



Genetic improvement of reproductive efficiency of sheep and goats[☆]

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ABSTRACT

Sheep and goats are produced in a wide range of production systems and climatic conditions and possess great genetic diversity in reproductive potentials. Mean litter sizes range from near 1 to 3 or more, and patterns of seasonal reproduction are often strongly synchronised to local conditions. Thus, optimisation, rather than maximisation, of reproductive potentials is required, and optimum reproductive rates are often well below those which could be achieved. However, changing employment patterns, increasing urbanisation, and emergence of new markets provide corresponding opportunities for sustainable intensification of small ruminant production, potentially requiring enhancements in reproductive potentials. Heritabilities for most reproductive traits are less than those for many other traits, usually ranging from 0.05 to 0.15, and opportunities for within-breed selection are therefore limited. Substantial changes in litter size or major changes in seasonal breeding patterns are thus best achieved by crossing of divergent breeds to rapidly reset genetic potentials for these traits, followed by within-breed selection to optimise reproductive potentials. Various mutations influencing ovulation rate and litter size in sheep provide additional opportunities to rapidly adjust genetic potentials, but require careful breeding management. Comparable major genes have not yet been found in goats or for traits associated with breeding season.

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1. Introduction

Sheep and goats are major contributors to global livestock production in essentially all agro-ecological regions. Genetic variation in reproductive potentials among populations is large and genetic variation within populations is commonly adequate to support reasonable rates of genetic improvement, even though reproductive potentials may be strongly canalised to synchronise breeding season, ovulation rate and age at first parity with the production environment and associated feed and management resources.

In many parts of the world, sheep and goats are produced under extensive, arid or semi-arid conditions, with little or no supplemental feeding. Thus, breeding seasons have evolved to synchronise parturition with periods of favourable forage availability and twinning is often rare. However, global demand for sustainable intensification of livestock production has led to opportunities to increase production, even if incremental increases in inputs of feed, labour and management are required. These changes in production conditions are commonly associated with optimal increases of reproductive performance, which leads us to ask how best to enhance reproductive potentials without unduly compromising associated fitness traits. Thus, establishment of optimal breeding programmes for reproductive capacity involves appropriate use of genetic variation among and within breeds, as well as judicious use of major genes (primarily for ovulation rate) and is an appropriate strategy in both developing countries and more highly developed market economies.

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This paper will first review genetic mechanisms controlling reproductive traits, with primary emphasis on ovulation rates and seasonal breeding, as these represent two particularly critical elements of the reproductive biology of small ruminants. The paper will then address the design and implementation of breeding and selection programmes to increase reproductive performance in both natural and accelerated lambing systems. Most of the material in this paper comes from the more voluminous and more thoroughly reviewed literature on sheep, with the expectation, unless specifically noted, of similar results for goats.

2. Genetic mechanisms controlling reproductive traits

2.1. Ovulation rate and litter size

Breed differ by up to three-fold (from near one to in excess of three) in mean ovulation rates of adult ewes and does, providing opportunity to enhance ovulation rates in favourable production environments or to control ovulation rates to production resources in more limiting environments. Genetic control of ovulation rates in many prolific breeds is polygenic, involving large numbers of genes with small individual effects (Fahmy, 1996). However, several important mutations in genes associated with ovarian function exist in sheep, with effects on ovulation rates in homozygotes of two or more ova relative to wild type ewes. Genes expressing these mutations include bone morphogenic protein receptor-1B (*BMPR-1B*, originally discovered in Booroola Merino sheep and designated *FecB*), bone morphogenic protein 15 (*BMP1*, which is X-linked, originally discovered in Romney sheep, designated as *FecX* and results in infertility in homozygotes) and growth and differentiation factor 9 (*GDF9*, an autosomal mutation originally discovered in Cambridge and Belclair sheep and associated with infertility in homozygotes). History, mechanisms of action and strategies for use of major genes affecting ovulation rates were reviewed by Davis (2005), McNatty et al. (2005) and Notter (2008). The *FecB* mutation is widespread among, and apparently exclusive to, Australasian breeds, whereas mutations in *FecX* and *GDF9* appear in breeds originating in Europe (Davis et al., 2006).

