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Inbreeding and its impact on the prolific Polish Olkuska sheep population

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ABSTRACT

The aim of this study was to assess the level of genetic variability in the Olkuska sheep population and evaluate inbreeding effects on birth weight, weaning weight (at 56 days of age), lamb survival up to 56 days and the litter size of ewes. Pedigree information over a 36 year period of Olkuska population (from 1976 to 2012) was used in this study. A small number of important ancestors, with only four individuals explaining over 50% of the total genetic variation of the population resulted in high levels of inbreeding, with mean values exceeding 10% for lambs born from 2007 till 2012. Animal model was used to test the effects of inbreeding depression on lamb weight and survival. Significant inbreeding depression was found for birth weight ($P < 0.01$), and for body weight at the age of 8 weeks, −0.0071 kg and −0.0325 kg per 1% increase in inbreeding respectively. The effect of inbreeding on lamb survival was statistically significant, but very small. No significant impact of inbreeding on litter size was observed, due to the segregation of the major gene affecting fecundity. The main factors determining lamb weight and survival were its gender and type of birth.

1. Introduction

In the last few decades, substantial efforts were made to prevent rare breeds from going extinct, but still much work remains (FAO, 2015). One of the main factors that decrease the chance of breed survival, is the scarce number of animals and small effective population size (N_e). Under such conditions, matings of close relatives are hard to avoid, what subsequently leads to an increase in inbreeding and the loss of genetic variability. Lack of genetic variation is disadvantageous, as it limits selection response and adaptation ability of the breed to future opportunities and conditions (Van Wyk et al., 2009). Increase in inbreeding can result also in inbreeding depression which has been shown in many sheep populations (Lamberson and Thomas, 1984; Ercanbrack and Knight, 1991; Analla et al., 1998; Van Wyk et al., 2009; Selvaggi et al., 2010).

In Poland, due to the lack of profitability of sheep production, a lot of breeds were facing the risk of extinction, especially in the 1990s and the beginning of the Twenty-first Century. Currently, due to successful *in-situ* conservation programmes, the population sizes of many rare breeds are continuously growing, but their genetic baseline is often very limited. An example of this is the Olkuska sheep population, with no more than 100 ewes left in the 1990s, compared to 10,000 heads in 1950s and 1960s. The breed is an important heritage resource particularly in its region of origin, Olkusz. Here they were traditionally kept on small private farms, with few animals used as multipurpose sheep to meet household needs. High litter size and good maternal abilities make this breed a very valuable genetic resource. High reproductive performance of Olkuska ewes, with prolificacy exceeding 200%, is determined by a single mutation of the BMP15 gene, localized on the X chromosome with a major effect on the ovulation rate (Demars et al., 2013). Due to its special characteristics, the breed is an excellent biological resource for the discovery of genes and regulatory mechanisms that underpin improved reproductive success (Juengel et al., 2013).

Due to a small population size and unequal contribution of a limited number of sires, the inbreeding in Olkuska sheep population currently exceeds 10% and is expected to increase at a high rate in the future (Drobik and Martyniuk, 2014a). High coancestry levels within the large number of small flocks showed that inbreeding can reach very high levels and needs to be taken into account in breed conservation programmes. The purpose of this study was to access the genetic variability level in the Olkuska sheep population and to evaluate inbreeding depression on lamb weight, survival and litter size.

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2. Material and methods

2.1. Material

Data for this study were obtained from number of different sources: private breeders, the National Research Institute of Animal Production, and regional branches of the Polish Union of Sheep Farmers. Also included in the study were a historical data collected over the years by the Department of Genetics and Animal Breeding, Warsaw University of Life Sciences. Available pedigrees, which comprised of 11344 records for the period 1976–2012 were used to calculate inbreeding coefficients of individual animals. All records contained individual, dam and sire identification codes, sex, birth date, and flock of origin, as well as the current (or last known) owner of each animal.

To minimize discrepancies in pedigree and ensure higher homogenousity of data, only lambs born after 1999, with the equivalent of a minimum of 5 complete generations, were included in the analysis of inbreeding depression. In total, 9957 lambs fulfilled this condition (Fig. 1). A database, contained data for 1693 ewes and their 10676 lambings taking place in years 1996–2012. A total of 860 ewes, with a minimum number of 3 litters were selected for analysis using chi-square test. Ewes were assigned to different classes based on their inbreeding coefficient and mean prolificacy. Ewes with the equivalent of complete generations equal or greater than 5 were selected for animal model based analysis.

2.2. Pedigree analysis

Pedigree completeness, inbreeding coefficients, effective population size and analysis of founders was performed using Endog 4.8 software (Gutiérrez and Goyache, 2005).

