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SI FAT TAILED SHEEP

Mini review: breeding Awassi and Assaf sheep for diverse management conditions

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Abstract The Local Awassi, a triple-purpose breed for meat, milk, and carpet–wool production, is a low-prolific, hardy breed that is well adapted to the unfavorable conditions of the Middle East, where it is managed under traditionally extensive to semi-extensive conditions. Breeding work with the Awassi has included within-breed selection, crossbreeding, and gene introgression. Those efforts resulted in a variety of Awassi-derived genotypes that successfully occupy semi-intensive as well as intensive production systems. Thus, within-breed selection resulted in development of the "Improved Awassi"—a dairy-type Awassi strain which, under intensive management, produces over 500 l milk/ewe annually; crossbreeding with the East Friesian breed led to the development of the Assaf dairy breed, which exceeds the Improved Awassi in prolificacy and in year-round breeding activity, and introgression of the *B* allele of the *FecB* locus into the Awassi and Assaf breeds resulted in the formation of the prolific Afec Awassi and Afec Assaf strains, with prolificacies of 1.9 and 2.5 lambs born per ewe lambing, respectively. Advanced molecular genetics tools have enabled a better understanding of how the Awassi breed was formed during domestication and have uncovered differences in its genetic structure compared to other breeds. Implementing large-scale selection schemes that implement emerging new information on the sheep genome, overcoming threats of inbreeding depression, and further breeding for high uterine capacity are the new breeding goals for the Awassi, Assaf, and their derivatives.

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Introduction

Sheep were domesticated in the Near East some 9,500–10,000 years ago (Zeder 2008). Among the approximately 1,400 sheep breeds known (Scherf 2000), the fat-tailed Awassi breed has attracted particular attention, not only because it is the most numerous breed in the Middle East (ME) region, but also due to its significant contribution, as a pure breed or by crossbreeding, to milk production in sheep production systems worldwide (Rummel et al. 2005; Galal et al. 2008). Although archeological evidence documents the presence of Awassi-like fat-tailed sheep in the ME region as early as about 5,000 years ago, details regarding the early stages of Awassi formation are still missing.

The Local (unimproved) Awassi is a hardy, low-prolific, and low-milk-producing breed which is managed in the ME mainly under extensive or semi-extensive conditions (Galal et al. 2008), where environmental constraints, such as food availability and climate, are the rate-limiting factors for production. By selection within the Local Awassi, and by crossbreeding with other breeds, several medium and high milk producers, and high-prolific Awassi-derived genotypes were developed (Galal et al. 2008). These are now kept under a range of management conditions, including intensive conditions in which the genetic architecture of the animal is the rate-limiting factor for production. The extent to which today's different Awassi-derived genotypes suit the different management conditions is of interest.

A comprehensive review was published recently on Awassi sheep (Galal et al. 2008) which provides information regarding characterization of the breed and its productive and reproductive traits, a description of the results of various breeding programs related to the Awassi, and details on the dissemination of the Awassi from its countries of origin to other parts of the world. However, with the development of DNA markers, genetic maps and whole-genome sequencing (Dodds et al. 2007), new information has been accumulated on the Awassi and its related genotypes. The aim of this communication therefore, is to review recent literature regarding the development of Awassi strains and crosses, and to address the use of molecular genetic tools in the study of the Awassi's origin and genetic makeup.

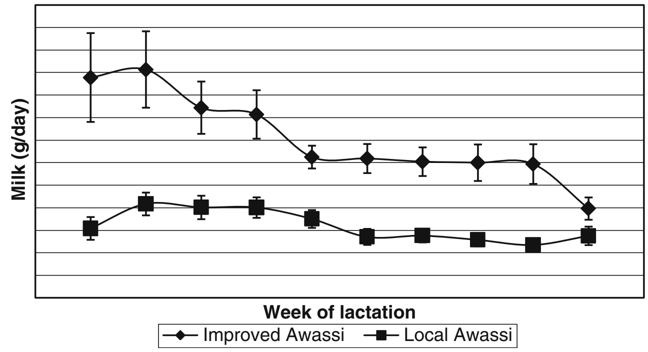

Fig. 1 Daily milk yield (mean±SE) on weekly tested days of local Awassi and improved Awassi sheep in their first lactation. Adapted from Alqaisi (2007)

