-lactation (101–105 DIM) only the higher Awassi% crossbred ewe group (>50%) showed significant differences from local and <30% Awassi (Table 3). The groups of ewes with >50% Awassi showed the highest TDMY in this period (0.96 kg day^{-1}). The average TDMY mainly decreased from the first to the last selected sub-periods of lactation. Overall, the group of ewes with >50% Awassi showed the highest average test-day milk yield in all three periods. However, there was no significant increase observed with the increase of Awassi blood level (%) neither for the entire nor in the selected days of sub-periods of lactation.

Discussion

In the present study, milk yields of groups of ewes of Menz and Wollo (Local) were compared with crossbred ewes having a variable percentage of Awassi. Using a limited number of ewes ($n = 115$) and records ($n = 466$) recorded over the entire lactation under field conditions in Ethiopia, the approach with modelling of lactation curves by genetic group had power enough to give some clear recommendations as to what breed percentages to be given preference with respect to milk yield. The group of ewes with a percentage of >50% Awassi produced consistently more milk than the Local breeds 0.40 kg day^{-1} over the entire calculated 120 days of lactation, or 70% more. The 30–50% Awassi group produced 0.31 kg day^{-1} (55% more) over the Local ewes. However, the >50% Awassi group did not improve significantly over the entire as well as sub periods of lactation over the 30–50% Awassi group. Considering the current management system at farmers' level, 30–50% Awassiewes suits best. If improved management can be provided, increasing Awassi percentage could be better for milk production.

The milk production of the Local group (0.56 kg day^{-1}) was more than double of that reported for the Afar breed (0.224 kg day^{-1}) in Ethiopia (Mirkena et al., 2011) and higher than what Mekoya et al. (2009) reported for Menz sheep breed (0.21 kg day^{-1}).

Use of Legendre polynomials within breed group allowed to utilize data for animals from different villages, parities and time of lactation period. Modelling of the contemporary group effect through village was chosen because each household had only a few ewes each (ranged from 1–30). A clear peak in the curve for most groups, expected to happen around 3–4 weeks after lambing (Assan, 2015) is lacking. Such a peak was only visible for the 30–50% Awassi group. These patterns made it difficult to compare the groups for their persistency, but also to compare them on average lactation yield (by integrating daily yield under the curve over the lactation). Comparison of lactation yield was done at 120 days, while the higher percentage Awassi groups milked longer. To become less dependent on the trajectory in comparisons, we chose to compare at lactation time points with most data.

To get Local x Awassi crossbreed ewes with 30–50% blood level in the field, it is necessary to disseminate breeding rams with a variable blood level of Awassi (25–75%). Local ewes (0% Awassi) could well be mated with rams with 75% Awassi initially. Thereafter, ewes with intermediate Awassi percentages could be mated to rams with 50% or 25% Awassi, or some intermediate percentage. The 50%Awassi rams would be the easiest to produce at the present stage. If a selection scheme for rams of a synthetic breed combining Local and Awassi is initiated, based on daughters' performances and BLUP, or based on genomic selection, proven individual rams of this type could be distributed.

Conclusions

With limited number of ewes and records from the field, modelling of the lactation curve within genetic groups can be used to draw some inference as to what breed percentage ewes should be given preference. The best performing ewes produced consistently more than local breeds over the course of the lactation, amounting to an average production improvement of close to 70% over Local ewes. This study shows the potential that exists for increasing milk production of ewes through the initiated crossbreeding programme with sheep in Ethiopia. A future evaluation could also rely on other traits than milk, like lamb survival, or udder morphometry to reach a more definite conclusion including large set of data. Further detailed economic analyses could also be required.

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PAPER II

Genetic analysis of test-day milk yield in sheep recorded at two governmental breeding and multiplication centers in Ethiopia

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Genetic analysis of test-day milk yield in sheep recorded at two governmental breeding and multiplication centers in Ethiopia

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ABSTRACT

One aim was to compare Local Menz (non-dairy, 0% Awassi), Awassi, and their available crossbred (50 and 75%) ewes for test-day milk yield (TDMY) recorded at two breeding and multiplication centers in Ethiopia. Another aim was to estimate variance components to exemplify the prediction of breeding values and their accuracy. A total of 1040 TDMY records of 211 ewes with different parity and days in milk (DIM) were used. A univariate repeatability model with Legendre polynomials coefficients (up to 3rd order) nested by genetic groups were used to model lactation curves from the TDMY data. The 100% Awassi ewes produced significantly ($p < 0.05$) more milk than the other studied ewe groups (0%, 50% and 75%Awassi) within 120 DIM. The Local (0% Awassi) ewes produced significantly less than the other groups. No significant differences in TDMY were observed between 50% and 75% Awassi ewes. The genetic advantage of the increased Awassi percentage was larger at the centers than under field conditions, i.e. for an improved environment. Moreover, the advantage of Awassi increased when comparison was done over more than 120 DIM. Estimates of heritability (h^2) and repeatability (r) of TDMY were 0.10 ±0.08 and 0.15 ±0.03, respectively. The genetic variance indicated for TDMY could give a genetic gain in the dissemination program if recorded for all ewes at the two centers (preferably with increased heritability and repeatability values).

Key words: Heritability; Legendre polynomials; Repeatability; Variance components

INTRODUCTION

In Ethiopia, there are around 31.3 million sheep (CSA, 2018). The sheep are mainly kept by smallholder farmers who raise them for meat, wool, and milk (Legesse *et al*., 2008). Sheep production is based on indigenous breeds except for mainly Awassi x Menz/Wollo crossbreds making up less than 1% of the national sheep population (Tibbo, 2006; Getachew *et al*., 2016). The current strategy employed in Ethiopia to increase production from sheep is to crossbreed locally adapted breeds with exotic breeds of high genetic merit, particularly Awassi. The exotic breeds are kept at governmental farms, and these have a mandate to disseminate crossbred rams for communal use by farmers (Getachew *et al*., 2016). In addition, some farmers specialize in production of crossbred rams (Gizaw and Getachew, 2009). The Awassi sheep breed is known for milk, meat and wool and has been widely spread to many countries (Epstein, 1985, Galal, 1985; Tzanidakis *et al*., 2014). In Ethiopia, especially the milking ability and meat production potential of Awassi are demanded. Moreover, milk production from sheep is an important trait in rearing of lambs and often directly for human consumption (Galal, 1985; Mekasha *et al*., 2016; Getachew *et al*., 2016; Mirkena *et al*., 2011; Legesse *et al*., 2008). Thus, there is a need to increase milk production from sheep through genetic selection.

The potential for genetic improvement of important traits of sheep in a selection program depends on the genetic variability, accuracy of the predicted breeding value, intensity of selection, and the generation interval. Prediction of the breeding value relies on the variance components as do the accuracy of the predicted breeding value of individuals (Lynch and Walsh, 1998). To maximize accuracy, it has become standard to use animal models to predict individual breeding values utilizing genetic relationships between animals (Kruuk, 2004). If repeated observations exist on the same individual for the same trait over time, e.g. for milk yield, repeatability, but also random regression, models can be used in estimation of variance components and prediction of breeding values (Schaeffer, 2016). In either of these models, regressions of orthogonal polynomials for DIM on the phenotype can be modelled, the most common being Legendre polynomials (Mrode, 2014). Repeatability and random regression models allow ewes to be evaluated based on any number of test-day records during a lactation, and hence all test-day information can be used in genetic evaluations. One aim of the present study was to compare ewes with different levels of Awassi percentage for their test-day milk yield at the governmental sheep farms, utilizing a repeatability animal model and pedigree relationship between animals. Another aim was to estimate variance components (genetic parameters) in order to predict breeding values and to calculate associated accuracies of the recorded animals and their ancestors, to exemplify the possibility to predict breeding value for test-day milk yield with such data.

MATERIAL AND METHODS

Site and Animal management

Data were obtained from two government farms: Debre-Berhan Sheep Breeding and Multiplication Center (DB-R) and Amed-Guya Sheep Breeding and Multiplication Center (AG-R), both located in the central highland of the Amhara regional state in Ethiopia (Table 1). These governmental sheep farms distribute selected breeding rams to farmers. Test-day records of ewes were used in the study. The flock management is semi-intensive. Animals are fed clover, straw, green fodder (during the rainy seasons), and concentrates. Ewes are mated throughout the year using natural service from about 12 months of age with a male to female ratio around 1:40-45. Rams are culled after three years of use. No artificial insemination has been used in the two flocks.

