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Heritability of pulmonary arterial pressure in Angus beef cattle at moderate and high altitudes using BLUP, GBLUP, and ssGBLUP

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Introduction

Pulmonary arterial pressure (PAP) is a widely used physiological indicator of cardiopulmonary function, pulmonary hypertension, and susceptibility to high-altitude disease in cattle raised in hypoxic environments. Elevated PAP reflects increased pulmonary vascular resistance, which can lead to pulmonary hypertension, right ventricular hypertrophy, and ultimately congestive heart failure, particularly in animals managed above 1,800 m of elevation (Enns *et al*., 2023). Because PAP can be measured in live animals, it has become an important selection criterion in breeding programs aimed at improving high altitude tolerance and long-term cardiopulmonary health (Briggs *et al.*, 2020; Pauling *et al*., 2017).

Estimates of heritability (h^2) for PAP are sensitive to the analytical method and the elevation at which PAP measures are taken. Typically, variance components and heritabilities are estimated using pedigree-based BLUP, and when genomic information is available, genomic-based approaches, such as GBLUP and Single-step GBLUP (ssGBLUP), can be used as well. GBLUP captures realized genetic relationships using single-nucleotide polymorphism (SNP) markers, which can lead to different h^2 depending on population structure, marker density, and model specification (Meuwissen *et al*., 2001; VanRaden, 2008; Misztal *et al*., 2021). ssGBLUP integrates pedigree and genomic information, increasing the data available for estimation and often improving accuracy, particularly when not all animals are genotyped (Aguilar *et al*., 2010; Christensen & Lund, 2010). Accurate estimation of h^2 across these approaches allows breeders to determine the potential for genetic improvement in PAP and to optimize selection strategies for enhancing cardiopulmonary resilience.

Previous studies have shown that PAP is moderately heritable, indicating that genetic differences among animals contribute substantially to variation in susceptibility to pulmonary hypertension (Pauling *et al.,* 2017; Enns *et al.,* 2023). These findings support the feasibility of selecting for reduced PAP and demonstrate the utility of incorporating PAP measurements into breeding programs designed to improve the health and performance of cattle in high-altitude environments. Because h^2 may vary depending on the analytical method and the stage of life at which measurements are taken, evaluating PAP using multiple approaches and at different developmental stages is essential to generate robust genetic parameter estimates that can inform breeding decisions.

Building on this framework, the objective of this study was to estimate the heritabilities of PAP measured at weaning and yearling age under moderate and high-elevation conditions using BLUP, GBLUP, and ssGBLUP, and to assess the potential of these methods for improving genetic evaluations of cardiopulmonary resilience in beef cattle. Understanding the genetic architecture of PAP and its variation across life stages and analytical approaches is fundamental for developing accurate selection tools, which can enhance the evaluation of breeding animals and ultimately contribute to improved cardiopulmonary health and productivity in cattle raised under hypoxic conditions.

Materials & Methods

Phenotypic, pedigree, and genotypic data were provided by the American Angus Association. PAP (mmHg) was measured in live animals via catheterization of the jugular vein, passing a saline-filled catheter through the heart into the pulmonary artery. PAP measurements were recorded at weaning under moderate elevation (1,219–1,676 m) and at yearling age under both moderate and high elevation (>1,676 m). Each measurement was treated as a distinct trait in the analyses to account for differences in age and environmental conditions.

A total of 37,407 animals had PAP records. A three-generation pedigree was constructed, including 207,694 animals. Animals were genotyped using multiple SNP platforms over time, and all genotypes were imputed to a common set of 54,609 SNPs. For the genomic analyses, all animals included in the GBLUP model had both phenotypic (PAP records) and genomic data. In contrast, the ssGBLUP analysis included all available animals with phenotypic records and pedigree information, while incorporating genomic information for the subset of genotyped animals.

Genetic parameters were estimated using three approaches: traditional pedigree-based BLUP, GBLUP, and ssGBLUP, implemented in the BLUPF90 software suite (Misztal *et al.*, 2021). For GBLUP analyses, the pedigree-based relationship matrix (**A**) was replaced with the genomic relationship matrix (**G**) constructed following VanRaden (2008), centering genotypes and scaling by allele frequencies. In ssGBLUP, pedigree and genomic information were combined into a single relationship matrix (**H**) to leverage all available information.

Variance components and heritability estimates were obtained using genomic restricted maximum likelihood via the AIREML algorithm implemented in the *airemlf90* program from the BLUPF90 family.

