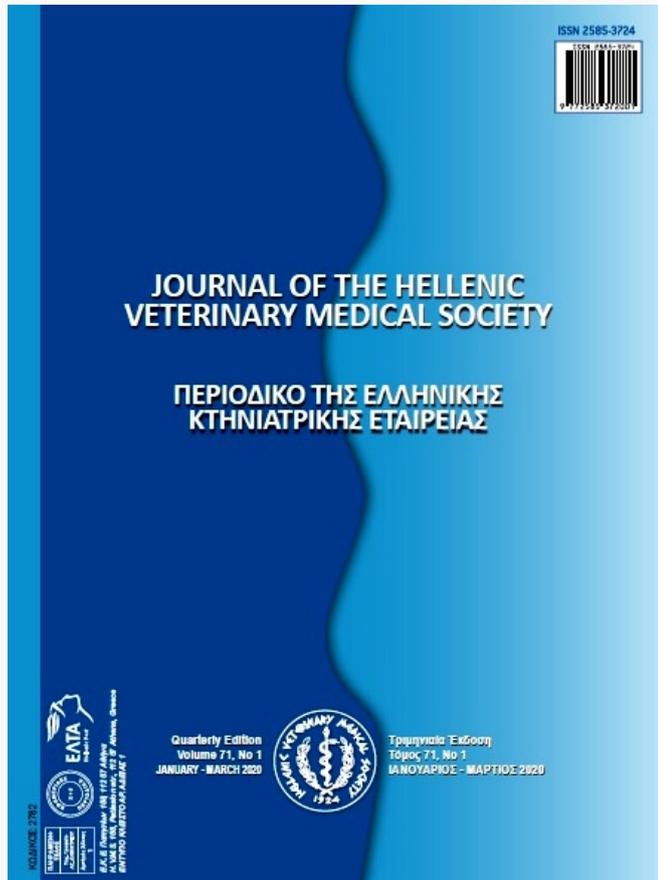


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Genetic improvement of indigenous Greek sheep and goat breeds

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ABSTRACT. The objective of the study was twofold: (i) to review the genetics of production and resilience traits of indigenous Greek small ruminant breeds as well as the evolution of national breeding programs, and (ii) explore innovative and feasible approaches to overcome the challenges and constraints towards improving these breeds and enhancing the sustainability of the small ruminant sector. Previous studies on the genetic basis of production and resilience traits of indigenous breeds revealed high improvement potential. However, the lack of follow-up action has failed to produce applicable results. Thus, implementation of scientific findings in existing breeding programs for these breeds is extremely limited. The latter has contributed to the overall poor success of such programs. Furthermore, due to the fact that most farmers do not comprehend the strategic importance of genetic improvement and lack motivation for self-funding, breeding programs have mostly relied on European or government funding; the latter has resulted in intermittent implementation. Therefore, most programs failed to improve performance of indigenous Greek breeds, many of which were consequently replaced by foreign breeds of higher productivity and documented merit. In order to facilitate the design of breeding schemes and overcome the challenges towards improvement of indigenous breeds, an integrative approach is necessary. The latter should be based on identification of specific breeding objectives, reflecting the priorities and needs of the sector, as well as the capacity of the indigenous populations. Scientific advances exemplified by genomic selection and novel reproductive technologies will enable faster and more effective genetic improvement. The overall approach is expected to enhance the competitiveness of indigenous Greek small ruminant breeds and the sustainability of the sector.

Keywords: genetic improvement, sheep, goats, indigenous breeds, Greece

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INTRODUCTION

Dairy sheep and goat farming is economically important in Mediterranean countries. It also has ecological and sociological impact, as it utilizes harsh and agriculturally low output areas thereby underpinning the sustainability of rural populations (Carta et al., 2009). Dairy small ruminant farming systems are quite diverse and mostly rely on natural resources for grazing. Under these systems, local breeds are considered the most suitable, as they are well-adapted to the local environment (Barillet, 2007; Gelasakis et al., 2010; 2017).

In Greece, small ruminant production dominates the livestock sector. In 2017, the national flock comprised about 8.6 million sheep and 3.8 million goats. With this population size, the Greek national goat herd was the largest and the national sheep flock was ranked fourth among EU-28 countries (Eurostat, 2017a). Small ruminants in Greece are mainly dairy and their milk is mostly processed into cheese and other dairy products (Gelasakis et al., 2010). In 2017, milk production was almost 800,000 tons, which represented about 57% of the total milk produced in Greece (Eurostat, 2017b). Based on the latest available data, annual sheep cheese production was 125,000 tons, rendering Greece the top sheep-cheese producing country worldwide; whereas, goat cheese production (40,000 tons) was the fourth largest globally (FAO, 2014). Meat production, although considered as a secondary activity, is also highly ranked among the EU-28 countries. Specifically in 2017, small ruminant meat production was ranked fourth (71,500 tons) representing 9.3% of the total EU-28 production (Eurostat, 2017a).

Greek small ruminant flocks are usually reared under semi-intensive or semi-extensive farming systems with a trend towards intensification (Gelasakis et al., 2012a; Gelasakis et al., 2017). Adaptation to more intensive farming relies on achieving high ewe and doe productivity. Despite the fact that indigenous breeds share a diverse genetic background and have considerable improvement potential (Hatziminaoglu et al., 1990), national genetic improvement programs have failed to achieve sufficient genetic gain, resulting in unprecedented import rates of foreign improved dairy breeds. In 2016, almost 435,000 sheep (increased by 33% compared to 2014) and 3,500 goats (decreased by 50%) were imported in Greece from EU countries, ranking Greece second and fifth regarding import rates in EU, respectively (European Commission,

2014; 2016).

Replacement of indigenous Greek breeds and uncontrolled crossbreeding with imported sheep and goats has caused the loss of invaluable autochthonous genetic material. Hence, population of most indigenous breeds has decreased dramatically, while even commonly used breeds are constantly losing ground. The objective of the study was twofold: (i) to review the genetics of production and resilience traits of indigenous Greek small ruminant breeds as well as the evolution of national breeding programs, and (ii) explore innovative and feasible approaches to overcome the challenges and constraints towards improving these breeds and enhancing the sustainability of the small ruminant sector.

