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Evidence of major gene(s) affecting milk traits in the Chios sheep breed

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ABSTRACT

This study investigates the mode of inheritance and estimates the genetic parameters of milk yield, milk fat content, and litter weight at birth in Chios sheep breed. A complex pedigree and repeated records for milk and fat content as well as litter weight from two distinct and unrelated populations, spanning over 20 and 31 years, were used for the detection of a major gene for milk yield in the Chios breed. The data originated from a closed nucleus in Northern Greece (6021 repeated records) and from a closed nucleus in Cyprus (6965 repeated records). The genetic parameters were estimated using both a polygenic model with maximum likelihood methodology and a mixed inheritance model (polygenes + major gene), using Bayesian segregation analysis. Segregation analysis results support the presence of a major gene for milk yield segregating in both populations. The mixed inheritance model for milk yield appears to be the most suitable model. The estimated additive effect of the putative major gene was 11% and 10.5% of the total additive genetic variance in the Cypriot and Greek populations, respectively, while the estimated dominance effect was negative in both populations. Although there are some indications for a major gene affecting fat content in Chios breed, there is no evidence for the presence of a major gene affecting litter weight at birth in either population.

1. Introduction

Segregation analysis has been used in several studies investigating major genes affecting production and reproduction traits in animals both before and after the introduction of molecular genetic technologies into animal production. Using such methods, several major genes have been reported in various species (e.g. pigs: Janss et al., 1995; Kadarmideen and Janss, 2005, dairy cattle: Pan et al., 2001; Ilahi and Kadarmideen, 2004; Karacaören et al., 2006, chickens: Szydłowski and Szwaczkowski, 2001 and fish (rainbow trout): Vallejo et al., 2009, 2010).

Particularly for sheep, segregation analysis has been successfully used for the detection of major genes affecting prolificacy. Many prolific breeds, including the Greek Chios breed population under study (Chatziplis et al., 2000), are considered to follow a monogenic inheritance pattern in reproductive traits such as litter size or ovulation rate (Fahmy, 1996). In most of these prolific sheep breeds, there is evidence of major genes segregating, and in some of these breeds, the genes responsible for increased prolificacy have been identified (Davis et al., 2002; Davis, 2005). In addition, ovine major genes affecting wool yield and quality have also been suggested (Purvis and Franklin, 2005).

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In relation to milk traits, segregation analysis studies have been carried out for the detection of major genes in cattle and goats (Pan et al., 2001; Ilahi et al., 2000; Ilahi and Kadarmideen, 2004). Karacaören et al. (2006) have suggested the existence of a major gene affecting milk yield in cattle, using segregation analysis. In the case of dairy sheep, although several genome studies support the existence of significant or suggestive quantitative trait loci (QTL) affecting ovine milk yield or quality in different sheep breeds (review: Barillet et al., 2005; Sarda × Lacaune: Carta et al., 2002, 2009; Churra: Gutiérrez-Gil et al., 2009; ovine candidate genes: Moioli et al., 2007), there is no segregation analysis study suggesting the existence of a major gene for ovine milk yield. Recently, Ilahi and Othmane (2011) proposed the polygenic inheritance mode for milk yield in the Churra dairy sheep breed, since by using Bayesian segregation analysis on milk yield data, the authors did not detect any major gene for milk yield.

The Chios breed is the main breed of sheep production in Cyprus and one of the most important breeds in Greece. It is considered to be among the most prolific and productive dairy sheep breeds in the world (Mavrogenis, 1985; Hatziminaoglou et al., 1996). Although segregation analysis could only be indicative in the detection of major genes, it can be used effectively in preliminary studies. Such methods could provide a valuable tool for the application of selective genotyping in genome association studies by reducing the cost of such experiments. Indeed, such analyses had been used prior to the detection of the booroola fecundity gene at the genomic and molecular levels (Montgomery et al., 1993).

Given the limited number of studies testing the existence of ovine major genes affecting milk yield and other production traits, this study aims to perform an initial data analysis concerning the mode of inheritance of milk yield, fat content and litter weight at birth as well as to estimate the genetic parameters for these traits in Chios sheep. Furthermore, this study aims to utilize the *a posteriori* results of the segregation analysis, in order to economically optimize our molecular genetic resources in a future association study using molecular genetic markers.