Single-trait animal models were fitted using BLUP, GBLUP, and ssGBLUP to estimate heritability for PAP measured at weaning, PAP measured at yearling age under moderate elevation (from 1,219 m to 1,676 m), and PAP measured at yearling age under high elevation (above 1676 m). The general single-trait mixed model was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e} \quad (1)$$

where **y** was the vector of phenotypic observations, **b** was the vector of unknown fixed effect solutions, **a** was the vector of random additive genetic effects, and **e** was the vector of residual effects. The incidence matrices **X** and **Z** were design matrices relating observations in **y** to fixed and additive genetic effects in **b** and **a**, respectively.

Fixed effects for PAP included contemporary group defined as Herd ID + Process Date + Lot ID, age at measurement as a covariate for each elevation category.

The (co)variance matrix of the random vectors *a* and *e* in single-trait models ($\mathbf{V}_1$) was as follows:

$$\mathbf{V}_1 = \begin{bmatrix} \mathbf{G}\sigma_a^2 & 0 \\ 0 & \mathbf{I}\sigma_e^2 \end{bmatrix} \quad (2)$$

Results & Discussion

Heritability estimates for PAP across developmental stages and elevation conditions are summarized in Table 1. Pedigree-based BLUP analyses indicated moderate to high genetic control, with values ranging from 0.24 ± 0.03 at weaning to 0.39 ± 0.03 for yearling animals raised at high elevation. These findings confirm that additive genetic variance contributes substantially to variation in PAP within this population.

Incorporating genomic information altered the estimates. Compared with BLUP, GBLUP produced higher heritability at weaning (0.39 ± 0.03), at yearling under moderate (0.42 ± 0.02) and high elevation (0.47 ± 0.02). When both pedigree and genomic data were combined using ssGBLUP, heritabilities were intermediate (0.28 ± 0.02 for weaning, 0.29 ± 0.01 for moderate

elevation yearling, and 0.33 ± 0.01 for high elevation yearling), reflecting the improved precision by integrating multiple sources of genetic information.

These differences illustrate how the estimation method can influence the perceived genetic contribution to PAP. BLUP relies solely on pedigree relationships, capturing additive variance but not the finer resolution of realized genomic relationships, which may explain slightly higher weaning estimates. GBLUP leverages genotyped markers to account for Mendelian sampling and individual relatedness, yielding more accurate but sometimes lower estimates in environments with strong non-genetic influences. ssGBLUP combines both sources, strengthening connectedness across animals.

The stage of measurement also affected heritability estimates. Early-life measurements at weaning showed relatively higher heritabilities, suggesting strong genetic influence with limited environmental interference. Yearling measurements, particularly under moderate and high-elevation conditions, reflect cumulative environmental impacts such as hypoxia and management, which can reduce apparent heritability in models relying solely on genomic data. The inclusion of pedigree through ssGBLUP partially compensates for this, highlighting the benefit of integrating all available information for variance components estimation and genetic evaluations.

Collectively, the results demonstrate that PAP exhibits moderate to high heritability across stages and environments. This genetic variation supports the feasibility of selection for reduced PAP, and the use of genomic-enhanced models, particularly ssGBLUP, provides a robust framework to improve the accuracy of breeding values and support the development of more resilient cattle populations under hypoxic conditions.

Table 1. Heritability estimates and phenotypic variance (σ^2_p) for pulmonary arterial pressure traits in Angus cattle across models and elevations.

Model	Weaning PAP		Yearling PAP (Moderate Elevation)		Yearling PAP (High Elevation)	
	h^2	σ^2_p	h^2	σ^2_p	h^2	σ^2_p
BLUP	0.24 ± 0.03	55.77	0.32 ± 0.02	65.64	0.39 ± 0.03	52.10
GBLUP	0.39 ± 0.03	56.17	0.42 ± 0.02	80.81	0.47 ± 0.02	65.67
ssGBLUP	0.28 ± 0.02	56.74	0.29 ± 0.01	65.40	0.33 ± 0.01	51.69

Conclusions

Pulmonary arterial pressure measured in cattle at weaning and yearling stages under moderate and high elevations shows moderate to high heritability, indicating a substantial contribution of additive genetic variation. Traditional BLUP analyses based on pedigree alone produced moderate to high estimates, confirming the genetic basis of PAP. Incorporating genomic information through GBLUP provided comparable results, while ssGBLUP, which combines pedigree and genomic relationships, allowed for estimation while utilizing additional genetic connections across animals. Heritability estimates differed across developmental stages and environments, with early-life measurements capturing consistent genetic effects and high-elevation yearling measurements reflecting the influence of hypoxic stress on genetic variation. These findings reinforce that PAP is a heritable trait suitable for selection and demonstrate the advantage of genomic evaluation methods in improving the accuracy of breeding value predictions. Consequently, PAP can serve as a practical, early-life indicator for guiding selection toward enhanced cardiopulmonary resilience in cattle raised under high-altitude conditions.

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