GENETICS OF PRODUCTION AND RESILIENCE TRAITS

Dairy-related traits

Research outcomes form the pillar of designing successful breeding programs. Indigenous Greek small ruminant breeds first gained scientific interest in the 1980s. The early studies focused on estimating heritability and genetic correlations of dairy-related traits (*i.e.* milk yield, udder traits) and lamb output of Chios sheep, using pedigree information and phenotypic data (Mavrogenis, 1982; Mavrogenis et al., 1988). Subsequently, genetic studies included more traits (*i.e.* milk content, somatic cell count, litter size, body weight) and sheep breeds (*i.e.* Boutsko, Sfakia and Lesvos). These studies showed that improvement of important traits was possible through selection (Kominakis et al., 1998; Ligda et al., 2000; Mavrogenis and Papachristoforou, 2000; Kominakis et al., 2002; Ligda et al., 2003; Nikolaou et al., 2004). Milk yield and composition were found to be antagonistically correlated indicating that selection for one trait would adversely affect the other (Volanis et al., 2002). Respective studies on indigenous Greek goats are limited. A study on Skopelos dairy goats showed that their milk yield is likely to improve through selection (Kominakis et al., 2000). All the above traits are important for dairy small ruminant production. However, inclusion of multiple traits in the same breeding scheme needs further investigation, especially when traits are genetically correlated.

Following the initial genetic studies based on the assumption of polygenic inheritance, Chatziplis et al. (2012) suggested that major genes are likely to be involved in the inheritance of milk traits of Chios sheep.

The same research team studied the acetyl-coenzyme A acyltransferase 2 (ACAA2) gene of Chios sheep and found a single nucleotide polymorphism (SNP) associated with milk yield (Orford et al., 2012). This SNP explained most of the milk yield variation in the same flocks even when analyzed along with 15 microsatellite markers; the latter were located close to Quantitative Trait Loci (QTL) that were found to affect milk yield in other sheep breeds (Chatziplis et al., 2013). Saridaki et al. (2017), performed a Genome-wide Association Study (GWAS) for total lactation milk yield on records of approximately 500 Frizarta ewes and found significant associations (only at chromosome level) with three SNPs located on chromosomes 5 and 23. Further analysis revealed a QTL related to milk yield, which was located close to the SNP found on chromosome 23. Another study on the same dataset, based on haplotype block regression analyses, identified 9 SNPs (4 of which were located in genomic areas associated with milk traits in other breeds) and 11 candidate genes that may be associated with milk yield and composition of Frizarta ewes (Saridaki et al., 2019). Interestingly, none of the SNPs reported in the first study of Saridaki et al. (2017), were verified in the second, after the alteration of the analysis protocol.

Another recent study, on the prolactin gene of Chios sheep, revealed a SNP positively associated with fat content and negatively with milk yield (Miltiadou et al., 2017). Polymorphisms in the caprine gene encoding α_{s1} casein (CSN1S1), known to be associated with goat milk traits (Moioli et al., 2007), have been studied on Skopelos dairy goats. Findings indicated that two out of the three most common genotypes were associated with higher protein and fat content (Arsenos et al., 2014; Kalamaki et al., 2014). Nevertheless, in all the above studies, sample size was quite small ranging from 230 to 318 animals; in order to use SNPs located in genes of interest as markers of selection for milk traits, the estimated effects need to be validated in bigger population samples.

Improvement of udder traits became crucial after the introduction of machine milking in dairy sheep and goat production. Machine milking efficiency depends on udder morphology, among other parameters (Marnet and McKusick, 2001). Many direct and indirect measurements have been used to describe udder morphology of small ruminants and improve their milkability (Fernandez et al., 1995; De la Fuente et al., 1996; Casu et al., 2006). However, the appropriate

udder traits for selection may differ among breeds and breed-specific studies are necessary to design genetic improvement programs. Gelasakis et al. (2012b) described the udder morphology of Chios sheep using both direct and indirect measurements, taking into account relationships with milking efficiency. Strong correlations among traits were observed indicating that udder improvement could be based on selection for only indirect linear traits, which can be assessed faster at a lower cost. A study on Frizarta sheep reported low to moderate heritability estimates (0.05 - 0.21) for indirect linear udder traits (Kominakis et al., 2013). Studies on a larger scale are necessary in order to make safe assumptions for selection of udder traits in Greek sheep.

Disease resistance

Response to infectious pathogens and susceptibility to disease are traits exhibiting considerable host genetic variation (Bishop, 2015). Studies of genetic variation underlying disease resistance in small ruminants have showed that selection for resistance to certain diseases is possible (Bishop and Morris, 2007). Respective studies on indigenous Greek sheep and goats have focused on scrapie, mastitis, footrot and nematode resistance.

Scrapie resistance

Resistance to classical scrapie has been associated with polymorphisms at codons 136 (alanine/valine), 154 (arginine/histidine) and 171 (glutamine/histidine/arginine) of the ovine *PRNP* gene in many sheep breeds (Bossers et al., 1996; Hunter et al., 1996). The aforementioned polymorphisms are most commonly combined into five haplotypes; namely ARR, ARH, ARQ, AHQ and VRQ. Combinations of the above haplotypes result in many genotypes, which are classified into five risk groups, according to the National Scrapie Plan (Warner et al., 2006). More than 25 *PRNP* genotypes have been detected in indigenous Greek sheep indicating high levels of genetic variation. Genotypes of risk groups 1 and 2, which are less susceptible to classical scrapie, have been reported in largely ranging frequencies (4.31 - 40% and 6.7 - 71.4% for risk groups 1 and 2, respectively) in both purebred and crossbred Greek sheep (Billinis et al., 2004; Ekateriniadou et al., 2007a; 2007b; Boukouvala et al., 2018). No significant associations of *PRNP* genotypes with milk production and reproduction traits have been found in Chios sheep, indicating that selection for scrapie resistance is not expected to ad-

versely affect these traits (Psifidi et al., 2011). Based on the latter findings, a selective breeding program has been implemented in Chios sheep aiming to increase the frequency of the resistant allele ARR.

In goats, more than 50 *PRNP* polymorphisms have been reported. Alleles 222K, 146S/D and 211Q in the caprine *PRNP* gene have been strongly associated with resistance to disease (Ricci et al., 2017). However, diverse frequencies of these alleles have been observed among and within breeds and countries. Thus, breed-specific studies are necessary for the development of selection schemes in each country (Ricci et al., 2017; Vouraki et al., 2018). Studies of both healthy and affected Greek goats have reported mutations that lead to amino acid substitutions in over 20 codons of the caprine *PRNP* gene, including the ones that have been associated with scrapie resistance (222K, 146S/D, 211Q) (Billinis et al., 2002; Bouzalas et al., 2010; Fragkiadaki et al., 2011; Kanata et al., 2014). However, the latter studies involved mostly small samples ($n = 51 - 436$ goats) of crossbred and undefined goat populations in Greece. Vouraki et al. (2018) reported frequencies of approximately 6% for the resistant allele 222K estimated over a larger population sample ($n = 551$ goats) of two indigenous Greek breeds (Eghoria and Skopelos). A follow-up study on the same dataset found no associations of allele 222K with dairy traits (Vouraki et al., 2019). Thus, selection for the resistant allele 222K is not expected to have adverse effects on dairy goat traits and could be the basis for the development of a breeding program to enhance scrapie resistance in the two breeds.

