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Caprine Genome Analysis Reveals Valuable Insights into Selection of Enhanced Phenotypic Traits to Enable Improved Goat Breeding Programs

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ABSTRACT

A commonly farmed bovid ruminant, the goat is often kept in low input production systems, frequently at subsistence levels. Under such conditions, the adoption of effective commercial breeding programs is limited, let alone engaging more advanced technologies such as those needed for marker-assisted selection. Developments have been made in gene mapping of the sheep, another small ruminant, with the marker map now consisting of more than 1,200 microsatellites, and a virtual genome sequence together with a very dense single nucleotide polymorphism map are expected. Gene mapping in goats has advanced far less, with mainly some activity in dairy herds, but historically this was hampered greatly by the expense of genotyping for genomic selection in goat breeding. However, rapidly reducing genotyping costs coupled with a better understanding of how to maximize benefits of genomic selection mean adoption is poised to rise dramatically. Integration of genotypic information into commercial genetic evaluation and optimal selection strategies is an ongoing challenge that deserves more research investment and industry stakeholder engagement. This review of current efforts serves to evaluate how far the work on the caprine genome is progressing and to highlight areas for future consideration.

Keywords: *bovid, goat, genome, sequence, genotype, phenotype, selection, breeding*

INTRODUCTION

One of the so-called ‘grand challenges’ in modern biology is to understand the genetic basis of phenotypic diversity among breeds within a single species and between distinct but closely related species. Thousands of years of selective breeding of animals domesticated by humans has created a diversity of phenotypes among breeds that is matched only by that observed among mammalian species by natural selection (Wright, 2015). Domestic animals therefore constitute a unique resource for investigating the genetic basis of phenotypic variation. As the genome sequences of domestic animals become increasingly available identifying the mutations that underlie the transformation from a wild to a domestic species is becoming a realistically achievable and important goal (Boichard et al., 2016).

Sheep and goat breeds are selected worldwide for meat, wool and dairy production, and breeding objectives also include improving other functional phenotypic traits such as reproductive performance and disease resistance. The advent of next-generation sequencing technology in 2007 facilitated the subsequent *de novo* sequencing of sheep (Jiang et al., 2014) and goat genomes (Dong et al., 2013). In turn, this offered an opportunity to create high-density single nucleotide polymorphism (SNP) DNA microarrays. Genomic studies in small ruminants were first possible in 2009 with the development of the 50K ovine SNP chip (Kijas et al., 2009). The

OvineSNP50 BeadChip (Illumina Inc., San Diego, USA) is a 54K SNP DNA analysis kit that was developed as part of the International Sheep Genomics Consortium (ISGC; www.sheephapmap.org). Similarly, the International Goat Genome Consortium (IGGC; www.goatgenome.org) was formed in 2010 to promote international efforts toward the development of a 52K SNP chip for goats (Tosser-Klopp et al., 2014). The first version of a draft assembled goat genome sequence was released at the end of 2011 and a commercial caprine microarray (53.3K SNP chip) produced by Illumina is soon to be made available. This genomic variant detection technology is a prime example of high throughput DNA methods that have revolutionized access to genome-wide information as a tool for breeding sheep and goats with enhanced genetics (Stock & Reents, 2013). Genomic evaluation has thus far been performed for sheep bred for wool in New Zealand and Australia, for dairy sheep in France, and for goats in France and the UK.

Genomic selection is now a leading means by which to address the science of animal breeding. Its application could considerably increase the genetic gain in traits of interest. However, the success of its practical utilization depends on selection scheme characteristics, which must be examined carefully in each particular case (van der Werf, 2013). For dairy cattle, especially in Holsteins, genomic selection is already a reality. In other livestock species (beef cattle, small ruminants, monogastrics and fish) thus far the application of genomic selection has been largely experimental (Meuwissen et al., 2013; Stock & Reents, 2013). At present, the major limitation to its widespread implementation is the high genotyping costs compared to the low selection value of the candidate animals.