Data

A total of 1040 test-day (TD) yields from 211 ewes that lambed and were milked during 2015 to 2017 were included in the study (Table 2). The test-day milk yield (TDMY, kg day^{-1}) data used in this study were from genetic groups of Menz (Local), Awassi x Menz crossbreds (50% and 75% Awassi), and 100% Awassi ewes. Milk production was measured on farm by trained local people and the first author. Milk measurements started from the 7^{th} day after lambing (after the colostral phase). On evenings prior to test days, lambs were separated from their mothers for 12 hours. The next morning, one half-udder was hand milked until it felt empty, while the other half udder was suckled by the lamb. The Weigh-Suckle-Weigh (WSW) method plus hand milking was used to measure milk production, recorded according to Benchohra *et al*. (2013). The weight difference of the lamb before and after suckling was used to estimate the milk suckled by the lamb. Then, TDMY was taken to be the sum of that hand milked and that consumed by the lamb multiplied by two, following the Method E suggested by ICAR (2002). The average number of TDMY per lactation per ewe was 5 (ranging 3 to 17).

The pedigree data included all ewes with recorded milk, and their ancestors, if available, up to 5 generations. Of the observed ewes, 201 had both parents known, and for 10 only one parent was known. The 211 ewes were from 51 different sires and 196 dams. The total number of males and females in the pedigree data amounted 92 and 620, respectively.

Statistical analysis

The analysis was performed in three steps. First, the variance components for TDMY were estimated using ASReml, version 4.1 (Gilmour *et al.,* 2015). Then, the estimates of variance components were used through own R programs to estimate contrasts between genetic groups and their confidence intervals. Finally, R was used to derive breeding values and associated accuracies.

Lactation curve

To model the effect of the lactation curve for each genetic group, regression coefficients for Legendre Polynomials (LP) were calculated according to Schaeffer (2016) by use of R programming (R Core Team, 2018). First, days in milk (DIM), with DIM_{min} = 7 and DIM_{max} = 120, were transformed to a normalized scale using: $t = -1 + 2(\text{DIM} - \text{DIM}_{min})/(\text{DIM}_{max} - \text{DIM}_{min})$. Then, the coefficients of the LP were obtained for each test-day observation as: ϕ_0 = 0.7071, ϕ_1 = 1.2247t, ϕ_2 = -0.7906 + 2.3717t^2, andϕ_3= -2.8062t+4.6771t^3.

Breed composition and heterosis effect

Breed composition of each ewe as either Menz or Awassi was derived, with the percentage of the Awassi breed of ewe i calculated as:

$$pA_i = 0.5\,(pA_{Si}+pA_{Di}),$$

where pA_i is the calculated percentage of the Awassi breed of ewe i;

pA_{Si} and pA_{Di} are, respectively, the percent of the Awassi breed of the sire (S) and dam (D) of ewe i. Calculation of the Menz proportion may be done likewise, or as:

$$pM_i = 1 - pA_i$$

since only two breeds were considered.

Then, retained heterozygosity (H_i) in each crossbred ewe (i) was calculated using the following equation (Dickerson, 1973):

$$H_i = 1 - (pM_{Si}*pM_{Di} + pA_{Si}*pA_{Di}),$$

where pM_{Si} and pM_{Di} represent the proportions of Menz in the sire and dam of animal i (Bourdon, 1999).

Estimation of variance components and genetic parameters

Variance components for additive genetic (σ_a^2), permanent environmental (σ_{pe}^2), and residual(σ_e^2) effects of TDMY were estimated by restricted maximum likelihood. They were used to obtain the phenotypic variance($\sigma_y^2 = \sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2$), heritability ($h^2 = \sigma_a^2/\sigma_y^2$), and repeatability ($r = (\sigma_a^2 + \sigma_{pe}^2)/\sigma_y^2$). Likelihood ratio testing (e.g., Wilson *et al.,* 2010) was carried out to test for significance of the variance components. The full model contained variance components, while the reduced model only contained the random error term. The heritability for the average TDMY based on n records was computed with the following formula: $h_{\bar{y}}^2 = \mathrm{n}h^2/[1 + (\mathrm{n} - 1)\mathrm{r}]$ (Bourdon,1999).

Models

After excluding non-significant fixed effects of birth type (single, multiple), farm (DB-R, AG-R), heterozygosity (0, 0.5, 1, as a regression) and sex of lamb (male, female, others), while keeping parity for biological reasons (even though it showed not to be significant), the data were analyzed with the following model:

$$\boldsymbol{y} = \boldsymbol{X\,b} + \boldsymbol{Z\,a} + \boldsymbol{W\,pe} + \boldsymbol{e}$$

where:

y is the vector of TDMY;

b is a vector of fixed regression coefficients for: DIM (7-157) of 3rd order (k = 0, 1, 2, 3) of LP within the 4 genetic groups: Local (0% Awassi), 50% Awassi, 75% Awassi and 100% Awassi (g = 1, 2, 3, 4); and fixed effects of 3 parities (first, second, later) and 3 seasons of lambing (long rainy, dry, short rainy);

X is a design matrix assigning fixed effects to the observations, including information on parity of ewes, season of lambing, and Legendre transformed functions of day of lactation for the observation within genetic group ($\phi_k(t)$);

a is a vector of additive genetic effects for all individuals in the pedigree;

pe is a vector of ewe permanent environmental effects;

Z and ***W*** are matrices linking the random additive genetic (***a***) and random permanent environmental ewe (***pe***) effects to the observations ***y***; and

e is the vector of random residual effects associated with ***y***.

Reduced models that excluded ***a*** and ***pe*** were also run.

Random effects were assumed normally distributed with zero means and the following covariance structures:

Var ($\boldsymbol{a}$) = $\sigma_a^2\mathbf{A}$ = $\mathbf{G}$;

Var ($\boldsymbol{pe}$) =$\sigma_{pe}^2\boldsymbol{I}_{pe}$ = $\mathbf{P}$;

Var ($\boldsymbol{e}$) = $\sigma_e^2\boldsymbol{I}_e$= $\mathbf{R}$; and so

Cov ($\boldsymbol{y}, \boldsymbol{y}'$) = $\mathbf{V} = \mathbf{ZGZ' + WPW' + R}$;

Above, **A** is the additive relationship matrix between the individuals included in the pedigree, $\boldsymbol{I}_{pe}$ represents an identity matrix of dimension equal to the number of observed ewes, and $\boldsymbol{I}_e$ is an identity matrix of dimension equal to number of observations.

R programs were used to calculate Least-Squares Means (LSM) and to plot lactation curves for TDMY using the estimated variance components from the full model. The $\boldsymbol{b}$ values were estimated with: $\hat{\boldsymbol{b}} = (\mathbf{X'V^{-1}X})^{-1}\mathbf{X'V^{-1}}\boldsymbol{y}$, where $\hat{\boldsymbol{b}}$ is a 20*1 vector including 4*4 = 16 $\hat{\boldsymbol{b}}$-s, to establish the form of the lactation curves within the 4 genotypes, in addition to 2 estimated fixed effects of parity and 2 for season of lambing (the third levels of parity and season were omitted to get consistent estimates). Variance of this estimator is: $\mathbf{var}\ (\hat{\boldsymbol{b}}) = (\mathbf{X'V^{-1}X})^{-1}$, and it was estimated by replacing the true variance components in **V** with their estimates.

Calculation of averages of TDMY for genetic groups

For genetic group g = 1, 2, 3, and 4, LSM yields over lactation days DIM=1, 2, …, 120 (the interval with positive $\tilde{\boldsymbol{y}}_g$ values for all groups), making up the lactation curve, were computed with: $\tilde{\boldsymbol{y}}_g = \boldsymbol{L}_g\hat{\boldsymbol{b}}$, where $\boldsymbol{L_g}$ is a 120*20 matrix with ϕ_0, ϕ_1, ϕ_2 and ϕ_3 for each of the 120 days in the genetic group g's positions of the matrix **X**, and 0 for the other groups, and averaging the main effects of parity and season of lambing. This means that the $\tilde{\boldsymbol{y}}_g$ is a vector with 120 estimated TDMY LSM values for group g.