Mastitis resistance

Mastitis resistance in small ruminants is commonly assessed using milk somatic cell count (SCC); increased values of SCC indicate udder inflammation. SCC in milk is a heritable trait. Furthermore, recent studies have revealed SNPs associated with mastitis resistance, which render genomic selection feasible (Bishop, 2015). Heritability estimates of SCC in Chios sheep were moderate (0.17) during the first weeks of lactation (Bramis et al., 2014). Further studies on the same data set reported SNPs associated with SCC and other mastitis traits (*i.e.* incidence of clinical mastitis, Total Viable Count - TVC, California Mastitis Test) and identified 24 Quantitative Trait Loci (QTLs), 19 of which had been previously reported in other unrelated dairy sheep breeds. Based on the above, 14 candidate genes were detected as most likely related to mastitis resistance in Chios sheep (Banos

et al., 2017). Detection of the same QTLs in unrelated dairy sheep breeds indicates that implementation of mutual genomic selection programs for the enhancement of mastitis resistance might be effective across breeds. However, further studies are necessary prior to implementation of such programs. Relative studies on other indigenous Greek sheep and goat breeds are largely missing.

Footrot resistance

Polymorphisms located within Class I and II regions of the ovine major histocompatibility complex (MHC) have been associated with resistance to footrot (Escayg et al., 1997). Gelasakis et al. (2013) investigated the genetic profile of *DQA2* gene (located in Class II region of the MHC) of Chios sheep and detected 20 alleles, indicating the highly polymorphic nature of the locus. Allele 1101 in that gene was associated with susceptibility to footrot. The latter finding is in agreement with earlier studies on other sheep breeds; however, the overall allelic frequencies were highly divergent. In general, such associations are inconsistent across breeds and populations rendering genetic selection for resistance to footrot complicated. GWAS, which enable the detection of multiple markers associated with ovine footrot, are considered a more efficient approach towards comprehending the genetic architecture of the disease (Raadsma et al., 2013; Bishop, 2015).

Nematode resistance

Nematode resistance in sheep has been associated with genes located in Class I to III regions of the MHC. Such associations are usually assessed using Fecal Egg Counts (FEC) (Dukkipati et al., 2006). *DRB1* gene (located in Class II region of the MHC) was investigated in Greek sheep and 39 alleles were reported. Genotypes heterozygous for three of the latter alleles were associated with lower FEC (Spetsariasis et al., 2016). Despite the variation observed in *DRB1* gene, further studies involving other genes are needed in order to incorporate the above findings into a breeding scheme. Furthermore, studies on nematode resistance based on FEC need to be interpreted with caution; since FEC are not distinguished among nematode species, inferences are not necessarily applicable for all nematode infections (Dukkipati et al., 2006).

Genetic structure and diversity

Characterization of genetic structure and diver-

sity within and between breeds is an important step towards revealing the genetic architecture of animal traits. Studies aiming to characterize indigenous Greek sheep breeds and assess genetic distances between them have been based on polymorphisms of blood proteins (Rogdakis et al., 1995; Koutsouli and Rogdakis, 2002) and different types of markers such as microsatellite loci (Bizelis et al., 2007; Koutsouli et al., 2007; Ligda et al., 2009; Mastranestasis et al., 2015; Loukovitis et al., 2016), Random Amplified Polymorphic DNA (RAPD) (Mastranestasis et al., 2011) and SNPs (Pariset et al., 2011; Kominakis et al., 2017a; Michailidou et al., 2018). Respective studies on indigenous Greek goats are limited and used either microsatellite markers (Cañon et al., 2006) or SNPs (Pariset et al., 2009).

Most of the above studies involved populations lacking pedigrees and small sample sizes per breed (30 - 100 animals). Only Mastranestasis et al. (2015) and Kominakis et al. (2017a) used relatively large sample sizes (350 Lesvos sheep and 503 Frizarta ewes, respectively) and published follow-up studies. The latter searched for possible associations of phenotypic traits (*i.e.* body traits, milk yield, litter size) with markers detected in the initial studies (Mastranestasis et al., 2016; Kominakis et al., 2017b; Saridaki et al., 2019).

Genetic studies of indigenous Greek sheep and goats indicate high genetic variability and, therefore, improvement potential of production and fitness traits. However, a notable lack of continuity between research activity and practical implementation is observed. Research objectives are altered on the basis of scientific trends resulting in intermittent studies and no further efforts are made towards the application of research outcomes. Consequently, implementation of scientific findings in breeding programs is extremely restricted.

BREEDING PROGRAMS

Introduction of breeding programs

Breeding programs of indigenous Greek small ruminant breeds were first introduced in the late 1970s. Since then, such programs of variable duration, some of which are still ongoing, have been implemented in 15 sheep and two goat breeds. The overall aim has been either improvement of production traits or, in case of rare breeds, conservation and diversity management. The only breeding objective has been milk yield except for the cases of Chios and Frizarta sheep.

Despite the improvement potential of indigenous Greek sheep and goats, breeding programs were not always successful, mostly because implementation was commonly interrupted for time periods varying from months to years. The vast majority of farmers do not comprehend the strategic importance and the long-term benefits of genetic improvement and thus, they are reluctant to invest in it. Reliance of breeding programs exclusively on European and/or government financial support has caused lack of consistency; animal recording paused due to shortage of other sources of financing, whenever funding was pending.

Chios sheep

Chios sheep are highly producing (average commercial lactation milk yield: 324 kg) and present a considerable amount of variance of dairy traits (*i.e.* milk yield, lactation length) indicating high improvement potential (Basdagianni et al., 2018). Hence, Chios sheep are among the most commonly reared indigenous sheep in Greece and the most extensively studied. Breeding objectives for Chios sheep include milk yield and resistance to scrapie. Selection for the latter has been based on genotyping rams for the associated gene, following the relevant study of Psifidi et al. (2011). Although scientific studies on several Chios sheep traits have been published, only the two aforementioned traits have been included in the breeding scheme. Since 2004, average commercial lactation milk yield has increased by ca. 20 kg (Basdagianni, 2006). However, full potential of the breed has not been reached and improvement rates are quite low given that the breeding program is ongoing for more than 15 years. The absence of systematic use of sire referencing schemes and artificial insemination (AI) across the breeding population is a major drawback in the genetic improvement program and contributes to the overall limited improvement of the traits included in the breeding goal.