2. Materials and methods

2.1. Data

Pedigree and milk yield records from two nucleus unrelated populations of Chios sheep, spanning over 20 years, have been used. The data originated from: (a) a closed nucleus flock kept at the Agricultural Research Institute of Cyprus (Nicosia 35°N 33°E) and (b) a closed nucleus flock kept at the Agricultural Research Station of Greece (Chalkidiki, National Agricultural Research Foundation of Greece, 40°N 23°E).

In the Cypriot nucleus flock during a 31-year period, 794 sires were mated to 2310 dams producing 6969 lambings from January to December every year. In total, 6965 repeated milk, fat content and litter weight at birth records were available. The milk yield records used in this analysis, for the Cypriot sheep population, were corrected for fat content at 4% as in previous studies (Mavrogenis and Papachristoforou, 1988).

In the Greek nucleus flock, during a 20-year period, 715 sires were mated to 3746 dams producing 6032 lambings from October to March every year. In total, 5636 repeated milk yield records were available. No fat correction was applied on the milk yield since there were no fat-content records.

Table 1
Description of different data sets and pedigrees for the Cypriot and Greek populations.

Effects	Number of levels	
	Cypriot population	Greek population
Year	31	20
Month of lambing	4	4
Parity (lactation number)	9	9
Permanent environmental effects	2473	2416
Days in milk (lactation length levels)	307	278
Average lactation length in days	159	181
Animals in the pedigree	10,087	6777

Special consideration has been taken in the matings of both populations to maintain minimum inbreeding. In the Cypriot nucleus flock, individual supervised matings were performed, while for the genetic management and control of inbreeding of the Greek population, the rotational mating system is used, in which the flock is divided into 10 families. The above considerations to maintain low inbreeding seem to be sufficient, since in a recent study of the Cypriot population, the rate of inbreeding after 42 years of selection was estimated to be lower than 0.3% per generation with a mean inbreeding coefficient of 5% for the 19 generations tested (Brown et al., unpublished data).

2.2. Genetic parameter estimation under polygenic model using maximum likelihood

Genetic parameters were estimated using a univariate individual animal model. Year, month of lambing and parity number were used as fixed effects in the analysis and, as random effects, the additive genetic, the permanent environmental and the residual effects. Moreover, for the traits of milk yield and fat content, a regression of milking days on milk yield and fat content was fitted. The V.C.E. 4.2 software (Groeneveld, 1994) was used for the estimation of the (co)variances and the genetic parameters.

The description of the different data sets and pedigrees for the two populations are given in Table 1.

2.3. Mixed inheritance model using Bayesian segregation analysis

The milk yield from the Greek and Cypriot nucleus populations and the fat content and litter weight at birth records from the Cypriot nucleus population were analyzed using a Bayesian mixed inheritance model (MaGGic 4.0: Janss, 1998). Fixed (year, month of lambing, parity), and random effects (polygenic effect) and a single major gene as an autosomal diallelic locus with an additive (a) and a dominant effect (d) were modeled. Moreover, in order to take into account environmental covariances between repeated measures and the length of the lactation as a covariate, the individual identification and the days in milk of each animal's lactation were fitted as random effects (MaGGic 4.0: Janss, 1998). The major gene was modeled as an autosomal biallelic (A and a) locus with Mendelian transmission probabilities. The genotypic value for animals with genotype AA at the putative major locus is a, −a for aa animals and d for Aa animals. The frequency of the A allele will be referred to as '*p*'. The following mixed inheritance model was used:

$$y = X\beta + Zu + Qpe + Gdm + ZWm + e \qquad (1)$$

where y is the vector of observations, β is a vector of non-genetic fixed effects including: year, season of lambing, lactation number (parity), u is a random vector of individual polygenic effects, pe is a random vector of permanent environmental effects, dm is a random vector of lactation length (days in milk), W is a design matrix that contains the genotype of each individual (i.e. AA, Aa, aa), m is the vector of genotype means (i.e. −a, d, a), e is a random vector of residual effects, and X, Z, Q and G are incidence matrices relating the observations to their respective effects. In the term modeling the single gene, both W and m are unknown and have to be estimated from the data with the use of segregation analysis.

Distributional assumptions for polygenic, permanent environmental effects, residual variances as well as prior distributions for genetic and non-genetic effects, variance components and allelic frequencies were as Janss et al. (1995).