The LSM average daily milk yield for a ewe in genetic group g over the 120 first days of lactation was calculated as follows:

$$\bar{\tilde{y}}_g = \frac{1}{120}\sum_{DIM=1}^{120} \tilde{\boldsymbol{y}}_g(DIM) = \mathbf{k}'\,\boldsymbol{L_g}\hat{\boldsymbol{b}}$$

where **k** is a vector with 120 equal elements: $\mathbf{k'} = [\frac{1}{120}, \frac{1}{120}, \dots, \frac{1}{120}]$.

Testing average TDMY differences between groups of ewes

LSM differences between genetic groups (g = 1 vs. 2, for example) of ewes over the first 120 days of lactation were found as:

$$\mathrm{L}\,\hat{b}_{12} = \bar{\bar{y}}_1 - \bar{\bar{y}}_2 = \mathbf{k}'\,\boldsymbol{L}_1\hat{\boldsymbol{b}} - \mathbf{k}'\,\boldsymbol{L}_2\hat{\boldsymbol{b}} = \mathbf{k}'\,(\boldsymbol{L}_1 - \boldsymbol{L}_2)\hat{\boldsymbol{b}}$$

The corresponding variance of the difference between the average daily milk yield for genetic groups 1 and 2 in the first 120 days was calculated as:

$$\mathrm{var}(\bar{\bar{y}}_1 - \bar{\bar{y}}_2) = \mathrm{var}(\mathbf{L}\hat{\boldsymbol{b}}_{12}) = \mathbf{k}'(\boldsymbol{L}_1 - \boldsymbol{L}_2)\,\mathrm{var}\big(\hat{\boldsymbol{b}}\big)(\boldsymbol{L}_1 - \boldsymbol{L}_2)'\,\mathbf{k} = \mathrm{SE}_{12}^2$$

A similar procedure was followed for the other groups and time periods. Above, SE_{12} is the standard error of the estimated difference. A 95% confidence interval for the difference was calculated using a t-distribution with the number of ewes as degrees of freedom:

$$\mathrm{L}\hat{b}_{12} \pm 1.987 * \mathrm{SE}_{12}$$

Similar confidence intervals were calculated for all the estimated differences, replacing SE_{12} with the relevant standard errors in each case. LSM differences between genetic groups were taken as non-significant at a 5% level if their confidence interval included 0.

Estimated Breeding Value

The estimated breeding value (EBV) over the 120 days were for each animal calculated as the sum of the fixed genetic group solutions of the relevant animal and the corresponding predicted individual additive genetic effects of animal i ($\hat{a}_i$) as:

$\mathrm{EBV}_\mathrm{i} = \bar{\bar{y}}_g + \hat{a}_i$

Determination of accuracy of Estimated Breeding Value

Accuracy of the estimated breeding value was calculated considering only the random part of the EBV, i.e. $\hat{a}_i$. This is in accordance with Henderson (1984) and known as the correlation between the predicted ($\hat{a}_i$) and true (a_i) additive breeding value for an individual i:

$$r_{a_i,\hat{a}_i} = \sqrt{\left(1 - C_{22ii}/G_{ii}\right)}$$

Where C_{22ii} is the diagonal element for individual *i* from the inverse left-hand side of the Mixed Model Equation, and G_{ii} is the diagonal element in **G** for individual *i*.

RESULTS

The likelihood-test statistics from inclusion of the permanent environmental effect over that of the environmental was 20.36, which is χ^2 distributed with 1 degree of freedom ($p < 0.00001$). The estimates of variance components and genetic parameters from a model with the permanent environmental, and from one that additionally models the additive genetic effect (***a***) are given in Table 3. In both models, the repeatability was of similar size (~ 0.15). However, in the full model, the standard error of the permanent environmental variance estimate increased considerably and for the additive genetic variance the standard error in this model was large (relative to the estimate). The additive genetic variance estimate of 0.016 kg^2 had a standard error of 0.013. For the full model heritability for TDMY was estimated as 0.10, with a standard error of 0.08. The heritability estimates for single observations translated into an estimate of 0.31 ($h_{\bar{y}}^2$) for an average TDMY based on the mean of 5 observations per ewe.

TDMY LSM for the genetic groups for 120 DIM were 0.81, 1.02, 1.06, and 1.69 kg day^{-1} for 0% Awassi, 50% Awassi, 75% Awassi, and 100% Awassi ewes, respectively (Table 4). The 100% Awassi ewes produced better ($p < 0.05$) than the other groups of ewes, whereas the

Local (0% Awassi) ewes produced significantly less than the others. The LSM values for 50% and 75% Awassi ewes were quite similar and not significantly different. The contrasts between the genetic groups can also be visualized through the fitted lactation curves, given in Figure 1. The lactation curve for the 0% Awassi lay consistently below the others, while the curves for 50% and 75% Awassi overlapped. Relative to the others, the 100% Awassi group started out with especially high values in early lactation and lay consistently over the others throughout the 120 DIM.

Ranges of estimated breeding values for ewes with TDMY records and their sires are given in Table 5. The table values show that the EBV's were mainly determined by $\bar{\bar{y}}_g$, but with individual variation due to the $\hat{a}_i$ term. In ewes the largest individual range was for 100% Awassi, followed by the two crossbred Awassi groups, and least range was calculated for Local. The larger ranges for the Awassi groups reflect also the accuracy of the estimated breeding value ($r_{a_i,\hat{a}_i}$) of ewes, being on average largest in the 100% Awassi group, and least in Local (Table 6). The largest individual accuracy was, however, found among the sires, due to sires being progeny tested with up to 43 offspring in the data.

DISCUSSION

In the two farms studied, the average TDMY over 120 DIM was higher for Local (0.81 kg day^{-1}) than the corresponding result earlier obtained in the farmers' environment by Haile *et al.* (2020) (0.56 kg day^{-1}). This indicates a more intensive environment at the two governmental farms than in the field. Relative to the Local, the 50% and the 75% Awassi groups produced significantly more (1.02 and 1.06 kg day^{-1}), with no significant difference between the two groups. The 100% Awassi produced 1.69 kg day^{-1}, more than double of that of the Local and significantly more than the other groups. Not only did the two crossbred ewe groups produce between the Local and the purebred Awassi, as also was obtained for the two intermediate Awassi groups by Haile *et al.* (2020), but the 100% Awassi now stood out with increased production in the improved environment. This resulted in a significant higher production compared to the other groups, despite only 21 ewes being purebred. Moreover, the larger number of ewes in the intermediate Awassi groups (125 and 37) relative to that of Haile *et al*. (2020) (both 19) together with the increased number of ewes (211 vs. 115) and records (1040 vs. 466), approximately halved the standard error of LSM contrasts and improved the power of detecting significant differences between the genetic groups in the present paper.

Inclusion of the LP as fixed effects in the genetic evaluation model allowed to estimate the trajectory of the lactation curves (Figure 1). For all genetic groups, these curves were continuously decreasing from the start of lactation, in analogy with the result of Haile *et al*. (2020). Moreover, the trajectory of the curves indicated shorter length of lactation ($\tilde{\boldsymbol{y}}_g$ close to 0 for Local at 120 DIM) for Local than for the three Awassi groups. In consequence, the comparison of genetic groups done here on the average yields for 120 DIM favored the Local ewes. Thus, the yield advantage of the three Awassi groups would have been even larger if comparison had included more than 120 DIM, which is considered as standard lactation length for many sheep breeds (Berger *et al*., 2010; Tzanidakis *et al*., 2014).

The three variance components for additive genetic, permanent environment and error for TDMY summarize the variance along the curve into only one parameter for each, the same for all genetic groups and individual ewes (σ_a^2, σ_{pe}^2 and σ_e^2, respectively). From these variance components, the repeatability and heritability of TDMY were estimated to be 0.15 ± 0.03 and 0.10 ± 0.08, respectively. The repeatability denotes the upper limit of the heritability

(Falconer and Mckay, 1996) and was estimated with a small standard error (irrespective of model), while the standard error for the heritability was close to as large as the estimate. When both genetic additive and permanent environment were included in the model, the permanent environmental effect was estimated with a much larger standard error than when a model not including the additive genetic was run. This indicates that there exists limited information in the data to separate these two effects. This could be due to the limited quality of the pedigree relationships, i.e., both depth and relationships between the sampled animals, and due to the limited size of the data set. Our estimates were considerably smaller than comparable estimates of repeatability and heritability, e.g. the 0.39 and 0.28 obtained by Bauer *et al*. (2012) and the corresponding estimates of 0.40 and 0.15 reported by Othmane *et al.* (2002). Bauer *et al*. (2012) found the flock-test day effect to be the most important systematic environmental factor in their data, whereas we in the present data considered to have too few observations per test day for this effect to be included in the model. If accounted for, it could have reduced the error variance and increased both our repeatability and heritability estimates.