Overview of breeding Awassi and its related genotypes

Within-breed selection and formation of the improved Awassi

The Local Awassi is a multipurpose fat-tailed breed raised for lamb, wool, and milk production (Galal et al. 2008). Prolificacy of the Local Awassi is low, about 1.1 lamb born/ewe lambing (LB/EL), as recently confirmed in several studies reporting 1.18 LB/EL in multiparous Local Awassi sheep (n=2,959) raised by Bedouins in the Negev region of Israel (Gootwine et al. 2009; Albaqain et al. 2010), and 1.08–1.16 LB/EL in Local Awassi ewes in three studies conducted in Jordan (Kridli et al. 2007; Lafi et al. 2009; Jawasreh et al. 2010).

Milk production of Local Awassi kept under extensive conditions is low, about 70 l/lactation (Epstein 1985), and several selection trials within the Awassi have been conducted in different countries to improve this parameter (Galal et al. 2008). The most significant selection program has been the development of the Improved Awassi in Israel, where under intensive conditions, these ewes produce on average 506 l/lactation (Gootwine and Pollott 2000, 2001). An appreciation of the genetic change in the Improved Awassi gained through its formation was recently obtained in a contemporary comparative study carried out at the Khanasry station in Jordan (Alqaisi 2007), where Local Awassi and Improved Awassi sheep were managed together in one flock under the same conditions, and their milk production in the first lactation was investigated for 10 weeks (Fig. 1). While Improved Awassi ewes (n=12) produced (mean±SE) 100.5±8.0 l of milk during that period, Local Awassi ewes (n=17) produced only 47±6 l. The genetic advantage of the Improved Awassi in milk production over the non-selected breed was also demonstrated in another contemporary comparative experiment, where milk production during the first 105 days of the lactation was investigated in Improved Awassi (n=22), Kazakh Fat Rump (KFR; n=16) and Improved Awassi× KFR F1 sheep (n=23). Milk production in that experiment was 152, 43, and 119 l for the three genotypes, respectively (Malmakov et al. 2006).

In response to selection for high milk production in the Awassi, the genetic variation for milk production ability is expected to decrease in the selected lines. It is thus not surprising that heritability estimates for milk yield in the Improved Awassi dairy strain are low as compared to those in non-selected Local Awassi populations (Table 1). The finding of low additive genetic variance for milk production in the Improved Awassi and, on the other hand, evidence for relatively high non-additive genetic variance, which may include dominance and epistatic effects (Pollott and Gootwine 2001), suggest that further genetic improvement of milk production in the Improved Awassi, as well as in other selected Awassi populations (Reiad et al. 2010), should include breeding strategies other than mass selection. However, for Local Awassi populations with low milk production, mass selection based on actual milk records on test days throughout the lactation will continue to be the main breeding strategy. Recently, Iniguez et al. (2009) showed that reliable evaluation of milk production in the Awassi can be obtained by assessing udder morphology, which may help in conducting large-scale selection for high milk production under semi-intensive conditions where milk monitoring might be difficult.

The development of the high milk producer Improved Awassi line from the Local Awassi was associated with an increase in ewes' body weight. Thus, when body weight and body condition score were documented by the same observer in multiparous non-pregnant Improved Awassi and local Awassi ewes (E. Gootwine, unpublished data), average body weight of the Improved Awassi ewes (n=41) was 79.2± 1.4 kg (mean±SE), heavier by about 22 kg than Local Awassi ewes (n=687) whose average weight was 57.1± 0.4 kg. Average body score on a scale of 1–5 of the two strains was 2.9±0.07 and 2.6±0.03 (mean±SE), respectively.

