Accuracy of genomic selection for reducing susceptibility to pendulous crop in turkey (*Meleagris gallopavo*)

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ABSTRACT Pendulous crop (**PC**) in the turkey occurs when the crop distends from its normal position, thereby preventing the movement of feed and water from the crop down into the digestive system. This condition negatively impacts the turkey industry at both production and welfare levels. In this study, we estimated the genetic parameters for PC incidence and its genetic correlation with 5 production traits. Additionally, we evaluated the prediction accuracy and bias of breeding values for the selection candidates using pedigree (**BLUP**) or pedigree-genomic (**ssGBLUP**) relationships among the animals. A total of 245,783 turkey records were made available by Hybrid Turkeys, Kitchener, Canada. Of these, 6,545 were affected with PC. In addition, the data included 9,634 records for breast meat yield (**BMY**); 5,592 records for feed conversion ratio (**FCR**) and residual feed intake (**RFI**) in males; 170,844 records for body weight (**BW**) and walking score (**WS**) between 18 and 20 wk of age for males (71,012) and females (99,832), respectively. Among this population, 36,830 were genotyped using a 65K SNP Illumina Inc. chip. While all animals passed the quality control criteria, only 53,455 SNP markers were retained for subsequent analysis. Heritability for PC was estimated at 0.16 ± 0.00 and 0.17 ± 0.00 using BLUP and ssGBLUP, respectively. The incidence of PC was not genetically correlated with WS or FCR. Low unfavourable genetic correlations with BW (0.12 and 0.14), BMY (0.24 and 0.24) and RFI (−0.33 and −0.28) were obtained using BLUP and ssGBLUP, respectively. Using ssGBLUP showed higher prediction accuracy (0.51) for the breeding values for the selection candidates than the pedigree-based model (0.35). Whereas the bias of the prediction was slightly reduced with ssGBLUP (0.33 ± 0.05) than BLUP (0.30 ± 0.08), both models showed a regression coefficient lower than one, indicating inflation in the predictions. The results of this study suggest that PC is a heritable trait and selection for lower PC incidence rates is feasible. Although further investigation is necessary, selection for BW, BMY, and RFI may increase PC incidence. Incorporating genomic information would lead to higher accuracy in predicting the genetic merit for selection candidates.

Key words: pendulous crop, single-step, genetic correlation, prediction accuracy, prediction bias

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INTRODUCTION

The crop is part of the esophagus found in most birds, with species-specific shapes and sizes (Kierończyk et al., 2016). The function of the crop in poultry is mainly related to temporary food storage, but also initial digestion through moistening of feed and activation of enzymes (Classen et al., 2016; Kierończyk et al., 2016). Studies have shown that between 30 and 50% of feed enters the crop before the proventriculus-gizzard, and that feed can be retained for up to 9 h in the crop in turkeys (Jackson and Duke, 1995; Cutler et al., 2005; Classen et al., 2016). Furthermore, the crop is thought to play a role in digestive tract health and in reducing contamination with food-borne pathogens (Cutler et al., 2005; Classen et al., 2016; Kierończyk et al., 2016). As such, 'healthy' crop function is thought to be beneficial for bird performance and health, but can be influenced by genetics, bird age, nutritional factors and flock management

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(Classen et al., 2016; Kierończyk et al., 2016; Crespo, 2019).

Pendulous crop (**PC**) syndrome is characterized by loss of muscle tone and distention of the crop which prolapses in front of the supportive tissue layers (Hinshaw, 2003; Ebling et al., 2015; Crespo, 2019; Çelik and Kıvanç, 2020), resulting in the crop not functioning as it should. PC cannot be identified early and there is no treatment, meaning that the crop never returns to its normal position (Hinshaw, 2003). Birds continue to eat but, the flow of feed from the crop to the proventriculus-gizzard is impaired due to the reduced muscle function (Ebling et al., 2015; Crespo, 2019). This can lead to impaired nutrition digestion and absorption in the digestive tract, ulceration of the crop lining, and ultimately, emaciation and mortality (Crespo, 2019). Furthermore, birds with PC may be condemned at the processing facility due to the risk of cross contamination (Crespo, 2019). As such, the main strategy is to cull birds with PC to avoid decreased bird well-being and financial losses due to reduced feed efficiency and carcass condemnation. Even though live weight can be normal, birds with PC generally have significantly lower carcass weight (Ebling et al., 2015). Hence, PC is a serious issue in poultry production from both a production and animal welfare perspective.