Breeding values and their accuracies were calculated assuming the estimated variance components were the true values. For the ewes in the 100% Awassi group, the estimated breeding values had the largest range and mean accuracy, which is beneficial because this group is the one to be multiplied, contributing the most, also through the 50 and 75% Awassi ewes. The ram lambs in the two latter groups are the product for dissemination from the station to farmers. Currently rams are selected for the field by mass selection based on own weight. These rams could also be selected based on breeding values for milk yield. This would require recording milk yield on ewes in the centres and to include the young ram selection candidates in an expanded relationship matrix **A**. With such a breeding scheme the accuracy of selection from only including the average 5 records of the animals' own mother would become 0.27 (= $0.5\sqrt{h_{\bar{y}}^2}$), using selection index theory, see e.g. Bourdon (1999), and become marginally higher by including information on more distant relatives, e.g. that from aunts. However, accuracy could increase if actions could be taken to increase the size of the genetic parameters. For example, assuming the heritability (h^2) and repeatability (r) values of Bauer *et al*. (2012) for the same 5 records would result in an accuracy of 0.37. Including additional information through genotyping would have the potential to further increase the accuracy. Selection within the purebred groups in the centers (with more than 3000 sheep in each of the two), both 100% Awassi and Local, could also be based on the same TDMY information. However, consideration needs to be taken for rate of inbreeding since both groups can be considered closed.

Recipients of the disseminated 50% and 75% Awassi rams are farmers locally organized as cooperative breeding groups (as given in Gizaw and Getachew, 2009) through the Community-Based sheep Breeding Program (CBBP) in the central highland of Ethiopia. These groups consist of 6-12 (sometimes more) farmers, and the rams are rotated across farmers and groups. Each third year, the ram is replaced with another ram from one of the governmental farms. Recently, Haile *et al.* (2020) have shown 30-50% Awassi ewes to produce best in the local villages. Thus, there is a need to disseminate rams from the governmental farms with a variable blood level (25 - 75%). An alternative would be to produce 25 - 50% Awassi rams locally, a development that anyhow seems to be practiced. Locally, in the villages, the ram lambs could, in the future, be selected on estimated breeding values given that herd recording became established and one was able to keep track of the genetic relationships between animals (could well be determined by the use of genetic markers in future). This would be pivotal in developing a breeding scheme relying on utilizing data from the field. By carrying out breeding value estimation, for example with variants of the model presented in this paper, a synthetic population could be established, converging towards the Awassi percentage favorable in the field. In the future, traits to be recorded should not be restricted to TDMY but also include growth, milk quality, survival, and wool traits. Such a development would be one in which the vision is that Ethiopia can utilize its own genetic resources and improve them through genetic selection over time. This would build infrastructure and contribute to increased knowledge that is essential for an efficient national sheep production.

CONCLUSION

The genetic advantage of an increased Awassi percentage for milk yield was larger at the two multiplication centers than under field conditions, i.e. for an improved environment. Moreover, the advantage of Awassi would increase if the comparison had been done over more than 120 DIM. An exploitable amount of genetic variance was indicated for TDMY. If information were recorded for all ewes at the two centers, preferably with higher heritability values than in the current study, there is potential for the dissemination program to considerably increase selection accuracy and genetic gain also for TDMY.

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Table 1. Characteristics of the two governmental farms located in the central highlands of Ethiopia.

Characteristic	**Governmental farm**[1)]	
	DB-R	**AG-R**
Distance from Addis-Ababa	125 km	282 km
Altitude (m.a.s.l)[2)]	2780	1680 – 3600
Latitude and longitude	9°36 N - 39°38 E	10°28 N - 39°5E
Rainfall (mm per year)	920	800 - 1600
Rainy season, pattern[3)]	June - September, bi-modal	June - September, bi-modal
Temperature[4)]	8.2 - 18.6 °C	8 - 18 °C

[1)] DB-R=Debre-Berhan Sheep Breeding and Multiplication Center; AG-R =Amed-Guya Sheep Breeding and Multiplication Center.

[2)] m.a.s.l. = meters above sea level.

[3)] June to September is the main rainy season. A weaker and unreliable second rainy season occurs from February to March (Getachew, 2015).

[4)] Average minimum and maximum per day in a year.

Table 2. Number of ewes with test-day milk yield records and number of records in each genetic group.

Genetic group	**No. of ewes**	**No. of records**
0% Awassi (100% Menz)	28	107
50% Awassi	125	579
75% Awassi	37	183
100% Awassi	21	171
Total	211	1040

Table 3. Estimated variance components and genetic parameters (± SE), for test-day milk yield (kg day^{-1}) obtained with statistical models with or without additive genetic effect ***a***.

Parameter	**Estimate ± SE**	
	With ***a***	Without ***a***
Additive genetic variance (σ_a^2)	0.016 ± 0.013	-
Permanent environmental variance (σ_{pe}^2)	0.009 ± 0.012	0.024 ± 0.005
Residual variance (σ_e^2)	0.139 ± 0.007	0.140 ± 0.007
Phenotypic variance (σ_y^2)	0.164 ± 0.007	0.164 ± 0.008
Heritability (h^2)	0.096 ± 0.078	-
Repeatability (*r*)	0.148 ± 0.031	0.145 ± 0.030

With ***a:*** $h^2 = \sigma_a^2/\sigma_y^2$, $r = (\sigma_a^2 + \sigma_{pe}^2)/\sigma_y^2$; without ***a:*** $r = \sigma_{pe}^2/\sigma_y^2$

Table 4. Least-squares means (LSM) of average test-day milk yield (kg day^{-1}) over 120 days in milk in each genetic group of ewes and estimated contrasts between groups. All estimates are given with standard error (SE).

Genetic group	LSM ± SE	LSM contrasts ± SE		
		50% Awassi	**75% Awassi**	**Awassi**
0% Awassi	0.81 ± 0.03	0.22 ± 0.04*[1]	0.25 ± 0.04*	0.88 ± 0.05*
50% Awassi	1.02 ± 0.02		0.04 ± 0.03	0.67 ± 0.04*
75% Awassi	1.06 ± 0.03			0.63 ± 0.04*
Awassi	1.69 ± 0.04			

[1] * = $p < 0.05$.

Table 5. Number of individuals in each genetic group and corresponding minimum and maximum estimates of breeding values (EBV, kgday^{-1}) for test-day milk yield (sum of average genetic group effect for an individual over 120 days in milk and individual animal genetic effect).

Genetic group	**Observed ewes**			**Sires of observed ewes**		
	N	**Min**	**Max**	**N**	**Min**	**Max**
0% Awassi	28	0.60	1.08	9	0.61	1.09
50% Awassi	125	0.76	1.39	6	1.01	1.18
75% Awassi	37	0.79	1.43	-	-	-
100% Awassi	21	1.39	2.17	36	1.55	1.97

Table 6. Mean, minimum and maximum accuracy of estimated breeding values for test-day milk yield in each genetic group of ewes and sires of ewes.