Table 1 Heritability estimates for milk production traits in Local Awassi, improved Awassi and Assaf populations

Breed type	Country	Population size (*n*) Sires	Ewes	Trait	Production level	Heritability estimate	Reference
Local Awassi	Iraq	29	187	TMY	73 kg	0.47	Al-Samarai and Al-Anbari (2009)
	Jordan	130	1,080	DMY	0.93 l	0.22	Jawasreh et al. (2010)
	Cyprus	68	1,213	PWMY	178 kg	0.56	Mavrogenis (1996)
	Syria		506	TMY	150 kg	0.60	Hossamo et al. (1985)
	Turkey	58	1,219	PWMY	113 kg	0.25	Pollott et al. (1998)
Improved Awassi	Israel	44	1,360	TMY	506 l	0.10	Pollott and Gootwine (2001)
Assaf	Israel	141	2,834	TMY	353 l	0.09	Gootwine and Pollott (2002)
	Spain	170	3,854	PWMY	432 kg	0.13	Gutierrez et al. (2007)

TMY total milk yield through the lactation, *DMY* daily milk yield, *PWMY* post-weaning milk yield

It is of interest, that a positive association was found between ewe weight at lambing and milk production also in a study conducted on different Awassi lines in Syria (Reiad et al. 2010).

While the Improved Awassi has been exported to many countries (Rummel et al. 2005; Galal et al. 2008), in its country of origin—Israel, it can be found as a flock in only one location: the Ein Harod flock. Being a closed flock, where replacements are only recruited from within, increased inbreeding is expected, which may lead to the manifestation of undesired recessive traits and to diminution in performances. Such a situation has been recently shown with the identification, within the Improved Awassi of the Ein Harod flock, of segregation of a novel recessive mutation that causes day blindness (Shamir et al. 2010). Using the candidate gene approach, it was found that the Awassi's day blindness is due to a mutation in the *CNGA3* gene that codes for the cone photoreceptor cyclic nucleotide-gated channel subunit α (Reicher et al. 2010). Eradication of the day blindness mutation from the Ein Harod flock is underway, by genotyping all ram lambs selected as replacements using a PCR-RFLP-based test, and culling carriers of the day blind mutation.

Crossbreeding of the Awassi with other breeds

Several crossbreeding trials have been conducted between the Awassi and other breeds to improve lamb and milk production in ME countries and elsewhere (Galal et al. 2008). By far the most successful trial has been the Improved Awassi×East Friesian cross in Israel (Goot 1986; Gootwine and Goot 1996), which resulted in the formation of the Assaf breed. Due to its relatively high prolificacy and high milk production, moderate seasonality, and good lamb growth ability (Pollott and Gootwine 2004), the Assaf has become an important dairy breed not only in Israel, but also in Spain (Ugarte et al. 2001; Gutierrez et al. 2007; Legaz et al. 2008). Assaf was first introduced to Spain in 1977, and its dramatic expansion occurred mainly via the formation of F1 populations with local breeds such as the Castellana, Churra, and Manchega, following continuous upgrading to the Assaf by using Assaf rams. Interestingly, as with the Improved Awassi, low heritability estimates for milk production have been obtained for Assaf populations in both Israel and Spain (Table 1).

Gene introgression

While milk production has been improved in the Awassi by selection, prolificacy remains low in the improved lines, about 1.3 LB/EL (Gootwine and Pollott 2000). Breeding for high prolificacy through introgression of the *B* allele of the *FecB* locus (Piper et al. 1985) into the Improved Awassi and Assaf breeds was begun in Israel in 1986 with the importation of five homozygous *BB* Booroola Merino rams from New Zealand. Introgression of the "Booroola mutation" led to the formation of the high-prolific Afec Awassi and Afec Assaf strains, with average prolificacies of about 1.9 and 2.5 LB/EL, respectively (Gootwine et al. 2008). With their high prolificacy, the Afec strains are managed under intensive conditions where animals are fed to meet all their metabolic needs and assistance is provided to ewes at lambing in the case of large litters. The desired genotype at the *FecB* locus in the Afec strains is heterozygous *B+* ewes, as homozygous *BB* ewes have disadvantages in terms of both prolificacy and growth (Gootwine et al. 2006, 2008). The "Booroola mutation" segregates in the Afec strains, and thus selection of ewe lambs as replacements is based on genotyping for the *FecB* locus.