A recent survey indicates that 25% of farmers listed PC as a reason for culling turkeys on their farms (van Staaveren et al., 2020). Prevalence of PC within flocks have been reported to range between 5 and 10% (Wheeler et al., 1960; Steimling, 2014), but more recent research indicates a prevalence under 5% in turkeys depending on genetic lines, sex, and management practices (Quinton et al., 2011; Willems et al., 2014; Vermette et al., 2016). The occurrence of PC has been proposed to be of genetic origin for many years (Asmundson and Hinshaw, 1938; Reed, 2009), but the precise etiology is still unclear. It has been demonstrated that genetic selection can be effective in reducing the susceptibility to infection in poultry such as Marek's disease, avian leucosis viruses, salmonellosis and colibacillosis (Kuhnlein et al., 2003), but limited work has been done on reducing susceptibility to non-infections conditions such as PC in turkeys. Several previous studies reported heritability estimates between 0.11 and 0.15 for PC incidence in turkeys (Quinton et al., 2011; Willems et al., 2014). This suggests that there is genetic variation in the susceptibility to PC in turkeys, and that the occurrence of PC might be reduced through genetic selection, thus improving turkey welfare and reducing economic loss in the turkey industry for both breeders and producers. Recent advances in selection programs allow for the incorporation of genomic data, which can successfully increase selection accuracy for several traits in turkeys (Abdalla et al., 2019, 2021). Therefore, the objectives of this study were to: 1) estimate genetic parameters of PC incidence and its genetic correlation with production traits in turkeys based on pedigree and genomic relationships and 2) estimate accuracy and bias of selection for lower PC incidence based on pedigree and genomic relationships.

Table 1. Total number, number of affected and not affected with pendulous crop (PC) and number of genotyped birds by sex used in the study.

Sex	Number of birds	Number of affected with PC	Number of genotyped
Males	153,781	2,452	10,659
Females	109,563	4,093	26,171
Total	263,344	6,545	36,830

MATERIALS AND METHODS

Data

Phenotypic and genomic data used in this study were provided by Hybrid Turkeys, Kitchener, Canada. As shown in Table 1, the data consisted of 263,344 observations for 153,781 and 109,563 purebred turkey males and females, respectively. The birds were hatched between 2010 and 2020 spanning 13 generations. Of the 263,344 birds, 2,452 males and 4,093 females were affected with PC. Body weight (**BW**) and walking score (**WS**) at 20 wek for these males and females were also obtained (Table 2). WS took values between 1 and 6 such that higher WS represented better walking ability. In addition, some males were also phenotyped for breast meat yield (**BMY**; N = 9,634), feed conversion ratio (**FCR**; N = 5,592) and residual feed intake (**RFI**; N = 5,592). Whereas FCR and RFI were obtained following Case et al. (2012), BMY was expressed as a percentage of breast meat out of live BW at slaughter.

The total number of animals in the pedigree was 863,850; 10,659 males and 26,171 females were genotyped (Table 1) using a proprietary 65K single nucleotide polymorphisms (**SNP**) panel (65,000 SNP; Illumina, Inc., San Diego, CA). Genomic data were not imputed and all genotyped animals had a call rate higher than 90%. Markers were excluded if they deviated significantly from Hardy Weinberg proportions ($P < 1 \times 10^{-8}$), had minor allele frequency lower than 5%, call rate lower than 90%, or were located in non-autosomal regions. Thus, the

Table 2. Descriptive statistics of the analyzed data set including the number of records, number of genotyped, mean and standard deviation for different production and fitness traits in a purebred turkey line.