Genetic group	**Observed ewes**			**Sires of observed ewes**		
	Mean (%)	Min (%)	Max (%)	Mean (%)	Min (%)	Max (%)
0% Awassi	48.7	33.3	57.8	51.8	40.7	63.7
50% Awassi	55.3	40.5	65.9	55.7	41.4	66.7
75% Awassi	55.3	42.3	64.9	-	-	-
100% Awassi	60.0	50.7	68.6	49.4	26.8	71.6

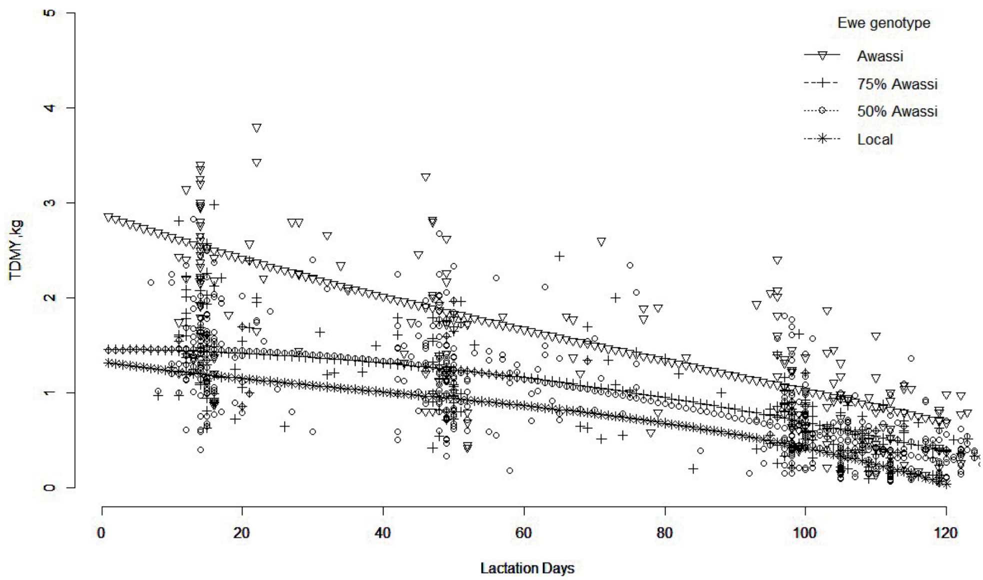

Figure 1. Observed test-day milk yields (TDMY, kgday^{-1}) and fitted lactation curves for each genetic group.

PAPER III

Genotype by environment interaction for test-day milk yield in sheep recorded in farmers' field and at breeding stations in Ethiopia, by stage of lactation and various proportions of Awassi

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Genotype by environment interaction for test-day milk yield in sheep recorded in farmers' field and at breeding stations in Ethiopia, by stage of lactation and various proportions of Awassi

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Abstract

Genotype by environment (G x E) interactions were evaluated by studying contrasts between test-day milk yield (TDMY) in breeding centres' environment (BE) compared to farmers' environment (FE), for combinations of similar breed proportions of Awassi and stages of lactation. A total of 1506 TDMY records from 326 ewes were analyzed: The records were made at different stages of lactation and parities, from the two environments during 2015 to 2017, with ewes having the sex of their lambs recorded. To be able to get information from a limited data set, a univariate repeatability model was fitted within each environment with Legendre polynomial (LP) coefficients (3^{rd} order) for both days in milk (DIM) and % Awassi describing fitted TDMY planes for the two environments. Over a 120 DIM, none of the genetic groups (based on % Awassi) showed significant differences in estimated contrasts for average TDMY between the two environments. This implies that genetic superiority at breeding centres will in large be realized in the farmers' environment. However, for early lactation the lower % Awassi groups had a significant higher production at the stations' environments. This was not the case for the >50 – 75% Awassi group. This G x E interaction implies that it is the high % Awassi (>50 - 75%) ewes that appear to be robust to environment change. The significant interaction in early lactation, being mostly physiological, will be avoided for most animals with the current regime for dissemination of rams that are either 50% or 75% Awassi.

Key words: Fixed effect contrast interaction; Legendre polynomial; Product of Legendre coefficients; Repeatability test-day model.

INTRODUCTION

Sheep production in Ethiopia is highly dependent on natural grazing of communal open natural pasture the year round (Tibbo, 2006). With high variation in the environmental conditions and in herd management, genotype by environment interaction (G x E) can potentially be important (Steinheim *et al*., 2004). Thus, it is important to examine G x E in the sheep crossbreeding program that has been implemented in the central highlands of Ethiopia. In this program, the Awassi breed from Israel has shown similar phenotypic appearance as indigenous sheep and been well accepted by producers (Gizaw and Getachew, 2009; Getachew *et al.*, 2016). Selection of animals is carried out in stations where the management is semi-intensive. Crossbred rams are transferred to local farmers taking part in the community-based breeding program (CBBP) to mate with local ewes (Gizaw and Getachew, 2009). The farmers' environments are quite different from those where the animals have been evaluated, at the breeding stations, and this can potentially be important. Thus, one breed may outperform another breed in one environment, but not in another (Falconer and Mackay, 1996), i.e. the performance obtained under the improved selection station conditions may not be relevant under the farmers' conditions. When the production environments vary widely, decisions on breed choices need due attention to possible G x E. In fact, differences in growth and reproduction performances of sheep have been reported that may be regarded as G x E (Demeke *et al*., 1995; Getachew, 2015). However, in Ethiopia, G x E for sheep milk production has not yet been studied.

There are different ways to assess G x E when the same genotypes are used in different environments. For fixed environments the average production of different genotypes may be assessed for combinations of genotype and environment (Lynch and Walsh, 1998). We propose a variant of this method through a mixed model. The study utilizes data from two previous studies (Haile *et al*., 2020a; Haile *et al.* 2020b) to assess the production potential in either the farmers' environment (FE) or in two breeding and multiplication centres (BE) in Ethiopia. We estimate contrasts between milk production estimates for the same proportions of Awassi in the two environments. In detail, lactation curves for ewes with varying % Awassi define different planes depending on environment. We check if there is any G x E when breeding stations is taken as one environment and farmers' field as the other. To be able to compare we need to have similar % Awassi and similar stages of lactation in the targeted environments. We do this by fitting models to each of the two environments, for a combination of DIM and % Awassi, and then check if any % Awassi seems to be better in one environment compared to the other. Using a model with Legendre polynomial (LP) regression for DIM makes this possible even with a limited and unbalanced dataset.

MATERIAL AND METHODS

Study animals, areas, and herd management

This study was carried out in two villages and at two sheep multiplication centers (breeding stations) located in the central highland areas of the Amhara regional state (Table 1). Data on genotypes with a variable % Awassi maintained by farmers involved in the CBBP and by the breeding stations were utilized in the study (Table 2).

Locally, the farmers' field environment (FE) is a mixed crop livestock husbandry system. Animals are housed under semi-shaded/open front barn, and they are ear tagged. During the rainy seasons the flocks were fed clover, straw, and green fodder (maize and natural pasture). Crop residues, hay, and often oat (*Avena sativa*) straw, and vetch (*Vicia sativa*) grass were commonly fed during the dry season. During crop harvesting, sheep had access to feed crop aftermath. Some farmers also gave supplementary feeds for the pregnant and nursing ewes (Amare, 2018). Ewes were first mated at about 12 months of age. Breeding rams (from the breeding stations) are assigned to mating groups of 20 - 35 ewes as described by Gizaw and Getachew (2009). Rams are culled after 3 years of use and replaced with new ones. The ewes were mated throughout the year using natural service.

In the breeding stations environment (BE), flock management is semi-intensive, and animals are housed semi-shaded. Animals graze on natural pasture and are fed on clover, straw, and green fodder (during the rainy season). Crop residues and hay were commonly fed during the dry season and lactating ewes were supplemented with concentrate: 250g (Local), 300g (crossbred), up to 1000g (pure Awassi) day^{-1}. Ewes were first mated at about 12 months of age. Breeding rams were assigned to mating groups of 40 - 45 ewes. Rams are culled after 3 years of use, and ewes are mated throughout the year using natural service.

Data

Test-day milk yield (TDMY) data used in this study consisted of 1506 records from 326 lactating ewes (Local, Awassi x Local crossbred, and pure Awassi) kept in either FE or BE (Table 2). The ewes were at different ages and different lactation stages, i.e. days in milk (DIM). The DIM of the ewes varied between 3 and 157. A total of 36 herds belonged to FE and two to BE. The pedigree file was not of good enough quality to be used in the analysis (primarily for FE ewes).

Milk yield recording

Milk measurements started after the colostral phase. On evenings prior to test days, lambs were separated from their mothers for 12 hours. The next morning, one half-udder was hand milked until it felt empty, while the other half-udder was suckled by the lamb. The Weigh-Suckle-Weigh (WSW) method plus hand milking was used to measure milk production, recorded according to Benchohra *et al*. (2013). The weight difference of the lambs after and before suckling was used to estimate milk suckled by lambs. Test-day milk yield (TDMY) was then taken to be the sum of the hand milked yield and that consumed by the lamb, multiplied by two, following the methods (Method E) suggested by ICAR (2002). Measurements were done by farmers, the first author and trained individuals.

Statistical analysis and generation of Legendre coefficients

Test-day records of milk yield were analyzed with a (univariate) repeatability test-day model for each of the two production systems. The same mixed model was run separately in the two environments, so fixed effects and variance components were nested within environment.