Frizarta sheep

Frizarta is another relatively highly producing indigenous Greek sheep breed with average commercial lactation milk yield of ca. 250 kg and average fat and protein contents of 6.2% and 5.5%, which are favorable for cheese production (Saridaki et al., 2019). Frizarta sheep have been subject to many studies. However, breeding objectives include only milk yield and quality (fat and protein content). Udder traits are recorded once a year in the beginning of lactation and are candidate traits for selection towards improv-

ing machine milkability (Agricultural and Livestock Union of Western Greece, n.d.). In recently published GWAS on milk and body size traits of Frizarta sheep, the idea of implementing genomic selection has been introduced (Kominakis et al., 2017b; Saridaki et al., 2019). A promising attribute of the breeding program of Frizarta sheep is the extensive implementation of AI across the breeding population.

Despite the few examples of efficiency, most breeding programs have failed to reach their full potential. Poor program management and lack of motivation for self-funding by farmers significantly affected the outcome. Thus, foreign improved breeds of higher productivity have replaced many indigenous small ruminant populations. The latter have decreased dramatically and some indigenous Greek breeds are now facing endangerment or even extinction issues.

TAKING THE NEXT STEP: AN INTEGRATIVE APPROACH

Tackling the challenges towards improvement of indigenous Greek small ruminant breeds requires collaboration of all stakeholders and experts involved in animal production, in an integrative holistic approach. This approach can be broken down into three levels; (i) setting appropriate breeding objectives, (ii) design of breeding schemes based on applied research outcomes, and (iii) practical implementation of breeding programs.

Determination of breeding objectives

In order to set genetic improvement objectives, specifying the needs of dairy industry comes first. Industry is mainly focused on processing milk of small ruminants into cheese (Moatsou and Govaris, 2011). Cheese yield is affected by milk quality traits and coagulation properties, which are characterized by genetic variation indicating improvement potential (Vacca et al., 2018). Milk hygiene traits are also important for dairy industry. According to the EU regulation, milk with increased SCC and TVC is inappropriate for human consumption (European Parliament and Council, 2004). Udder health is commonly compromised due to poor adaptation to machine milking (Gelasakis et al., 2015). Hence, udder conformation improvement for better milkability is also crucial.

Farmers, on the other hand, prioritize milk yield because it is their main source of income (Pulina et al., 2018). Unfortunately, Greek farms producing milk of higher quality are not rewarded; thus, a lack

of motivation for improvement is observed. Animal resilience is also critical for farms as it limits animal replacement needs and enhances their welfare. Animals more resistant to diseases and well adapted to rearing conditions are necessary to maintain a sustainable production (Theodoridis et al., 2018; Rose et al., 2019).

Breeding program design

Integration of the aforementioned multiple objectives in selection schemes requires careful design. Investigation of the genetic background of traits and possible intercorrelations is crucial. Respective studies on milk, udder and resilience traits of indigenous Greek small ruminant breeds are largely missing. Therefore, scientific research should focus on the above and engage in delivering results that are applicable to breeding schemes. To this purpose, genomics is a promising approach as it addresses issues of complex heritability (Hayes et al., 2013). Vast amounts of genomic data are available through high-density genotyping, making it possible to detect genomic regions associated with phenotypic traits of interest (Zhang et al., 2012). Increasing the accuracy of early-life selection is another key advantage of genomic technologies (Hayes et al., 2009; Pryce and Daetwyler, 2012). Furthermore, inclusion of environmental and climate data in genomic studies may simplify investigation of complex resilience traits (Lv et al., 2014).

Although initially expensive, genomic technologies have become affordable, making their implementation on a larger scale easier (Mrode et al., 2018). Advances in imputation techniques enable genomic strategies based on an optimal mixture of strategically targeted genotyping with high-density arrays combined with large-scale genotyping with inexpensive low-density arrays (Aliloo et al., 2018). Therefore, genomic selection is a feasible solution for breeding schemes of multiple objectives.

Practical implementation of breeding programs

Implementation of breeding programs may be based on a three-tier pyramid structure that ensures efficiency and facilitates dissemination of genetic improvement (Figure 1). To this purpose, after the initial screening of the population, a nucleus of animals of high improvement potential can be formed. These animals should be reared in an elite group of well-monitored flocks warranting high welfare standards and sufficient rearing conditions; under such practices animals are more likely to reach full potential. Perfor-

mance recording and genome-wide genotyping of the animals of the nucleus should be thoroughly implemented. Thus, the nucleus will produce sires of high breeding value, which will be used for breeding purposes in the rest of the purebred farms. The main role of the second tier, where a bigger number of flocks are involved, is to generate more animals with the desired genotypes of the top tier population. Animals of the second tier, that are proved to be of high breeding value, can also be used as sires or dams to enhance genetic diversity in the top tier when necessary. Thus, animal performance in second tier flocks is recorded, yet to a smaller extent than in the nucleus, and in some flocks low-density genotyping is also implemented. Finally, flocks involved in the third tier do not record animal performance and rely on the first two tiers for sires and dams of higher breeding value. Thus, flocks at the bottom of the structure benefit from genetic improvement achieved in the first two tiers, although it would take a longer time for them to improve. Such programs have been successfully implemented mainly in poultry and swine, and more recently in dairy ruminants (Harris & Newman, 1994).

Prerequisite for the successful implementation of genetic improvement programs is securing pedigree accuracy, which can be compromised when matings

are done by natural service. On the contrary, use of AI ensures closer monitoring, resulting in more accurate paternity records. Furthermore, AI achieves more efficient use of valuable genetic material and faster collection of progeny performance data, allowing for earlier evaluation of sires (Baldassare and Karatzas, 2004). The latter can be further facilitated through combining AI and genomic selection. Studies on French Lacaune and Manech sheep have showed that incorporation of genomic prediction based on parent performance assists accurate evaluation of candidate sires in a younger age. Such practices increase annual genetic gain without inflating cost (Buisson et al., 2014). Therefore, in the frame of a well-designed breeding scheme, introduction of AI and genomic selection in the nucleus and expansion of its use across the whole population accelerates genetic improvement.

The suggested approach is expected to improve indigenous Greek small ruminant breeds, given that the initial population is sufficiently large and presents improvement potential. Efficient collaboration among all stakeholders involved is expected to provide feedback that can be used for re-evaluation of the scheme, integration of novel technologies and approaches, and inclusion of new breeding objectives.