ECONOMIC CONTEXT FOR GOAT GENOMIC ANALYSIS

Goat genomics has evolved at a slow pace due to a lack of molecular tools and sufficient investment. While thousands and hundreds of quantitative trait loci (QTL) have been identified in cattle and sheep, respectively, only around 10 genome scans have been performed in goats to identify favourable traits including improved birth weight, rate of growth, wool fibre quality, and resistance to nematode infections (e.g. Esmailizadeh, 2014). In contrast, a considerable effort has been devoted to the characterization of candidate genes and their association with increased milk, meat and reproduction phenotypes (e.g. Martin et al., 2017). In this regard, causal mutations have been identified in the αS1-casein-encoding gene (*CSN1S1*) that has a strong effect on milk composition and the *PIS* locus that is linked to intersexuality and polledness. The development of massive parallel sequencing technologies has facilitated the construction of a reference caprine genome as well as enabling the expression of mRNAs and microRNAs to be monitored in a wide range of tissues and experimental conditions. In addition, the recent design of a 52K SNP chip (Tosser-Klopp et al., 2014) is expected to have a broad impact on the analysis of the genetic architecture of caprine traits of economic interest as well as in the study of the population structure of goats on a worldwide scale.

Globally, goats have a lower economic value than other farmed animals including cattle and pigs (Dubeuf et al., 2004). They are raised primarily in Asian (~500 million head) and African (~290 million head) countries, whilst their commercial relevance to agricultural production in Europe (~21 million head) and North America (~3 million head) is relatively modest (Aziz, 2010). This scenario may explain why the study of caprine genetics has lagged substantially behind those performed on bovines, porcines and even sheep, a closely related species. While the genomic analysis of quantitative traits has undergone substantial advances in the three other animal types mentioned, in several successful cases leading to the identification of causal mutations, to date a small number of studies has identified QTL in goats (Wientjes et al., 2015). However, there are compelling signs that this situation is set to change, chiefly because of the development of high throughput genotyping and sequencing tools that enable the generation of huge amounts of data with only a moderate investment of time and money.

GENOMICS OF REPRODUCTION IN GOATS

In aiming to understand how caprine reproduction is controlled, genomics plays an important role. Thus, Wang et al. (2010) cloned the cDNA encoding the *hnRNP K* gene in goats. Expression of this gene was detected in the uterus, ovary, mammary gland, kidney and muscle, but not in the heart, pituitary and thalamencephalon. This indicated that the *hnRNP K* gene is expressed mainly in the urogenital system and may influence the reproductive ability of goats. In Chinese goat breeds, an association between litter size and a wide array of polymorphisms mapping to the *BMP4* (Chu et al., 2011), *CART* (Wang et al., 2011), *GDF9* (Feng et al., 2011; An et al., 2013a), *GNRH1* (An et al., 2013a), *INHA* and *INHBA* (Hou et al., 2012), *KISS1* (Cao et al., 2010, 2011; An et al., 2013b), *KITLG* (An et al., 2012), *POUF1* (Feng et al., 2012), and *TSHB* (Huang et al., 2013) genes, among others, has been screened. However, the most significant finding in the field of caprine reproduction genetics has been the elucidation of the molecular basis of goat polled intersex syndrome (PIS). Bacterial artificial chromosome sequencing revealed that the causal mutation of caprine PIS is a 11.7 kb deletion affecting the expression of *PISRT1*, a long noncoding RNA, and *FOXL2*, a forkhead transcription factor involved in ovarian development and the maintenance of granulosa cell function (Pailhoux et al., 2001). The deleted region may contain a long-range regulatory element affecting the expression of these two loci that lie 20 kb (*PISRT1*) and 200-300 kb (*FOXL2*) apart from it

GENOMICS OF DAIRY CHARACTERISTICS IN GOATS

New molecular tools, such as those offered by genomics and proteomics, are being harnessed in milk production by goats. Zidi et al. (2010) studied the relationship between the stearoyl-CoA desaturase 1-encoding gene (*SCD1*) and milk fatty acid composition in Murciano-Granadina goats, observing an association between the two, which may be explained by the global effects that stearoyl-CoA desaturase 1 exerts on mammary gland lipid metabolism through the down-modulation of key transcription factors.

Safayi et al. (2010a) examined with genomic technology mammary remodeling in primiparous and multiparous dairy goats during lactation. Differences in genes between primiparous and multiparous goats were observed, but it was not possible to identify any specific genomic factor(s) that could account for the variation between primiparous and multiparous goats with respect to mammary gland development and mammary epithelial cell type. The same research group investigated the effect of continuous lactation on mammary remodeling during late gestation and lactation, reporting that the continuously lactating gland resembles a normally mammary gland in an advanced stage of lactation (Safayi et al. 2010b). Montaldo et al. (2010) concluded that the presence of unfavourable genetic relationships between milk yield and kidding interval indicates a need to include reproductive performance as a selection criterion in the breeding of dairy goats.