DIM with DIM_{min}, the earliest test-day, and DIM_{max}, the latest test-day, were transformed to a normalized scale using $t = -1 + 2(DIM - DIM_{min}) / (DIM_{max} - DIM_{min})$. The coefficients of the Legendre polynomial (LP) used were: $\phi_0 = 0.7071$, $\phi_1(t) = 1.2247t$, $\phi_2(t) = -0.7906 + 2.3717t^2$, and $\phi_3(t) = -2.8062t + 4.6771t^3$. The same procedure was followed for Awassi percentage (A) using A_{min} (0%), and A_{max} (100%) to generate four coefficients for the normalized scaled $a : Z_q(a)$ where q = 0,1,2,3. To model the effect of any stage of lactation for any % Awassi the product of each of the four coefficients for t is multiplied by each of the coefficients for a thus yielding 4*4 = 16 combined Legendre coefficients gathered in a 1*16 vector:

$$\boldsymbol{L(t,a)} = [\phi_0 * Z_0, \phi_0 * Z_1(a), \phi_0 * Z_2(a), \phi_0 * Z_3(a), \phi_1(t) * Z_0, \phi_1(t) * Z_1(a), \phi_1(t) * Z_2(a), \phi_1(t) * Z_3(a), \ldots, \phi_3(t) * Z_3(a)]$$

The Model

The same model, used for both environments, had the following general characteristics;

$$y_{ijklmn} = \boldsymbol{L(t,a)}\, \boldsymbol{b}_{ta} + P_i + Yr_j + S_k + Sex_l + pe_m + e_{ijklmn}$$

where:

y_{ijklmn} is the nth TDMY of a ewe m;

$\boldsymbol{L(t,a)}$ is a 1*16 vector denoting 3rd order (p = 0, 1, 2, and 3) LP coefficients of test day (*t*) of the observation $_{ijklmn}$ multiplied by similar 3rd order LP coefficients of % Awassi (*a*) of the ewe of the same observation $_{ijklmn}$, making up altogether 16 coefficients for each $_{ijklmn}$;

$\boldsymbol{b}_{ta}$ is a 1*16 vector containing 16 regression parameters (same for all observations in the same environment, BE or FE);

P_i is the fixed effect of parity *i* (i= 1, 2, and $\geq$3);

Yr_j is fixed effect of year *j* of lambing (j = 2015, 2016 and 2017);

S_k is fixed effect of seasons *k* of the dam at lambing (k= long rainy season, dry season and short rainy season);

Sex_l is fixed effect of sex *l* of lamb (1= male, 2 = female, 3 = others, twins of any kind);

pe_m is random permanent environmental effect of identity of ewe *m;* and

e_{ijklmn} is a random residual.

To make the effects estimable, only two levels (of the 3) of the 4 main effects were kept, in addition to the 16 regressions; in total 24 fixed effects were estimated.

In matrix form the above model can be summarized:

$$\boldsymbol{y} = \boldsymbol{X}\,\boldsymbol{b} + \boldsymbol{Z}\,\boldsymbol{u} + \boldsymbol{e}$$

where $\boldsymbol{y}$ is a vector of observations for TDMY in each environment; $\boldsymbol{b}$ is a vector of the 24 fixed effects to be estimated; $\boldsymbol{X}$ is a design matrix made from the $\boldsymbol{L(t,a)}$ vectors for DIM and % Awassi for each observation in $\boldsymbol{y}$, as well as indicating which level of the 4 fixed effects each observation belongs to, linking the parameters in $\boldsymbol{b}$ to the observations in $\boldsymbol{y}$; $\boldsymbol{u}$ is a vector for permanent environmental effect of ewes; $\boldsymbol{Z}$ is a design matrix assigning the permanent environmental effect of ewe ID to its observations; and $\boldsymbol{e}$ is the vector of residual effects in each environment.

The model assumptions were:

Cov($\boldsymbol{y}, \boldsymbol{y}'$) = $\boldsymbol{V} = \boldsymbol{ZGZ}' + \boldsymbol{R}$,

Cov($\boldsymbol{u}, \boldsymbol{u}'$) = $\boldsymbol{G} = \sigma^2_{ewe}\,\boldsymbol{I}$, where $\boldsymbol{I}$ is an identity matrix with size equal to the number of ewes in each environment, and σ^2_{ewe} is the variance component for ewes in each environment (FE or BE), and

Cov($\boldsymbol{e}, \boldsymbol{e}'$) = $\boldsymbol{R} = \sigma^2_e\,\boldsymbol{I}$, where $\boldsymbol{I}$ is an identity matrix of size equal to the number of observations in each environment, and σ^2_e is the residual variance component per environment.

The variance components (σ^2_{ewe} and σ^2_e) of $\boldsymbol{G}$ and $\boldsymbol{R}$ were estimated for each environment separately using the ASReml software (Gilmour *et al.,* 2015) with the model given above, and used as true values to generate the $\boldsymbol{V^{-1}}$. The R program was used to estimate fixed effects of the model and carry out statistical testing. The $\boldsymbol{b}$ in each environment was estimated with Generalized Least Squares means: $\boldsymbol{\hat{b} = (X'V^{-1}X)^{-1}X'\,V^{-1}y}$, where $\boldsymbol{\hat{b}}$ is a 24*1 vector including the 4*4 = 16 $\boldsymbol{\hat{b}}$-s to establish the form of the lactation yield planes for the %Awassi by DIM, in addition to 8 estimated fixed effects of: parity, year of lambing, season of lambing and sex of lamb. The variance of this estimator is: $\mathbf{var}(\boldsymbol{\hat{b}}) = (\boldsymbol{X'V^{-1}X})^{-1}$.

Estimation of lactation plane in each environment

The daily least-squares mean (LSM) lactation yield per % Awassi (t x a), per environment f (f = FE or BE), was calculated as:

$$\tilde{y}(t,a,f) = \boldsymbol{M}(t,a)\boldsymbol{\hat{b}}_f$$

where

$\boldsymbol{M}(t,a)$ is a 1 x 24 vector with the combined Legendre $\boldsymbol{L(t,a)}$ coefficients in 16 columns for the combination of days in milk (t) with the Awassi percentage (a) and with 1/3 in the remaining 8 columns. The $\boldsymbol{\hat{b}}_f$ contains the corresponding fixed effect solutions for each environment f. The $\tilde{y}(t,a,f)$ make two (undulating) planes in 3D over the 2D t,a-coordinate system (see Figure 1).

Estimation of yields in genetic groups** g **and sub period** h **of lactation

We defined five genetic groups according to % Awassi: g = 1 (0% Awassi), 2 (<30% Awassi), 3 (30 - 50% Awassi), 4 (>50 - 75% Awassi), and 5 (100% Awassi). Except group 2 and 5 the groups have reasonable numbers of observations in both FE and BE and are comparable to those used in Haile *et al*. (2020a) where the largest % Awassi in FE was 72%.

In addition to the first 120 DIM the three ranges of 5 milking days (h = *early*: 11-15, *mid*: 46-50, *late*: 101-105 DIM) with most observations were used for the calculation of LSM yields of three sub-periods of lactation per defined genetic group, in correspondence with Haile *et al*. (2020a).

The average LSM daily milk yield for ewes of environment f in genetic group g for a DIM interval h was calculated by summing the relevant $\tilde{y}(t,a,f)$ and dividing by the number of estimated observations summed over ($n_{f,g,h}$):

$$\bar{\bar{y}}_{f,g,h} = \frac{1}{n_{f,g,h}} \sum_{a,t\ elements\ of\ g,h} \tilde{y}(t,a,f) = \frac{1}{n_{f,g,h}} \sum_{a,t\ elements\ of\ g,h} \boldsymbol{M}(t,a)\, \widehat{\boldsymbol{b}}_f = \boldsymbol{N}_{f,g,h} \widehat{\boldsymbol{b}}_f \quad ,$$

where $\boldsymbol{N}_{f,g,h}$ is a vector of 1*24 numbers. The average $\bar{\bar{y}}_{f,g,h}$ is thus a linear combination of the estimated $\widehat{\boldsymbol{b}}_f$.

For example for group g = 2 we use 0% $<a<$ 30% (i.e., 29 values of a) and for h = *early* we have 10 $<t<$ 16 (i.e., 5 values of t) in all 29 * 5 = 145 = $n_{f,2,early}$ different $\tilde{y}(t,a,f)$ values.