Crossbreeding with prolific breeds or introgression of major genes for ovulation rate is recommended if a substantial increase in litter size is desired. Heritabilities are approximately 0.15 for ovulation rate, 0.13 for litter size and 0.05 for number of lambs weaned (Safari et al., 2005). These values are low and, even though substantial phenotypic variance are present for these traits, the potential increase in litter size from selection seldom exceeds 0.02 lambs per year and a value of 0.01 lambs per year with multiple-trait selection is probably more realistic. Thus, within-breed selection for litter size is recommended as a primary genetic improvement strategy only if environmental adaptation is long-established and remains critical or if an increase in litter size of 0.10 lambs or less is adequate to optimise production.

Crossing with prolific breeds can generate new breeds with modest increases in prolificacy and prolific breeds can

be found with adaptation to a wide range of environmental conditions, including damp temperate (Finnish Landrace, Romanov), warm arid (D'Man) and humid subtropical (Barbados Blackbelly). With polygenic control of prolificacy, anticipated increases in ovulation rate and litter size can be titrated to desired levels by varying the contribution of a prolific breed to descendant populations. Dickerson (1977) postulated that each 1% increase in Finnish Landrace breeding in crosses with North American breeds would result in an increase of 1% in mean litter size. Thus, the Polypay breed was created in the USA with 25% Finnish Landrace breeding and a mean litter size in spring-lambing adult ewes of 2.1–2.3 lambs, whilst the Rideau Arcott was developed in Canada with approximately 40% Finnish Landrace breeding (Fahmy and Mason, 1996).

Use of major genes to increase prolificacy involves unique opportunities and challenges. Several ovulation rate mutations increase litter size by 0.5–1.0 lambs in heterozygotes and can be introgressed into any breed by repeated backcrossing and DNA testing, resulting in enhanced ovulation rates in an otherwise unmodified genetic background. Use of mutations in *BMP15* (*FecX*) or *GDF9* is especially challenging, because of infertility in homozygous ewes and usually involves mating carrier males and females with DNA testing of offspring to identify the desired heterozygous replacement females. Thus, individual-animal identification (at least with regard to genotype), regular DNA testing and control of mating are required and may preclude effective use of these genes in extensive or poorly controlled breeding programme.

Individuals that carry two copies of the *FecB* allele are fertile, but increases in ovulation rates may exceed two, with corresponding increases in litter size greater than one. High frequencies of triplet or greater numbers of births in homozygous ewes may result in excessive neonatal deaths relative to non-carrier ewes and mandate specialised breeding programmes to generate heterozygous *FecB* ewes and exclude homozygous ewes from the breeding flock. The suitability of heterozygous ewes depends on the prolificacy of the recipient breeds. Thus, in the USA, prolificacy of adult ewes of common commercial breeds ranges from 1.75 to 1.95. Insertion of a single copy of *FecB* into this genetic background increases litter size by approximately one lamb, generally with unacceptable increases in frequency of large (>3) litters and with little or no increase in numbers of lambs weaned (Notter et al., 2009). In contrast, however, introgression of *FecB* into intensively managed commercial dairy flocks of Awassi and Assaf (an Awassi × East Friesian composite) ewes in Israel with baseline litter size of approximately 1.3 and 1.65, respectively, increased litter size to acceptable levels of 1.90 and 2.40, respectively, in heterozygotes and 1.92 and 2.55, respectively, in homozygotes (Gootwine, 2009).

Use of *FecB* in low-input smallholder flocks in India permitted a rapid increase in prolificacy in lowly prolific Decani ewes (mean litter size of 1.03 (Nimbkar et al., 2009). In that study, heterozygous ewes had average litter size of approximately 1.5 live lambs at birth and average litter size for a small number of homozygous ewes was 1.65. When coupled with outreach and training activities to achieve incremental improvements in management and

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