Although dairy goats are a potential source of animal protein the increased farming of which can help to address the new world challenges (Norris et al., 2011), milk and dairy products are the principal source of total fat and saturated fatty acids (FA) in many European countries (Caroli et al., 2009). Epidemiological studies have shown that saturated and trans FA are the main risk factors for coronary heart disease (Funaki, 2009; Kennedy et al., 2009). On the contrary, polyunsaturated FA, and in particular linoleic acid (C18:2c9c12) and its conjugated acids, play a role in the modulation of plasma lipid concentrations, showing anti-carcinogenic, anti-inflammatory and immunological effects (Haug et al., 2007). Since drastically reducing the consumption of dairy-based foods is not a practicable option, a viable alternative is to act on the composition of the FA profile. The biosynthesis of milk fat is a complicated process regulated by many genes belonging to several metabolic pathways (Bionaz & Loor, 2008; Chessa et al., 2009). Especially in cattle, candidate gene approaches, quantitative trait loci and genome-wide association studies have attempted to identify regions and polymorphisms associated with milk fat composition (Schennink et al., 2009; Stoop et al., 2009; Bouwman et al., 2011, 2012), but very few markers were identified. A preliminary investigation was conducted to verify if, using genomic data, the canonical discriminant analysis could be adopted to distinguish goats producing different FA levels. The approach had been applied successfully already for bovine breed assignment and traceability purposes (Dimauro et al., 2013). Chessa et al. (2014) reported that canonical discriminant analysis worked well for saturated FA. The separation was particularly good for SFA, whereas it was less efficient for capric acid (C10:0) and stearic acid (C18:0). Also, all examined individuals were correctly assigned to the three categories (high, medium or low content) except for two: for the capric acid (C10:0) and stearic acid (C18:0) an individual with a low and a high production level, respectively, were assigned to medium level production.

GENOMICS OF MORPHOLOGICAL CHARACTERISTICS IN GOATS

The genetic analysis of production and disease-related traits in goats has been rarely performed at a genome-wide scale (Manunza et al., 2016). This is largely due to a lack of well-established microsatellite panels covering the whole genome, which has greatly hindered the implementation of genome scans aimed at detecting QTL (Amills, 2014). The limited extent of the investigation of growth and conformation includes the identification of QTL for: head length (1, 4 chromosomes), body length (8 chromosomes), chest depth (2 chromosomes) and circumference (9 chromosomes) in Angora goats (Marrube et al., 2007); body weight (chromosomes 4, 8, 17, 27) in the Angora breed (Visser et al., 2013); and weaning weight (chromosomes 16, 19), body weight and average daily gain (chromosomes 1, 2, 5) in Rayini goats (Abadi et al., 2009). Belonging to the transforming growth factor-β superfamily myostatin (MSTN) is recognized to repress muscular growth (Bellinge et al., 2005). In cattle, mutations inactivating *MSTN* expression lead to a muscular hypertrophy phenotype known as 'double muscling' (Grobet et al., 1997). In goats, variation at the *MSTN* gene has been associated with fluctuations in body weight, length and height (Zhang et al., 2012). In the case of *GH* and *MSTN*, genetic variability may affect growth rate because both molecules are considered to play a key role in this physiological process; however, causal mutations have yet to be identified. For other loci, this relationship is less obvious; for example, the polymorphism of the diacylglycerolacyltransferase 2 (*DGAT2*) gene that regulates triacylglycerol synthesis has been associated with withers height in Chinese goats without mechanistic explanation being provided (Fang et al., 2012). Cai et al. (2014) reported that polymorphism of the *GF11B* gene revealed significant differences among genotypes for three indigenous Chinese goat breeds.

In the absence of positional information, investigation of the genetic factors that determine phenotypic variation of economically important traits has been based on physiological candidate gene approaches. It is important to note, however, that this strategy has important limitations. The involvement of one gene in a metabolic pathway does not necessarily imply that it contains variation affecting the trait under study (Georges, 2007). A common pitfall of association studies is to present significance as raw *P* values, instead of correcting for multiple testing. Other extensive flaws are to report associations without proposing any biological mechanism to support them or to infer that a trait is associated with a given genotype on the basis of divergent allelic frequencies among populations with extreme phenotypes (Glazier et al., 2002). Erroneous experimental practices can lead to the publication of spurious associations that do not have any biological basis. The recent opportunity to carry out genome-wide association studies in goats is expected to alleviate this concern by making possible the generation of positional information at an affordable cost and relatively high resolution.