Testing of differences between the two environments

LSM differences between environments f (FE and BE) for genetic group g (g=1, 2,.., 4) of ewes over the early DIM were for example found as:

$$d_{g,early} = \boldsymbol{N}_{BE,g,early} \widehat{\boldsymbol{b}}_{BE} - \boldsymbol{N}_{FE,g,early} \widehat{\boldsymbol{b}}_{FE}$$

The variance of this difference between the average daily milk yield for genetic group g of environments FE and BE (since there are no covariances between the estimates and since the coefficients and vectors are the same for both environments, i.e., $\boldsymbol{N}_{BE,g,early} = \boldsymbol{N}_{FE,g,early} = \boldsymbol{N}_{g,early}$) was calculated as:

$$var\left(\boldsymbol{N}_{BE,g,early} \widehat{\boldsymbol{b}}_{BE} - \boldsymbol{N}_{FE,g,early} \widehat{\boldsymbol{b}}_{FE}\right) = \boldsymbol{N}_{g,early} var\left(\widehat{\boldsymbol{b}}_{BE} - \widehat{\boldsymbol{b}}_{FE}\right) \boldsymbol{N}_{g,early}' =$$

$$\boldsymbol{N}_{g,early}\,[var(\hat{\boldsymbol{b}}_{BE}) + \; var(\hat{\boldsymbol{b}}_{FE})]\,\boldsymbol{N}_{g,early}{}' =$$

$$= SE^2_{g,ealy,BE,FE}$$

, and similarly, for the other groups and time periods. Above, *SE* is the standard error of the estimated difference. A 95% confidence interval for the difference was calculated using a t-distribution with the number of ewes as degrees of freedom:

$$d_{g,early} \pm 1.987 * SE_{g,early,BE,FE}$$

Similar confidence intervals were calculated for all presented estimated differences, replacing $SE_{g,early,BE,FE}$ with the relevant standard error in each case. LSM differences were taken as non-significant (NS) at a 5% level if their confidence interval included 0.

RESULTS

Table 3 shows that TDMY of ewes at both the breeding stations and in the field were affected ($P < 0.05$) by the parity and year of lambing. The lambing season effects was significant in the BE environment only, while lamb sex (including twinning) was not significant in any of the two environments.

The estimated variance components are presented in Table 4. Numerically, the ewe variance component (σ^2_{ewe}) was higher in FE (0.04 ± 0.01) than in BE (0.02 ± 0.01). Contrarily, the residual variance (σ^2_e) was lower in FE (0.08 ± 0.01) than the value obtained for BE (0.14 ± 0.01).

The predicted average TDMY of genetic groups of ewes by environments over 120 DIM are summarized in Table 5 and Figure 1. Even if the ewes in BE on average produced more milk than the ewes in FE for all studied genetic groups, none of the contrasts over 120 DIM were significant within the genetic groups studied. This suggests little G x E for average TDMY over 120-days of lactation. TDMY yield in both environments showed increments with increased percentage of Awassi blood level in ewes. As seen in Figure 1, the model was fitted beyond 120 DIM, but LSM were only calculated up to 120 DIM because some genetic groups had negative TDMY for >120 DIM. In FE the largest % Awassi was 72% so LSM differences were not calculated for 100% Awassi.

Table 6 shows effect of the environments on average TDMY over the 3 selected 5-day sub-periods of lactation (11 - 15, 46 - 50 and 101 - 105 DIM) for the 5 chosen % Awassi intervals. In the early stage of lactation (DIM 11 - 15) the 0%, <30% and 30 - 50% Awassi ewes had higher TDMY at the stations than in farmers' environment (P< 0.05). However, for ewes being in the >50 - 75% Awassi group the difference was not significant. In mid lactation (DIM 46 - 50) only the <30% Awassi ewes gave significantly higher TDMY at the stations. During the late stage of lactation (DIM 101 - 105), no significant differences were found for the genotype groups contrasted in the study. However, for all groups, the ewes kept under farmers' condition were calculated with somewhat higher average TDMY values at the late lactation stage than at the breeding stations, whereas for earlier stages lower averages were registered.

DISCUSSION

In this study, data from the farmers' field (previously analyzed by Haile *et al*., 2020a) and from two breeding and multiplication centres (analyzed by Haile *et al*., 2020b) were utilized to evaluate G x E interaction for TDMY. As before, the trajectory over DIM was modelled by a flexible Legendre polynomial, but here it was also combined with the continuous trajectory of Awassi percentages of the ewes. The data used was unbalanced in terms of number of ewes and blood percentage of exotic breed for the two targeted environments. For easy comparison we need to have similar % of Awassi blood level and similar stage of lactation (DIM) in both environments. With limited numbers of observations as we had here, we could not make an adequate balanced data set. We analyzed by fitting models to each of the two environments, for a combination of days of lactation and % of Awassi, and then further checked if any % of Awassi seemed to be better in one environment compared to the other at some stage of lactation. For each environment a variance component for ewe and residual were estimated. Estimation of the effects of all the products (16) of the two Legendre coefficients (each with 4 coefficients) within each environment (BE and FE) resulted in two flexible planes, one for each environment (see Figure 1 for an illustration). The G x E interaction effect was estimated by forming contrasts between solutions in the two planes. Contrasts between BE and FE considered by us were average TDMY for 4 defined genetic groups across 120 DIM, and across 5-day intervals in early, mid and late lactation. As in Haile *et al*. (2020a; 2020b) lactation length was found to be shorter for 0% Awassi (Figure 1). Our comparison did not include milk produced after 120 DIM, so the genetic groups with longer lactations did not benefit.

Over 120 DIM and in BE, the LSM estimates were close to those obtained by Haile *et al*. (2020b), while the corresponding estimates in FE for 0% Awassi and <30% Awassi were considerably higher than those estimated by Haile *et al*. (2020a) (see Table 2). Also now, the production in FE was lower than in BE and seemed to increase with the blood percentage of Awassi. The production advantage of the 30 - 50% Awassi group found by Haile *et al*.

(2020a) became less clear. None of the contrasts between the genetic groups in the two environments stood out as especially different from the others for any of the 4 genetic groups. In this study modelling of the trajectory of DIM was done across the trajectory of the exact Awassi percentage of ewes, while in Haile *et al*. (2020a; 2020b) the trajectories of DIM were done within predefined genetic groups, classified according to % of Awassi, which might be high or low within the classes. This continuum as well as the product of the coefficients for the two trajectories is considered as reasons for the somewhat changed LSM estimates, especially for FE with the least data (Table 2). Note that the form of the Legendre fit for % of Awassi will also be affected by TDMY values outside the genetic group studied.

For the genetic groups with the least % Awassi, the new model leads to somewhat higher LSM in early, mid and late lactation relative to the estimates of Haile *et al*. (2020a) for FE. At early lactation the lower % Awassi groups (although only 0% and 50% Awassi ewes were observed at BE) a significant TDMY increase was found for the stations' environments, but not for the highest, >50 - 75% Awassi, genetic group. This G x E interaction implies that it is the high % Awassi (>50 - 75%) ewes that appear to be robust. Awassi has been bred for increased milk production, normally resulting in a more peaked lactation curve (Rummel *et al*., 2005), irrespective of environment. Especially in FE resources for early milk production comes from body reserves. These have to be replaced in the dry period, otherwise it might result in a shorter productive life (Puillet *et al*., 2016). Consequently, the seemingly increased robustness of the increased % of Awassi in early lactation may result in a G x E at a later stage of life. Ideally, the G x E interaction should have been examined for more traits to have gained more insight. Our G x E result imply that selection carried out at the breeding and multiplication centres (discussed by Haile *et al*., 2020b) for lactation yield to a large degree should also be realized in the field. Furthermore, the more physiological G x E interaction found in early lactation can be utilized most efficiently by establishing a synthetic population, where all the ewes (given that all become crossbreeds) produce more milk in early lactation. This can be important because high rate of lamb mortality has been reported in the area, with a phenotypic relation to both survival and growth of lambs (Snowder and Glimp, 1991; Tibbo, 2006; Getachew, 2015). The approach can be further developed by adopting a higher order LP that would generate more flexible planes. With adequate additive genetic relationship between animals in the two environments, a joint genetic analysis of the data in the two environments could have been carried out. Moreover, estimation of genetic group specific residual and permanent environmental variances in either of the two environments could have been obtained with more data and would have added information about the environmental sensitivity of the genetic groups at the micro and macro level, in analogy with Bytyqi *et al*. (2007) and Steinheim *et al*. (2008).