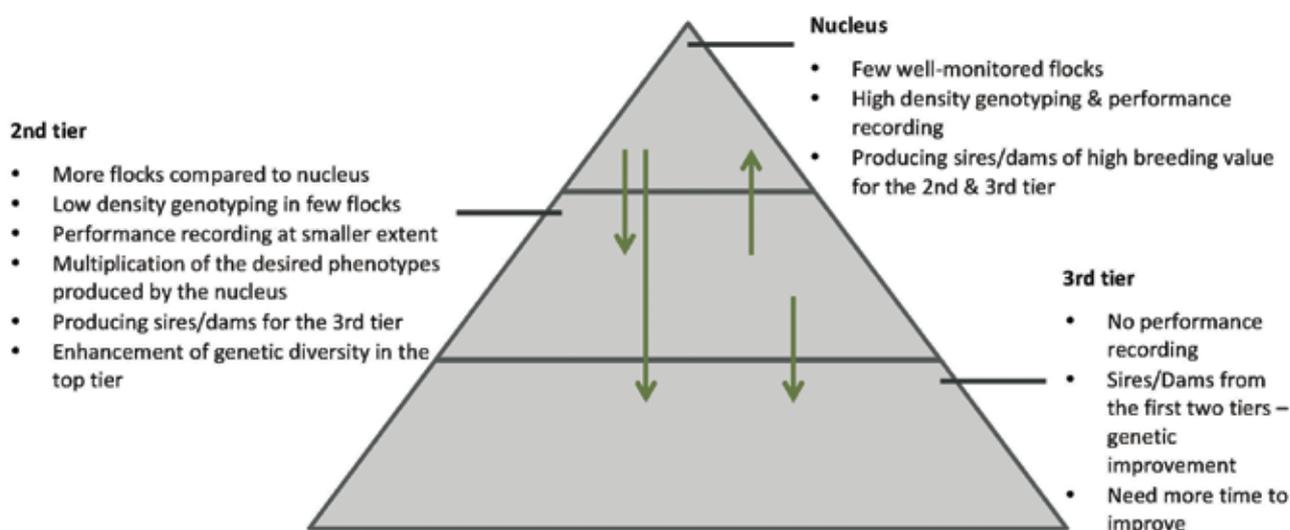


Figure 1: Three-tier pyramid structure that facilitates dissemination of genetic improvement in breeding programs (green arrows indicating supply of sires/dams among tiers)

CONCLUSIONS

Indigenous Greek small ruminant breeds exhibit substantial genetic diversity, which indicates high improvement potential. The latter is supported by scientific publications on production and fitness traits. However, no follow-up action has been taken to systematically incorporate research outcomes into breeding programs. Furthermore, implementation initiatives of such programs have been interrupted more than once due to lack of funding and failed to achieve substantial improvement.

Setting appropriate breeding objectives is the first key step to designing sophisticated breeding schemes that take into account the needs of the sector, market demands and the capacity and potential of indigenous small ruminant populations. Consistent population

monitoring and accurate record keeping are essential. Integration of scientific advances, especially in genomics and reproductive technologies, is expected to underpin the successful implementation of breeding programs and acceleration of genetic improvement. Most importantly, commitment and good communication among all stakeholders, including farmers, industry and scientists, is necessary to ensure efficiency of such programs. Implementation of breeding programs incorporating all the above features is expected to improve the competitiveness of indigenous Greek small ruminant breeds and enhance the sustainability of the sector.

CONFLICT OF INTEREST

None declared.

REFERENCES

- Abdoli R, Zamani P, Mirhoseini SZ, Ghavi Hossein-Zadeh N, Nadri S (2016) A review on prolificacy genes in sheep. *Reprod Domest Anim* 51(5):631-637.
- Agricultural and Livestock Union of Western Greece (n.d.) <http://www.frizarta.gr/> [accessed 12 October 2018].
- Aliloo H, Mrode R, Okeyo AM, Ni G, Goddard ME, Gibson JP (2018) The feasibility of using low-density marker panels for genotype imputation and genomic prediction of crossbred dairy cattle of East Africa. *J Dairy Sci* 101(10):9108-9127.
- Arsenos G, Gelasakis AI, Kalamaki MS (2014) Effect of aS1-casein genotypes on yield and chemical composition of milk from Skopelos goats. In: Book of abstracts of the 65th Annual Meeting of the European Federation of Animal Science, Copenhagen, Denmark: pp 401.
- Baldassarre H, Karatzas CN (2004) Advanced assisted reproduction technologies (ART) in goats. *Anim Reprod Sci* 82-83:255-266.
- Banos G, Bramis G, Bush SJ, Clark EL, Mcculloch MEB, Smith J, Schulze G, Arsenos G, Hume DA, Psifidi A (2017) The genomic architecture of mastitis resistance in dairy sheep. *BMC Genomics* 18(1):624.
- Barillet F (2007) Genetic improvement for dairy production in sheep and goats. *Small Rumin Res* 70(1):60-75.
- Basdagianni Z (2006) Contribution to the genetic improvement of sheep in Greece: Utilization of milk recording of the Chios dairy sheep. PhD thesis, Aristotle University of Thessaloniki.
- Basdagianni Z, Sinapis E, Banos G (2018) Evaluation of reference lactation length in Chios dairy sheep. *Animal* 13(1):1-7.
- Billinis C, Panagiotidis CH, Psychas V, Argyroudis S, Nicolaou A, Leontides S, Papadopoulos O, Sklaviadis T (2002) Prion protein gene polymorphisms in natural goat scrapie. *J Gen Virol* 83(3):713-721.
- Billinis C, Psychas V, Leontides L, Spyrou V, Argyroudis S, Vlemmas I, Leontides S, Sklaviadis T, Papadopoulos O (2004) Prion protein gene polymorphisms in healthy and scrapie-affected sheep in Greece. *J Gen Virol* 85(2):547-554.
- Bishop SC (2015) Genetic resistance to infections in sheep. *Vet Microbiol* 181(1-2):2-7.
- Bishop SC, Morris CA (2007) Genetics of disease resistance in sheep and goats. *Small Rumin Res* 70(1):48-59.
- Bizelis J, Koutsouli P, Rogdakis E (2007) Genetic structure of semi-tailed Greek sheep breeds: I. Gene frequencies, genetic variation and F-statistics. *Animal Science Review* 36:55-69.
- Bossers A, Schreuder BE, Muileman IH, Belt PB, Smits MA (1996) PrP genotype contributes to determining survival times of sheep with natural scrapie. *J Gen Virol* 77(10):2669-2673.
- Boukouvala E, Katharopoulos E, Christoforidou S, Babetsa M, Ekateriniadou LV (2018) Analysis of the PRNP gene polymorphisms in healthy Greek sheep during 2012-2016. *J Hell Vet Med Soc* 69(1):839-846.
- Bouzalas IG, Dovas CI, Banos G, Papanastasiopoulou M, Kritas S, Oevermann A, Papakostaki D, Chatzinasiou E, Papadopoulos O, Seuberlich T, Koptopoulos G (2010) Caprine PRNP polymorphisms at codons 171, 211, 222 and 240 in a Greek herd and their association with classical scrapie. *J Gen Virol* 91(6):1629-1634.
- Bramis G, Arsenos G, Psifidi A, Banos G (2014) Genetic parameters of mastitis related traits in dairy sheep. In: Proceedings of the Annual Conference of the British Society of Animal Science, Nottingham, UK: pp 194.
- Buisson D, Lagriffoul G, Baloché G, Aguerre X, Boulenc P, Fidele F, Frégeat G, Giral-Viala B, Guibert P, Panis P, Soulas C, Astruc JM, Barillet F (2014) Genomic breeding schemes in French Lacaune and Manech dairy sheep: design and expected genetic gain. In: Proceedings of the 10th World Congress of Genetics Applied to Livestock Production, Vancouver, BC, Canada.
- Cañon J, García D, García-Atance MA, Obexer-Ruff G, Lenstra JA, Ajmone-Marsan P, Dunner S, ECONOGENE Consortium (2006) Geographical partitioning of goat diversity in Europe and the Middle East. *Anim Genet* 37(4):327-334.
- Carta A, Casu S, Salaris S (2009) Invited review: Current state of genetic improvement in dairy sheep. *J Dairy Sci* 92(12):5814-5833.
- Casu S, Pernaizza I, Carta A (2006) Feasibility of a linear scoring method of udder morphology for the selection scheme of Sardinian sheep. *J Dairy Sci* 89(6):2200-2209.
- Chatziplis D, Orford M, Tzamaloukas O, Hadjipavlou G, Brown C, Koumas A, Mavrogenis A, Papachristoforou C, Miltiadiou D (2013) A genomic association analysis of milk production traits in Chios sheep breed using microsatellite (SSR) and SNP markers. In: Proceedings of the 4th Pan-Hellenic Congress in Technology of Animal Production, Thessaloniki, Greece: pp 333-343.
- Chatziplis DG, Tzamaloukas O, Miltiadiou D, Ligda C, Koumas A, Mavrogenis AP, Georgoudis A, Papachristoforou C (2012) Evidence of major gene(s) affecting milk traits in the Chios sheep breed. *Small Rumin Res* 105(1-3):61-68.
- De La Fuente LF, Fernandez G, San Primitivo F (1996) A linear evaluation system for udder traits of dairy ewes. *Livest Prod Sci* 45(2-3):171-178.
- Dukkipati VSR, Blair HT, Garrick DJ, Murray A (2006) 'Ovar-Mhc'—Ovine major histocompatibility complex: Role in genetic resistance