The inherently high prolificacy in the Afec Assaf uncovered hidden variability in uterine capacity. Uterine capacity is defined as the maximal number of fetuses that the uterine environment can support to birth (Bazer 1969). Whereas in the Afec Awassi, litters of four or more are very rare—about 2%, in the Afec Assaf they comprise about

15% of the litters (Gootwine et al. 2008). It was found that only part Afec Assaf ewes can successfully carry large litters of four or more lambs to term. To fully exploit the economic benefits of the high prolificacy of the Afec Assaf, further research is needed to uncover the genetic and managerial factors underlying the phenomenon of intra-uterine fetal growth restriction (Gootwine et al. 2007).

Despite the fact that Afec Assaf ewes are fed under intensive conditions to meet their metabolic needs, some animals are affected by pregnancy toxemia (PT). The most common treatment for PT is to drench the affected ewe with propylene glycol. However, it is seldom possible to save the mother and lead her to normal lambing. Aiming to develop appropriate management for handling high-prolific Afec Assaf ewes, Zamir et al. (2009) found that combining the propylene glycol treatment with flunixin meglumine, a potent analgesic and antipyretic non-steroidal anti-inflammatory drug, dramatically improves both ewe and lamb survival rates.

Gene–environment interactions in Awassi and Awassi-derived genotypes

By improving environmental conditions, Local Awassi output can be increased, as was demonstrated in Jordan where stationary rather semi-nomadic management and the provision of supplemented feeds were suggested to support improvements in fertility, twinning rate, and lamb survival (Lafi et al. 2009). However, like other traditional breeds (Moav et al. 1976), the Local Awassi has a limited capacity to respond to an increase in management input. Together, selection and crossbreeding efforts with the Awassi have resulted in the formation of a variety of genotypes that can facilitate the transition from traditional extensive sheep production with low input to intensive, high-input management (Fig. 2). However, further research is needed to exploit the most efficient genotype–environment combinations for the different Awassi-related genotypes (Valle Zárate et al. 2009). In this respect, the performance of the prolific Afec Awassi that, so far, has been utilized under intensive conditions, was recently investigated in flocks kept by Bedouin farmers in the Negev—the southern arid part of Israel, under semi-extensive management. In this production system, the animals rely for about half the year on pasture. Dissemination of the Booroola mutation into the Bedouins' flocks was achieved by mating/inseminating Local Awassi sheep with homozygous *BB* Afec Awassi rams. Results showed the prolificacy of the F_1 *B*+ ewes to be, on average, 1.83 and 1.88 LB/EL in the first and second parities, respectively, with overall lamb survival rate at birth of 0.84 (Gootwine et al. 2009; Albaqain et al. 2010), giving about 0.5 more lambs born alive/lambing as compared to the Local Awassi.

Applying molecular markers to study Awassi and Assaf genetic architecture

Autosomal markers Following the use of protein polymorphism, DNA-based molecular markers were used to assess the origin and diversity of livestock species and breeds. Both nuclear and mitochondrial DNA markers were applied to ascertain the genetic basis for differences between the Awassi, Assaf, and other breeds. Thus, using eight microsatellite loci (Buchanan et al. 1994; Forbes et al. 1995), the Awassi was grouped separately, as expected, from various Merino lines and from three British breeds: Romney, Border Leicester, and Suffolk. In a large-scale evaluation of genetic diversity among 29 diverse breeds, using 23 microsatellites, the Awassi was grouped among the fat-tailed breeds, deviating from various European breeds (Lawson Handley et al. 2007). Using a panel of 25 microsatellite markers, the Assaf was clustered apart from several Portuguese breeds (Santos-Silva