CONCLUSION

No significant G x E interaction was found for any of the genetic groups across 120 days in milk. This implies that the selection can be performed at the breeding stations, and the genetic superiority multiplied will in large be realized in the farmers' field. Moreover, the significant interaction in early lactation, being mostly physiological, will be avoided for most animals with the current regime for the dissemination of rams that are either 50% or 75% Awassi.

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Table 1. Study area characteristics as well as number of herds and ewes observed in the two villages and two stations included in the study.

Study area characteristics	Farmers' environment[1)]		Breeding environment[2)]	
	Faji (North Shoa)	**Chiro (South Wollo)**	**DB-R (North Shoa)**	**AG-R (North Shoa)**
Distance from Addis-Ababa, km	120 km	501 km	125 km	282 km
Altitude, m.a.s.l.[3)]	2770	1500 – 3700	2780	1680 - 3600
Latitude and longitude	10º00N - 39º00 E	11º00N - 39º00 E	9°36 N - 39°38 E	10°28 N - 39°5E
Rainfall, mm	920	700 – 1200	920	800 - 1600
Rainy season, pattern[4)]	June - September, bimodal	June - September, bimodal	June - September, bimodal	June - September, bimodal
Temperature (annual), ºC[5)]	6.7 – 19.9	7.3 - 23.7	8.2 - 18.6	8 – 18

[1)] Sixteen herds in Faji and 18 in Chiro.

[2)] DB-R=Debre-Berhan Sheep Breeding and Multiplication Center; AG-R = Amed-Guya Sheep Breeding and Multiplication Center.

[3)] m.a.s.l. = meters above sea level.

[4)] June to September is the main rainy season. A weaker and unreliable second rainy season is from February to March.

[5)] Minimum and maximum average per day in a year.

Table 2. Number of ewes and records in genetic groups, and test-day milk yield averages (LSM ± SE) from two previous studies for the animals in the present study.

Environment	**Proportion of Awassi (%)**	**Ewes, n**	**Test-day records**		**Reference**
			n	**TDMY, kg**[1)]	
Farmers' field	0% Awassi	46	196	0.56 ± 0.08	Haile *et al.* (2020a)
	<30% Awassi	19	85	0.67 ± 0.09	
	30 - 50% Awassi	19	77	0.87 ± 0.07	
	>50% Awassi	31	108	0.96 ± 0.07	
Breeding and multiplication centres	0% Awassi	28	107	0.81 ± 0.03	Haile *et al.* (2020b)
	50% Awassi	125	579	1.02 ± 0.02	
	75% Awassi	37	183	1.06 ± 0.03	
	100% Awassi	21	171	1.69 ± 0.04	
Total		326	1506		

[1)] Least-squares mean over first 120 days in milk.

Table 3. Analysis of variance results for fixed effects examined to affect test-day milk yield of ewes recorded in either the farmers' field (FE) or at the breeding and multiplication centres (BE).

Effects	**Df**	**FE**			**BE**		
		Mean square	**F**	***p***	**Mean square**	**F**	***p***
DIM and % Awassi[1)]	16	370.7	105.21	<0.001	815.5	365.10	<0.001
Parity	2	113.3	5.91	0.004	192.0	3.45	0.034
Year of lambing	2	121.5	4.13	0.018	180.3	5.74	0.004
Season of lambing	2	114.0	1.91	0.153	185.9	4.46	0.013
Lamb sex (and twinning)	2	80.8	0.51	0.605	185.7	0.42	0.656

[1)] *3*rd order Legendre polynomials of test day (t) and % Awassi (a) including the mean effects.

Table 4. Estimated ewe and residual variances (± SE), within farmers' (FE) and breeding stations' (BE) environments.

Parameter	Environment	
	FE	BE
Ewe variance (σ^2_{ewe})	0.04 ± 0.01	0.02 ± 0.01
Residual variance (σ^2_{e})	0.08 ± 0.01	0.14 ± 0.01

Table 5. Least-squares means (LSM ± SE) of average test-day milk yield (kg) over the first 120 days in milk (in either farmers' or breeding stations' environments, FE or BE) for chosen genetic groups; and a test if the estimated contrasts between environments within genetic group were significant.

	Environment (LSM ± SE)		
Genetic group	**FE**	**BE**	**LSM contrasts ± SE[1)]**
0% Awassi	0.76 ± 0.06	0.82 ± 0.09	0.06 ± 0.10
<30% Awassi	0.87 ± 0.06	1.07 ± 0.09	0.20 ± 0.11
30 - 50% Awassi	0.93 ± 0.06	1.05 ± 0.07	0.12 ± 0.09
>50 - 75% Awassi	0.99 ± 0.08	1.00 ± 0.07	0.01 ± 0.10
100% Awassi	-	1.70 ± 0.08	-

[1)] * Test if contrast is significantly different from 0 with $p < 0.05$.

Table 6. Least-squares means (LSM ± SE) of average test-day milk yield (kg) over 3 selected sub-periods of lactation (DIM) (in either farmers' or breeding stations' environments, FE or BE) for genetic groups; and a test if the estimated contrast between environments within genetic group was significant.

DIM 11 - 15	**Genetic group**	**Environment (LSM ± SE)**		**LSM contrast ± SE**[1)]
		FE	**BE**	
	0% Awassi	1.00 ± 0.07	1.25 ± 0.10	0.25 ± 0.12*
	<30% Awassi	1.26 ± 0.08	1.65 ± 0.11	0.39 ± 0.14*
	30 - 50% Awassi	1.20 ± 0.07	1.53 ± 0.07	0.33 ± 0.10*
	>50 - 75% Awassi	1.40 ± 0.09	1.36 ± 0.08	-0.04 ± 0.12
	100% Awassi	-	2.62 ± 0.08	-
DIM 46 - 50				
	0% Awassi	0.87 ± 0.07	0.98 ± 0.10	0.11 ± 0.12
	<30% Awassi	0.96 ± 0.08	1.31 ± 0.11	0.35 ± 0.13*
	30 - 50% Awassi	1.11 ± 0.07	1.28 ± 0.07	0.17 ± 0.10
	>50 - 75% Awassi	1.14 ± 0.10	1.21 ± 0.08	0.06 ± 0.12
	100% Awassi	-	1.87 ± 0.09	-
DIM 101 - 105				
	0% Awassi	0.48 ± 0.06	0.37 ± 0.09	-0.10 ± 0.11
	<30% Awassi	0.53 ± 0.07	0.47 ± 0.10	-0.06 ± 0.12
	30 - 50% Awassi	0.55 ± 0.06	0.49 ± 0.10	-0.06 ± 0.10
	>50 - 75% Awassi	0.56 ± 0.09	0.55 ± 0.10	-0.01 ± 0.11
	100% Awassi	-	0.95± 0.08	-

[1)]* Test if contrast is significantly different from 0 with $p < 0.05$.

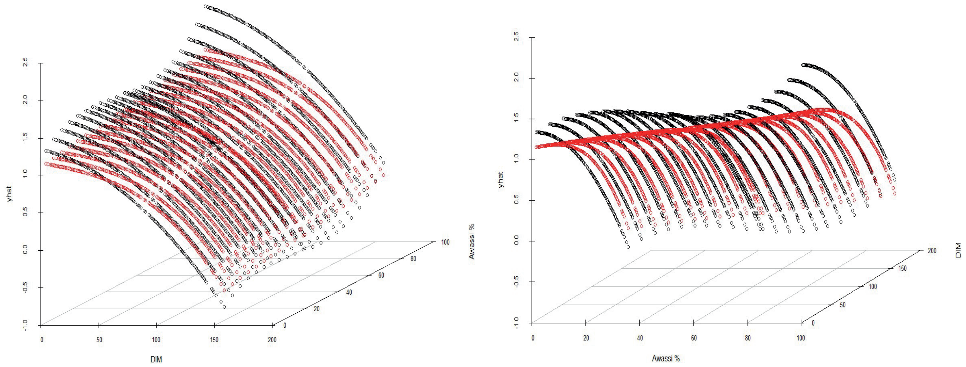

Figure 1. Estimated least-squares means (LSM) of test-day milk yield (TDMY) in the farmers field (FE) (Red, o) and at the breeding stations (BE) (Black, **o**) by days of lactation (DIM) and for % Awassi, when modelling up to third order cross products of their Legendre coefficient.

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