- to diseases. *N Z Vet J* 54(4):153-160.
- Ekateriniadou LV, Kanata E, Panagiotidis C, Nikolaou A, Koutsoukou E, Lymberopoulos AG, Sklaviadis T (2007a) PrP genotypes in scrapie-affected sheep in Greece—The contribution of the AHQ 1 polymorphism. *Small Rumin Res* 73(1-3):142-149.
- Ekateriniadou LV, Panagiotidis CH, Terzis A, Ploumi K, Triantafyllidis A, Deligiannidis P, Triantafyllidis C, Sklaviadis T (2007b) Genotyping for PrP gene polymorphisms in rare Greek breeds of sheep. *Vet Rec* 160(6):194-195.
- Escayg AP, Hickford JGH, Bullock DW (1997) Association between alleles of the ovine major histocompatibility complex and resistance to footrot. *Res Vet Sci* 63(3):283-287.
- European Commission (2014) https://ec.europa.eu/food/sites/food/files/animals/docs/ahsc_report_2014_en.pdf [accessed 12 October 2018]
- European Commission (2016) https://ec.europa.eu/food/sites/food/files/animals/docs/ahsc_report_2016_en.pdf [accessed 12 October 2018]
- European Parliament and Council (2004) Regulation (EC) No 853/2004 of the European Parliament and of the Council of 29 April 2004 laying down specific hygiene rules for food of animal origin. *OJ L139(30.4.2004)*:55-205.
- Eurostat (2017a) https://ec.europa.eu/eurostat/statistics-explained/index.php?title=Agricultural_production_-_livestock_and_meat#Sheep_and_goat_meat [accessed 22 July 2019]
- Eurostat (2017b) https://ec.europa.eu/eurostat/statistics-explained/index.php/Milk_and_milk_product_statistics#Milk_production [accessed 22 July 2019]
- Fernandez G, Alvarez P, San Primitivo F, De La Fuente LF (1995) Factors Affecting Variation of Udder Traits of Dairy Ewes. *J Dairy Sci* 78(4):842-849.
- Food and Agriculture Organization of the United Nations - FAO (2014) <http://www.fao.org/faostat/en/#data/QP> [accessed 22 July 2019]
- Fragkiadaki EG, Vaccari G, Ekateriniadou LV, Agrimi U, Giadinis ND, Chiappini B, Esposito E, Conte M, Nonno R (2011) PRNP genetic variability and molecular typing of natural goat scrapie isolates in a high number of infected flocks. *Vet Res* 42(1):104.
- Gelasakis AI, Arsenos G, Valergakis GE, Oikonomou G, Kiossis E, Fthenakis GC (2012b) Study of factors affecting udder traits and assessment of their interrelationships with milking efficiency in Chios breed ewes. *Small Rumin Res* 103(2-3):232-239.
- Gelasakis AI, Arsenos G, Hickford J, Zhou H, Psifidi A, Valergakis GE, Banos G (2013) Polymorphism of the MHC-DQA2 gene in the Chios dairy sheep population and its association with footrot. *Livest Sci* 153(1-3):56-59.
- Gelasakis AI, Mavrogianni VS, Petridis IG, Vasileiou NG, Fthenakis GC (2015) Mastitis in sheep - The last 10 years and the future of research. *Vet Microbiol* 181(1-2):136-146.
- Gelasakis AI, Rose G, Giannakou R, Valergakis GE, Theodoridis A, Fortomaris P, Arsenos G (2017) Typology and characteristics of dairy goat production systems in Greece. *Livest Sci* 197:22-29.
- Gelasakis AI, Valergakis GE, Fortomaris P, Arsenos G (2010) Farm conditions and production methods in Chios sheep flocks. *J Hell Vet Med Soc* 61(2):111-119.
- Gelasakis AI, Valergakis GE, Arsenos G, Banos G (2012a) Description and typology of intensive Chios dairy sheep farms in Greece. *J Dairy Sci* 95(6):3070-3079.
- Harris DL, Newman S (1994) Breeding for profit: Synergism between genetic improvement and livestock production (a review). *J Anim Sci* 72(8):2178-2200.
- Hatziminaoglou J, Zervas NP, Boyazoglu J (1990) Prolific dairy sheep breeds in Greece. In: *Options Méditerranéennes: Série A. Séminaires Méditerranéens*; n. 12, "Les petits ruminants et leurs productions laitières dans la région Méditerranéenne", Montpellier, CIHEAM: pp 25-30.
- Hayes BJ, Bowman PJ, Chamberlain AJ, Goddard ME (2009) Invited review: Genomic selection in dairy cattle: Progress and challenges. *J Dairy Sci* 92(2):433-443.
- Hayes BJ, Lewin HA, Goddard ME (2013) The future of livestock breeding: genomic selection for efficiency, reduced emissions intensity, and adaptation. *Trends Genet* 29(4): 206-214.
- Hunter N, Foster JD, Goldmann W, Stear MJ, Hope J, Bostock C (1996) Natural scrapie in a closed flock of Cheviot sheep occurs only in specific PrP genotypes. *Arch Virol* 141(5):809-824.