Candidate Genes for Coat Colour

Goats display a wide array of pigmentation patterns, even at the intra-breed level, that contrast strongly with the monochromous brown colour of the wild bezoar ibex from which the domestic goat is descended. The development of multiple coat colours is probably the result of human artificial selection of certain pigmentation phenotypes because of cultural, religious and/or breeding practices (Nicoloso et al., 2012). Our understanding of the genetic basis of coat colour in goats is more limited than that of other species, such as cattle and sheep, for which causal mutations with well-established effects have been identified (Sponenberg & LaMarsh, 1996). Pigmentation is a polygenic trait influenced by the combined action of many genes that often interact in a tissue-specific epistatic mode (Sturm et al., 2001). Although the list of candidate genes for pigmentation patterns is very large, there are certain loci that appear to play a prominent and consistent role across species. An example of this is *MC1R* that encodes the G protein-coupled melanocortin 1 receptor with 7 transmembrane-spanning domains. The activity of this protein determines if either eumelanin (black) or pheomelanin (red/yellow) will be synthesized within the melanocyte (Schaffer & Bolognia, 2001), hence influencing coat colour.

CHALLENGES TO GENOMIC SELECTION IN GOATS

Specific issues of genomic selection for domesticated bovid species include small reference population sizes, low linkage disequilibrium, multi-breed evaluations, lack of phenotype recording in many countries, and marginal cost-benefits. The data recording scheme for goats, in particular, is limited and therefore the genetic gain using current genomic selection strategies may be less favourable than that obtained through traditional selection methods (van der Werf, 2009). Genomic selection could offer new opportunities for achieving the genetic enhancement of farmed small ruminants if an adapted version of the dairy cattle model is applied (Taylor-Robinson et al., 2014). However, this concept may be undermined if commercial interests continue to lead sheep and goats towards a closed nucleus breeding programs of pyramidal structure (Banks & van der Werf, 2009). An experimental nucleus flock has been created in Australia to obtain data on new traits for genome-wide association studies (van der Werf et al., 2010), while New Zealand has implemented a genomic evaluation for sheep meat traits, although the practical implementation is still restricted. Nevertheless, these ovine trials are the forerunners for similar studies in goats.

The historically high cost of genotyping has been a principal limitation of the application of genomic selection in most breeding domestic animal programs. The adoption of low-density SNP panels represents an interesting strategy for reducing the sequencing cost involved in selecting candidate traits. Habier et al. (2009) and Weigel et al. (2009; 2010) confirmed small losses in accuracy on the genomic predictions of selection candidates genotyped by low-density SNP panels compared to when high-density SNP panels are used. Further to this, recent increased sophistication of assembly algorithms has facilitated a near-finished, accurate reference genome for the domestic goat to be published (Bickhart et al., 2017), the most continuous de novo mammalian assembly currently known. This exciting development provides a new standard reference for caprine genetics. This valuable asset should enable easier identification of adaptive variants in sequence data from descendent breeds and thereby facilitate genomic selection of productive traits.

CONCLUSION

Genomic selection is acknowledged as one of the fundamental challenges in farmed animal breeding. Its judicious application could considerably increase the genetic gain in traits of interest. Still, the success of its practical implementation depends on the selection scheme characteristics, so these should be examined in each particular case. In dairy cattle, especially in Holsteins, genomic selection is a now a routine occurrence. Yet, in other livestock species (beef cattle, small ruminants, monogastrics and fish) genomic selection lags behind at the experimental research stage. Until recently, the main limitation to its adoption for these farmed animals – including sheep and goats – has been the high cost of genotyping compared to the low selection value of the candidate. Nowadays, the use of SNP chips of low density to make genomic selection applications economically feasible in breeding programs is under development. Hence, in order to achieve genetic enhancement within a goat herd the benefits of bringing genomic selection to identify novel traits remains a distinct possibility. While it is evident that genomic selection offers great potential, a suitable genotyping strategy and recording system for each case is required in order to maximize commercial exploitation.

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