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ORIGINAL SCIENTIFIC PAPER

Partition of genetic trend for milk yield by gender and flock in Pag sheep

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Abstract

Breeding programs for dairy sheep seek to improve a set of economically and/or functionally important traits. Their success is measured by genetic trends, and their partitioning allows the contributions of different selection pathways to be quantified. This study aimed to estimate the genetic trend for daily milk yield in Pag sheep and to partition it by gender and flock. The estimated genetic gain was ~1 kg per production year (120 days). Females contributed to selection gain much more than males, while the within-flock contribution varied over the years, making it difficult to rank their contribution in the overall gain. The results imply that rams should be selected more carefully, preferably based on estimated breeding values.

Key words: Pag sheep, genetic trend, partition, gender, flock

Introduction

Pag sheep is a Croatian autochthonous breed with great traditional, cultural, ecological, and economical importance. The high purchase prices of ovine milk (~1.7 €/L) and ovine cheese (~30 €/kg) on the island of Pag encourage breeders to raise this breed and also to produce more milk per ewe. Some breeders made significant improvements in dairy sheep management (housing, nutrition, machine milking), and further improvements could be obtained by intermating genetically superior animals. Genealogical and performance recording in this population started about two decades ago. BLUP genetic evaluation has been conducted for several dairy traits in order to support breeders in their selection decision. The evaluation relies on the pedigree based test-day repeatability animal genetic model (Špehar et al., 2020), but a substantial part of the population has been genotyped (50K SNP chip) in order to establish single-step genomic evaluation (Legarra et al., 2009). The breeders are advised to select based on EBVs, but they are not obliged to do so. Trait-orientated selection usually provides genetic gain for trait(s) of interest. In order to check the success of selection, genetic trends need to be examined. They have been traditionally obtained by averaging estimated breeding values (EBVs) by birth year of animals (Blair and Pollak, 1984) or by regressing EBVs on birth year (Bernardes et al., 2018). However, evaluating single parts of the selection scheme is more complicated due to different selection intensities from different sources. One approach in tackling this issue is to calculate selection differentials for the different paths (Van Tassell and Van Vleck, 1990), which is not a trivial task (overlapping pedigrees). The more sophisticated method, proposed by Garcia-Cortes et al. (2008), relies on a direct transformation of EBVs by pedigree. Decomposition of EBVs with this methodology has already been carried out in cattle (Gorjanc et al., 2011; Gorjanc et al., 2012; Špehar et al., 2011), pigs (Škorput et al., 2015), and sheep (Špehar et al., 2021). Success of past selection work in this population has never been examined on such level, so we aimed to determine genetic trend for milk yield and decompose EBVs by gender and flock to examined their different contribution in the overall genetic trend for daily milk yield.

Material and methods

Genetic evaluation

Test day-records (n=113,075 collected on 9,629 ewes) for daily milk yield (DMY), information on systematic effects, (age, days in milk, parity, flock, litter size, season), and genealogical information (n=10,594 animals) were provided by the Ministry of Agriculture. Test-day records were obtained in accordance with ICAR guidelines (ICAR, 2018). Covariance components (estimated with REML) and BVs (predicted with BLUP) were estimated using the same multi-trait repeatability test-day genetic animal model (Špehar et al., 2020). Parity, litter size, season of lambing, and flock were fitted as class, while days in milk (DIM) and age at lambing (AL) as continues fixed predictors. The Ali-Schaeffer lactation curve (Ali and Schaeffer, 1987) nested within parity and litter size was used to model DIM. Age at lambing was modelled as a linear regression nested within parity. Flock test-day, permanent environmental effect within lactations, and direct additive genetic effect were fitted as random effects. The matrix notation of the model was: $y = Xb + W_cc +$ $W_pp + W_aa + e$ where: y was a vector of the phenotypes and, X and W were incidence matrices for the fixed and random effects, respectively. W_c, W_p, W_a were incidence matrices; and c, p, and a were vectors of unknown random effects, for the flock-test-day, permanent environmental, and additive genetic effects, respectively.

Decomposition of genetic trends

Genetic trends were obtained as the average of \hat{a} (BVs) by year of birth for animals born from 2010 to 2018, and the \hat{a} was partitioned by the gender and flock in R (R Core Team, 2020) with the package AlphaPart 0.8.1. (Gorjanc et al., 2021). This was done by following the method of Garcia-Cortes et al. (2008) with the formula $\hat{a} = TP_1T^{-1}\hat{a} + TP_2T^{-1}\hat{a} + \cdots + TP_kT^{-1}\hat{a}$. T traces gene flow from one generation to another, i.e., it describes the expected genetic contribution of genes identical by descent between each individual and all its ancestors, while P_i matrix is the 'path' matrix for the i-th origin that selects a partition of animals' BV attributed to the selection work performed by the i-th origin. Only a subset of the population (21 flocks) was included in this part of the study.