- Kalamaki MS, Gelasakis A, Arsenos G (2014) Genetic polymorphism of the CSN1S1 gene in the Greek-indigenous Skopelos goat. In: *Proceedings of the 4th ISOFA Scientific Conference, 'Building Organic Bridges' at the Organic World Congress, Istanbul, Turkey*: pp 575-578.
- Kanata E, Humphreys-Panagiotidis C, Giadinis ND, Papaioannou N, Arsenakis M, Sklaviadis T (2014) Perspectives of a scrapie resistance breeding scheme targeting Q211, S146 and K222 caprine PRNP alleles in Greek goats. *Vet Res* 45(1):43.
- Kominakis A, Antonakos G, Karagianni V, Voulgari M, Vafiadakis T (2013) Genetic parameters of udder morphological traits in the Frizarta dairy sheep. In: *Proceedings of the 4th Pan-Hellenic Congress in Technology of Animal Production, Thessaloniki, Greece*: pp 393-399.
- Kominakis A, Hager-Theodorides AL, Saridaki A, Antonakos G, Tsiamis G (2017a) Genome-wide population structure and evolutionary history of the Frizarta dairy sheep. *Animal* 11(10):1680-1688.
- Kominakis A, Hager-Theodorides AL, Zoidis E, Saridaki A, Antonakos G, Tsiamis G (2017b) Combined GWAS and 'guilt by association'-based prioritization analysis identifies functional candidate genes for body size in sheep. *Genet Sel Evol* 49:41.
- Kominakis A, Rogdakis E, Koutsotolis K (1998) Genetic parameters for milk yield and litter size in Boutsico dairy sheep. *Can J Anim Sci* 78(4):525-532.
- Kominakis A, Rogdakis E, Koutsotolis K (2002) Genetic Aspects of Persistence of Milk Yield in Boutsico Dairy Sheep. *Asian-Australas J Anim Sci* 15(3):315-320.
- Kominakis A, Rogdakis E, Vasiloudis C, Liaskos O (2000) Genetic and environmental sources of variation of milk yield of Skopelos dairy goats. *Small Rumin Res* 36:1-5.
- Koutsouli P, Bizelis J, Rogdakis E (2007) Genetic structure of semi-fat tailed Greek sheep breeds: II. Genetic relationships among breeds and use of microsatellite genotypes for breed assignment. *Animal Science Review* 36:71-82.
- Koutsouli P, Rogdakis E (2002) Genetic structure of Greek sheep breeds: III. Genetic variation within and between breeds. *Animal Science Review* 30:29-44.
- Ligda C, Altarayrah J, Georgoudis A, ECONOGENE Consortium (2009) Genetic analysis of Greek sheep breeds using microsatellite markers for setting conservation priorities. *Small Rumin Res* 83(1-3):42-48.
- Ligda C, Gabriilidis G, Papadopoulos T, Georgoudis A (2000) Estimation of genetic parameters for production traits of Chios sheep using a multitrait animal model. *Livest Prod Sci* 66(3):217-221.
- Ligda C, Papadopoulos T, Mavrogenis A, Georgoudis A (2003) Genetic parameters for test day milk traits and somatic cell counts in Chios dairy sheep. In: *Options Méditerranéennes: Série A. Séminaires Méditerranéens*; n. 55, "Breeding programmes for improving the quality and safety of products. New traits, tools, rules and organization", Zaragoza, CIHEAM: pp 55-59.
- Loukovitis D, Siasiou A, Mitsopoulos I, Lymberopoulos AG, Laga V, Chatziplis D (2016) Genetic diversity of Greek sheep breeds and transhumant populations utilizing microsatellite markers. *Small Rumin Res* 136:238-242.
- Lv FH, Agha S, Kantanen J, Colli L, Stucki S, Kijas JW, Joost S, Li MH, Ajmone-Marsan P (2014) Adaptations to climate-mediated selective pressures in sheep. *Mol Biol Evol* 31(12):3324-3343.
- Marnet PG, McKusick BC (2001) Regulation of milk ejection and milkability in small ruminants. *Livest Prod Sci* 70(1-2):125-133.
- Mastranestasis I, Ekateriniadou LV, Ligda C, Theodorou K (2015) Genetic diversity and structure of the Lesvos sheep breed. *Small Rumin Res* 130:54-59.
- Mastranestasis I, Kominakis A, Hager-Theodorides AL, Ekateriniadou LV, Ligda C, Theodorou K (2016) Associations between genetic polymorphisms and phenotypic traits in the Lesvos dairy sheep. *Small Rumin Res* 144:205-210.
- Mastranestasis I, Ligda C, Theodorou K, Ekateriniadou LV (2011) Genetic structure and diversity among three Greek sheep breeds using Random Amplified Polymorphic DNA-PCR. *J Hell Vet Med Soc* 62(4):301-313.
- Mavrogenis AP (1982) Environmental and genetic factors influenc-