Pedigree completeness was estimated on the basis of equivalent of complete generations, the number of fully traced generations and the maximum number of generations traced (Maignel et al., 1996). The equivalent of complete generations was calculated as $\sum(½)^n$ for all known ancestors of the individual, where n is the number of generations separating individual from its ancestor. The number of fully traced generations is the number of generations (g) separating the offspring from the furthest generation in which 2^g of ancestors for an individual is known. The maximum number of generations traced, is the number of generations separating an individual from its furthest ancestors.

Inbreeding can be defined as the probability that two alleles at any locus randomly sampled among all loci in the genome are identical by descent (Malécot, 1948 Wright, 1922) and in this study was calculated using the algorithm proposed by Meuwissen and Luo (1992). Trends in inbreeding were assessed by the mean individual inbreeding coefficients in each lambing season.

Due to a dispersed population and substantial differences in contribution of individual parents to the next generation, the effective population size was calculated. The effective population size (N_e) is the number of breeding animals that would lead to the observed increase in inbreeding if they contributed equally to the next generation (reference). Effective population size was calculated based on increase in inbreeding per generation (ΔF) according to the following Formula (1):

$$\Delta F = \frac{F_t - F_{t-1}}{1 - F_{t-1}} = \frac{1}{2N_e} \tag{1}$$

where F_t is the inbreeding coefficient in t generation.

An analysis of the contributions of founders and ancestors to current Olkuska population was conducted based on all pedigrees available in the database. A founder is an individual with both parents unknown, while ancestors were identified based on their genetic contributions to the population; marginal genetics contributions of all ancestors should sum to one (Boichard et al., 1997). The ancestors contributing the most were chosen in iterative process, where at round n, the marginal genetic contribution (p_k), is defined as the genetic contribution of ancestor k, not yet explained by the n-1 already selected ancestors. The effective number of ancestors was than calculated as (2):

$$f_{a=}\frac{1}{\sum_{k=1}^{f} p_k^2} \tag{2}$$

where p_k is the marginal probability of gene origin from k ancestor. The effective number of founders was calculated similarly, but probabilities of gene origin form k founder (q_k) were used instead of p_k. The effective number of ancestors (f_a) is always less than the f_e and the comparison of both numbers can be used to find the bottlenecks that have occurred in the population; the greater the f_e/f_a ratio, the stronger the bottlenecks.

2.3. Statistical analysis

The effects of inbreeding coefficient and other factors on lamb weight and survival were analysed using generalized linear mixed models implemented in MCMCglm package (Hadfield, 2010) in R environment version 3.0.2 (R Development Core Team, 2008). The analysed traits included lamb weight at birth, lamb weight at 56 day (8 weeks), lamb survival over the birth and up to 56 day of life, and litter size of ewes. An linear model was used for lamb body weight and litter size, while lamb survival was fitted with the logistic model.

Models for body weight and litter size were run for 1,000,000 iterations with a thinning parameter of 100. The first 50,000 iterations were removed as burn in period. A model for lamb survival was run for 2,000,000 iterations with a thinning interval of 200 to improve mixing of mcmc chains. Non informative priors were used for body weight at birth and litter size with V = 1e−6 and nu = −2, so the marginal distribution of the variance component was equivalent to the REML estimator. Flat priors were used for logistic model with variance for residuals fixed at 1.

The animal model was used to assess the impact of inbreeding on lamb and ewe traits and can be represented in matrix notation as (3):

$$y = Xb + Za + e \tag{3}$$

where y is a vector of observation, b is a vector of fixed effects, a is a vector of random effects, e is a vector of residual effects and X and Z are known incidence matrices.

The flock of the lamb origin was fitted as a random effect. The reproduction season was not significant as the fixed effect and was correlated with inbreeding coefficient, what decreased model performance. Therefore, it was removed from the models. Fixed effects in the models included: sex (with female as reference level), type of birth (in 5 classes: 1, . . ., 4, 5 and more), age of dam (in 7 classes: 1, . . ., 6, 7 and older), the inbreeding coefficient of lambs, and the maternal inbreeding coefficient. Categorical variables like sex, age of dam and type of birth were included in the model as dummy variables by transforming categorical variable with *k* levels into k-1 variables each with two levels (0 and 1). A lme4 package (Bates et al., 2014) and a maximum likelihood (ML) method using ANOVA was used to test the significance of fixed and random effects, and to choose the best model. Akaike's Information Criterion (AIC) was used to compare different models. To access its effects, individual inbreeding coefficient and inbreeding coefficient of dams were included in all models, regardless of their significance. Inspection of residuals for models with a normal error distribution was used to check assumptions of normality and homoscedasticity. Variance inflation factor (VIF) and simple linear regression models were used