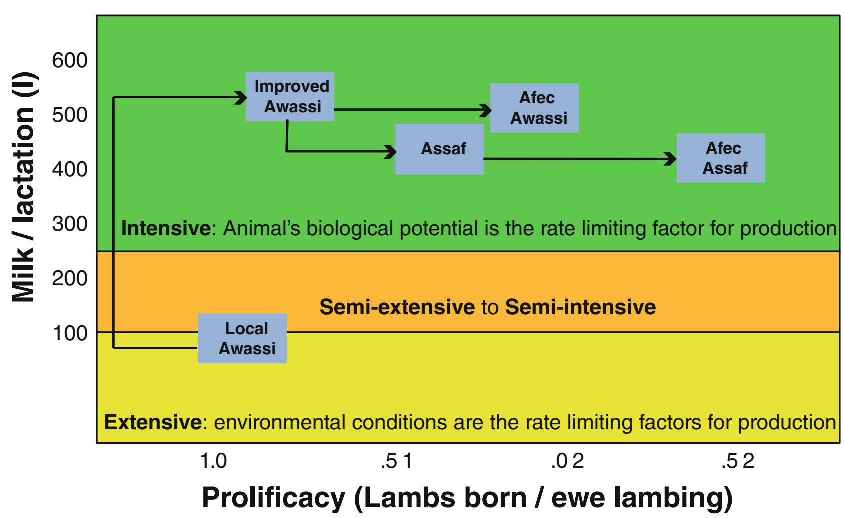

Fig. 2 Distribution of Awassi and Awassi-derived genotypes in relation to their prolificacy and milk-production ability

et al. 2008), and by applying of 14 microsatellite markers, the Spanish Assaf, designated Assaf.E, found to have high genetic distance with respect to native Spanish dairy sheep breeds (Legaz et al. 2008).

Endogenous retrovirus markers Utilizing information on endogenous retrovirus sequences in the sheep genome became a novel way of tracing the history of the domestication of sheep breeds, including the Awassi (Chessa et al. 2009). The sheep genome contains more than 27 sequences related to the pathogenic Jaagsiekte sheep retrovirus (enJSRV). Those sequences, spread over different chromosomal locations, are the result of integration events of retroviruses into the sheep germ line, each event occurring at a particular time during evolution, in a different individual. Once the retrovirus genome integrates into the sheep genome, it is transmitted through generations in a Mendelian fashion. Most enJSRV loci are fixed in domestic sheep, indicating that the integration event took place before sheep breed diversification. However, some enJSRV are polymorphic, as they are not present in all individuals. Six of those polymorphic enJSRVs were used as genetic markers to follow sheep phylogeny and it became apparent that the Awassi does not belong to the "primitive" breed group, where the Mouflon as well as other breeds such as the Orkney, Soay, and Nordic short-tailed breeds are clustered. Rather, it belongs to the group of relatively recently evolved sheep breeds that are characterized by having improved production traits.

Mitochondrial markers Studying mitochondrial DNA polymorphism provides an additional way to follow sheep domestication. As opposed to nuclear DNA, mitochondrial DNA is maternally inherited. To date, five distinct mitochondrial haplogroups have been revealed in sheep: A, B, C, D, and E (Meadows et al. 2007; Pedrosa et al. 2007). Haplogroup A is predominantly found in Asian breeds, haplogroup B in European breeds and haplogroup C in Chinese and Turkish breeds. Four of the haplogroups, A, B, C, and E, were found in the Awassi (Meadows et al. 2007; Pedrosa et al. 2007), suggesting that at least four different maternal lineages contributed to its formation.

As the Awassi served as a maternal parent breed for the Assaf (Gootwine and Goot 1996), it is not surprising that the Awassi's diversity in mitochondrial haplogroups was also observed in the Assaf (Gootwine et al. 2010). However, contrary to the Israeli Assaf, the Spanish Assaf.E is homogenous for the B haplogroup (Pedrosa et al. 2007), reflecting the way in which this breed was formed: by crossing Assaf rams obtained from Israel with local Iberian breeds, in which B is the most frequent haplogroup.

The question is whether mitochondrial polymorphism in the Awassi and Assaf populations contributes to the within-breed variation in productive and reproductive traits. Recent results (Gootwine et al. 2010) suggest that mitochondrial polymorphism affects prolificacy, where prolificacy of animals carrying the B and C haplogroups is higher by 0.10 and 0.22 LB/EL, respectively, than the prolificacy of sheep carrying the A haplogroup.