- ing milk production and lamb output of Chios sheep. *Livest Prod Sci* 8(6):519-527.
- Mavrogenis AP, Papachristoforou C (2000) Genetic and phenotypic relationships between milk production and body weight in Chios sheep and Damascus goats. *Livest Prod Sci* 67(1-2):81-87.
- Mavrogenis AP, Papachristoforou C, Lysandrides P, Roushias A (1988) Environmental and genetic factors affecting udder characters and milk production in Chios sheep. *Genet Sel Evol* 20(4):477-488.
- Michailidou S, Tsangaris G, Fthenakis GC, Tzora A, Skoufos I, Karkabounas SC, Banos G, Argiriou A, Arsenos G (2018) Genomic diversity and population structure of three autochthonous Greek sheep breeds assessed with genome-wide DNA arrays. *Mol Genet Genomics* 293(3):753-768.
- Miltiadou D, Orford M, Symeou S, Banos G (2017) Short communication: Identification of variation in the ovine prolactin gene of Chios sheep with a cost-effective sequence-based typing assay. *J Dairy Sci* 100(2):1290-1294.
- Moatsou G, Govaris A (2011) White brined cheeses: A diachronic exploitation of small ruminants milk in Greece. *Small Rumin Res* 101(1-3):113-121.
- Moioli B, D'Andrea M, Pilla F (2007) Candidate genes affecting sheep and goat milk quality. *Small Rumin Res* 68:179-192.
- Mrode R, Tarekegn GM, Mwacharo JM, Djikeng A (2018) Invited review: Genomic selection for small ruminants in developed countries: How applicable for the rest of the world? *Animal* 12(7):1333-1340.
- Nikolaou M, Kominakis AP, Rogdakis E, Zampitis S (2004) Effect of mean and variance heterogeneity on genetic evaluations of Lesbos dairy sheep. *Livest Prod Sci* 88(1-2):107-115.
- Orford M, Hadjipavlou G, Tzamaloukas O, Chatziplis D, Koumas A, Mavrogenis A, Papachristoforou C, Miltiadou D (2012). A single nucleotide polymorphism in the acetyl-coenzyme A acyltransferase 2 (ACAA2) gene is associated with milk yield in Chios sheep. *J Dairy Sci* 95(6):3419-3427.
- Pariset L, Cuteri A, Ligda C, Ajmone-Marsan P, Valentini A, ECONOGENE Consortium (2009) Geographical patterning of sixteen goat breeds from Italy, Albania and Greece assessed by Single Nucleotide Polymorphisms. *BMC Ecol* 9:20.
- Pariset L, Mariotti M, Gargani M, Joost S, Negrini R, Perez T, Bruford M, Ajmone-Marsan P, Valentini A (2011) Genetic diversity of sheep breeds from Albania, Greece, and Italy assessed by mitochondrial DNA and nuclear polymorphisms (SNPs). *Sci World J* 11:1641-1659.
- Pryce JE, Daetwyler HD (2012) Designing dairy cattle breeding schemes under genomic selection: a review of international research. *Anim Prod Sci* 52(3):107-114.
- Psfidi A, Basdagianni Z, Dovas CI, Arsenos G, Sinapis E, Papanastassopoulou M, Banos G (2011) Characterization of the PRNP gene locus in Chios dairy sheep and its association with milk production and reproduction traits. *Anim Genet* 42(4):406-414.
- Pulina G, Milán MJ, Lavín MP, Theodoridis A, Morin E, Capote J, Thomas DL, Francesconi AHD, Caja G (2018) Invited review: Current production trends, farm structures, and economics of the dairy sheep and goat sectors. *J Dairy Sci*, 101(8):6715-6729.
- Raadsma HW, Dhungyel OP (2013) A review of footrot in sheep: New approaches for control of virulent footrot. *Livest Sci* 156(1-3):115-125.
- Ricci A, Allende A, Bolton D, Chemaly M, Davies R, Fernández Escámez PS, Gironés R, Herman L, Koutsoumanis K, Lindqvist R, Nørrung B, Robertson L, Ru G, Sanaa M, Skandamis P, Speybroeck N, Simmons M, Ter Kuile B, Threlfall J, Wahlström H, Acutis PL, Andreleotti O, Goldmann W, Langeveld J, Windig JJ, Ortiz Pelaez A, Snary E (2017) Genetic resistance to transmissible spongiform encephalopathies (TSE) in goats. *EFSA J* 15(8):4962.
- Rogdakis E, Kutsuli P, Surdis I, Panopulu E (1995) Untersuchungen zur genetischen Struktur der wichtigsten Schafrassen Griechenlands. *J Anim Breed Genet* 112(1-6):255-266.
- Rose I, Martin-Collado D, Orsini S, Zanolli R, Yañez-Ruiz D, Zaralis K, Arsenos G (2019) Using the multi-stakeholder approach to match potential innovations with challenges experienced by European sheep and goat farms. In: *Innovative Approaches and Applications for Sustainable Rural Development*, 8th International Conference, HAICTA 2017, Chania, Crete, Greece, September 21-24, 2017, Selected Papers, Springer Earth System Sciences: pp 119-130.
- Saridaki A, Antonakos G, Hager-Theodorides A, Zoidis E, Tsiamis G, Bourtzis K, Kominakis A (2017) Genomic markers and candidate genes associated with milk yield in the Frizarta dairy sheep. In: *Proceedings of the 6th Pan-Hellenic Congress in Technology of Animal Production*, Thessaloniki, Greece: pp 90-92.
- Saridaki A, Antonakos G, Hager-Theodorides A, Zoidis E, Tsiamis G, Bourtzis K, Kominakis A (2019) Combined haplotype blocks regression and multi-locus mixed model analysis reveals novel candidate genes associated with milk traits in dairy sheep. *Livest Sci* 220:8-16.
- Spetsariasis S, Koutsouli P, Theodorou G, Theodoropoulos G, Bizelis I (2016) Allelic polymorphism of Ovar-DRB1 exon2 gene and parasite resistance in two dairy sheep breeds. *HAF* 3(1):1-19.
- Theodoridis A, Ragkos A, Rose G, Roustemis D, Arsenos G. (2017) Defining the breeding goal for a sheep breed including production and functional traits using market data. *Animal* 12(7):1508-1515.
- Vacca GM, Stocco G, Dettori ML, Pira E, Bittante G, Pazzola M (2018) Milk yield, quality, and coagulation properties of 6 breeds of goats: Environmental and individual variability. *J Dairy Sci* 101(8):7236-7247.
- Volanis M, Kominakis A, Rogdakis E (2002) Genetic analysis of udder score and milk traits in test day records of Sfakia dairy ewes. *Arch Anim Breed* 45(1):69-77.
- Vouraki S, Gelasakis AI, Alexandri P, Boukouvala E, Ekateriniadou LV, Banos G, Arsenos G (2018) Genetic profile of scrapie codons 146, 211 and 222 in the PRNP gene locus in three breeds of dairy goats. *PLoS One* 13(6): e0198819.
- Vouraki S, Gelasakis AI, Ekateriniadou LV, Banos G, Arsenos G (2019) Impact of polymorphisms at the PRNP locus on the performance of dairy goats reared under low-input pastoral farming systems. *Small Rumin Res* 174:77-82.
- Warner R, Morris D, Dawson M (2006) PrP genotype progression in flocks participating in the National Scrapie Plan for Great Britain. *Vet Rec* 159(15):473-479.
- Zhang H, Wang Z, Wang S, Li H (2012) Progress of genome wide association study in domestic animals. *J Animal Sci Biotechnol* 3(1):26.