Results and discussion

The overall genetic trend for DMY in the Pag sheep breed and its decomposition by gender is presented in Figure 1. The overall genetic trend during the studied period was positive. By regressing BVs on birth year, the annual DMY was estimated to be 0.0087 kg. This result arose from the BVs obtained by the fixed regression repeatability test day animal model, which means that this estimate reflects annual genetic progress for average DMY. Multiplying this estimate by 120 days of lactation, cumulative lactation gain per year was estimated to be ~1 kg. Decomposition of the trend by gender revealed that females were the main source of genetic gain in this population. This result was quite unexpected at first, because raw means of EBVs by year and gender suggested the opposite conclusion. However, after detailed inspection of the data, applied procedures, and feedback from the field, it was determined that a positive response to selection could be attributable to the female selection path. The results obtained suggest that rams should be selected more carefully, preferably based on BVs. A similar pattern, i.e., a higher contribution of females to the overall genetic trend has been obtained by Abdollahi-Arpanahi et al. (2021) in the population of a selected maternal pig line. Their explanation for such a result was that selection decisions in a maternal pig line were placed more on the females because 40% of the traits under selection were measured only in females and because the selected females had more progenies than the sires. The former reason can be applied to some extent to our population, where all traits were measured on females and selection of replacement ewes is

based on female ancestral performance. This is rarely the case in selection of rams. Decomposition of genetic trends with this methodology has been insufficiently applied on real data and the patterns obtained on simulated data (Garcia-Cortes et al., 2008; Obšteter et al., 2021) can hardly be compared with our results due to the large discrepancy in data structure and applied selection schemes.

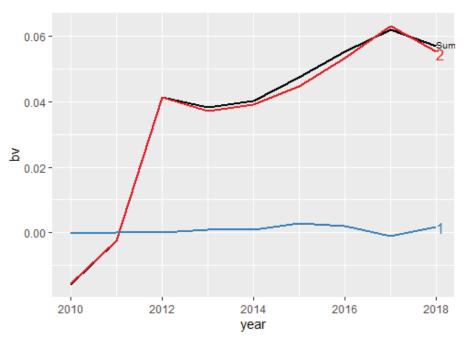


Figure 1. The estimated genetic trend (black) and contribution of sires (blue) and dams (red) in selection on daily milk yield in the Pag sheep breed

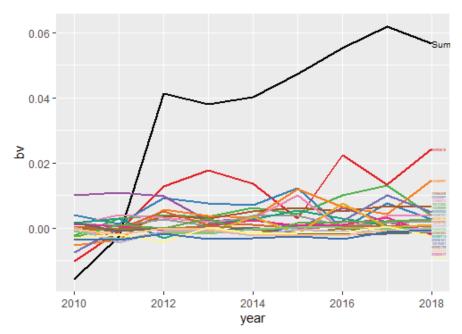


Figure 2. Flocks' contributions to the overall genetic trend for daily milk yield in the Pag sheep breed

The decomposition of genetic trend by flock (Figure 2) was less conclusive, however it revealed to some extent which flocks contributed most to the overall genetic trend. According to the estimated partitions, it seems that their relative importance to the overall

genetic gain was inconsistent between years, suggesting non-systematic selection with changeable success. Genetic progress of the population under consideration usually comes from different selection pathways that are exposed to different selection pressures, making this task very challenging. When attempting to study the impact of genetic effects on any complex (quantitative) trait, it is necessary to eliminate, or to account for and control, other potential sources of phenotypic variation. Studies conducted on livestock field data therefore heavily rely on the appropriate statistical model used to disentangle genetic from environmental effects. In this study, all available information (as explained in M&M) was used to estimate EBVs as accurately as possible (true breeding value is never known), and a purposely developed method and software was used to decompose them by gender and flock. Despite some shortcomings of the data (low genetic connectedness between flocks and insufficient pedigree information for some animals), we think that the estimates are a credible reflection of the true genetic change and the main contributors of genetic gain in this population. In addition to answering some important questions about past selection work in this population, we hereby demonstrated the "power" of decomposition of genetic trends on real data. Implementation of such procedures is necessary in practice in order to reveal benefits and pitfalls of applied selection schemes and to take actions to guide future selection activities in right direction.

Conclusion

The decomposition of genetic trends is an important "tool" to monitor past breeding activities in a population, ant it should be regularly applied in advanced breeding programs. Results of this study revealed that females were the main contributors of selection gain in this population and that flocks included in the national genetic evaluation system had non-uniform contribution. The results should serve to improve selection practices in this population, but also to demonstrate the importance and power of comprehensive genetic trend analysis in livestock populations under selection.

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Particija genetskog trenda prema spolu i stadu za dnevnu količinu mlijeka Paške ovce

Sažetak

Uzgojni programi u mliječnom ovčarstvu nastoje unaprijediti skup ekonomski i/ili funkcionalno važnih osobina ovaca. Uspjeh njihove provedbe se iskazuje genetskim trendovima, čija dekompozicija omogućuje kvantifikaciju doprinosa pojedinih selekcijskih puteva. Cilj rada bio je procijeniti genetski trend za dnevnu količinu mlijeka Paške ovce i napraviti njegovu dekompoziciju temeljem spola i stada. Trend je bio pozitivan, sa stopom promjene od 0,0087 kg/dan/godina (~1 kg po laktaciji). Ovce su imale veći doprinos selekcijskom napretku od ovnova, dok je doprinos pojedinih stada varirao tokom godina i time otežao rangiranje doprinosa pojedinih stada. Rezultati upućuju na potrebu veće pažnje kod odabira ovnova koji bi se trebao temeljiti prvenstveno na procijenjenim uzgojnim vrijednostima.

Ključne riječi: Paška ovca, genetski trend, dekompozicija, spol, stado