Y-specific markers Awassi sheep were included in a study investigating polymorphism on the ovine Y chromosome in individuals representing 65 breeds from different parts of the world (Meadows et al. 2006). The results indicated the presence of at least two male lineages, both present in the Awassi.

Detecting quantitative trait loci affecting production traits in Awassi×Merino crosses

As panels of molecular genetic markers became available in sheep, the search for genomic regions carrying polymorphisms associated with variation in quantitative trait loci (QTL) became feasible (Barillet 2007; van der Werf et al. 2007; Carta et al. 2009). The Improved Awassi is a large-framed fat-tailed dairy breed while the Merino is a small-framed, non-dairy, wooly breed. Thus, crosses between those two divergent breeds were utilized for QTL identification. About 200 genetic markers were investigated in a crossbred population of 172 ewes, looking for QTL controlling milk traits such as milk, fat, protein and lactose yields, and somatic cell score (Raadsma et al. 2009a). A total of 15 significant and 25 suggestive QTL were detected in this study. QTL affecting milk production traits were also found in another study in which a population of 258 Awassi×Merino crossbred ewes were genotyped for 13 microsatellite loci distributed on ovine chromosome 6 (Arnyasi et al. 2009). QTL were also detected in the Awassi–Merino crosses for growth rate and body weight traits (Raadsma et al. 2009b), and for carcass composition traits (Cavanagh et al. 2010).

The development of Illumina's OvineSNP50 BeadChip (http://www.illumina.com/pages.ilmn?ID=319/) has provided an assay for 50,000 evenly spaced single-nucleotide polymorphic loci across the sheep genome, contributing a new tool to comprehensive mapping of this genome. Sequencing Awassi's DNA, as well as that of another five breeds, was one of the first steps in the preparation of the OvineSNP50 BeadChip. Using this new tool, it will be possible to carry out a detailed investigation of the genetic changes that occurred during the selection leading to the formation of the Improved Awassi from the Local Awassi, and to the development of other Awassi-derived genotypes. Furthermore, the OvineSNP50 BeadChip may serve in genomic selection within Awassi and Assaf populations for various production and reproduction traits.

Conclusions

Studying the genetic architecture of Awassi sheep using Y-chromosome and mitochondrial molecular markers shows that the Awassi was constructed from several maternal and paternal lineages, common to many other Asiatic and European breeds. This may indicate that the Awassi did not originate from an isolated, small, uniform population but rather, from sheep populations with multiple origins. A different situation has been described for most Iberian sheep (Pedrosa et al. 2007). Whether the different maternal and paternal lineages were already present in the original population from which the Awassi was constructed, or multiple lineages were introduced with time by assimilation in the Awassi males and females from other breeds, is not yet clear.

The Awassi has a quite uniform phenotype with respect to coat color, wool traits and carrying fat tail, which is one of the characteristics of this breed. However, it can be assumed that selection for carrying fat tail was probably carried out at an early stage of the breed's formation. Not much is known about the inheritance of fat tail. However, a study on Lori-Bakhtiari fat-tailed sheep indicates that carrying fat tail has moderate (0.36) heritability (Vatankhah and Talebi 2008) and thus, was not difficult to select for. The conclusion that carrying fat tail may be governed by a few genes is supported by carcass analyses of Awassi and Awassi-Merino crossbreeds (Goot et al. 1991), where it was found that carrying fat tail is inherited in a semi-recessive mode.

Following selection and crossbreeding trials conducted in various countries (Galal et al. 2008), the Awassi, Assaf, and their related genotypes provide a set of genotypes that are adapted to ME conditions and carry the favorable traditional fat tail phenotype. The different genotypes can be tailored to a range of management conditions, from extensive management to higher intensity dairy milk production. New breeding goals like udder morphology and health and ewe longevity (Barillet 2007) have emerged as selection for high milk production has narrowed the genetic base of the improved genotypes (Table 1), and introducing a major gene for high prolificacy uncovered genetic variability for uterine capacity. Incorporating new genome-based technologies in modern Awassi breeding may contribute to achieving those future breeding goals.

Competing interests The author declares that he has no conflict of interest.

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