Trait	Number (genotyped)	Mean	Standard deviation
Feed conversion ratio (kg/kg)	5,592 (2,417)	2.58	0.39
Residual feed intake (kg)	5,592 (2,417)	0.00	2.51
Body weight (kg)	170,844 (31,409)	17.50	5.32
Breast meat yield (%)	9,634 (979)	24.37	2.33
Walking score[1] (1–6)	170,844 (31,409)	2.10	0.86
Pendulous crop[2] (0–1)	263,344 (36,830)	0.03	0.17

[1]Higher walking score represents better walking ability.
[2]Values 0 and 1 represent not affected and affected with pendulous crop, respectively.

number of markers retained for subsequent analyses was 53,455 out of the 65K.

Statistical Model

*Best linear unbiased prediction model (**BLUP**).* The data were analyzed using the following multitrait animal model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e},$$

where, $\mathbf{y}$ is a vector of observations of PC, FCR, RFI, BMY, BW and WS sorted within animals; $\mathbf{b}$ is a vector with the fixed effects of hatch week-year for all traits and sex for PC, BW and WS; $\mathbf{u}$ is a vector of additive genetic effects, distributed as $\mathbf{u} \sim N(\mathbf{0}, \mathbf{A}\otimes\mathbf{K})$, where $\mathbf{A}$ is the numerator relationship matrix including the inbreeding coefficients and $\mathbf{K}$ is the additive genetic variance-covariance matrix among traits; $\mathbf{e}$ is a vector of residual effects, distributed as $\mathbf{e} \sim N(\mathbf{0}, \sum_i^+ \mathbf{E}_{iy})$ where $\mathbf{E}_{iy}$ indicates a $m_i \times m_i$ matrix corresponding to the traits that were present for animal i, and m_i is the number of traits present for animal i; $\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices for the respective fixed and random effects.

*Single-step genomic best linear unbiased prediction model (**ssGBLUP**).* The ssGBLUP was implemented by replacing the $\mathbf{A}$ matrix in BLUP by $\mathbf{H}$ (Aguilar et al., 2010); which is a matrix combining pedigree and genomic relationships:

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & (w \times \mathbf{G} + (1 - w)\mathbf{A}_{22})^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix}.$$

In the above, $\mathbf{H}^{-1}$ is the inverse of the modified relationship matrix; $\mathbf{A}^{-1}$ is the inverse of the pedigree-based relationship matrix; $\mathbf{G}$ is the genomic relationship matrix; $\mathbf{A}_{22}$ and $\mathbf{A}_{22}^{-1}$ are the pedigree-based relationship matrix for genotyped animals and its inverse, respectively, and w is a constant weighting factor (Vitezica et al., 2010; Abdalla et al., 2019). The value of w was 0.90 and was chosen as it gave the highest accuracy (Abdalla et al., 2019) for predicting the breeding values for PC incidence. The $\mathbf{G}$ matrix (VanRaden, 2008) was obtained based on the observed allele frequencies in the population as follows:

$$\mathrm{G} = \frac{(\mathrm{M} - \mathrm{P})(\mathrm{M} - \mathrm{P})'}{2\sum_{\mathrm{j}=1}^{\mathrm{m}} p_{\mathrm{j}}(1 - p_{\mathrm{j}})}$$

where $\mathbf{M}$ is the matrix of genotypes, with columns representing markers and rows representing individuals. Each element in $\mathbf{M}_{\mathrm{ij}}$ was coded as 0, 1, or 2 if the genotype of individual i for SNP j was homozygous for the first allele, heterozygous, or homozygous for the second allele, respectively. $\mathbf{P}$ is a matrix with average allele frequencies calculated as $2(p_i - 0.5)$, where $\mathrm{p_i}$ is the frequency of the second allele at locus (column) i. Genetic parameters were estimated using each model as well as estimated breeding values (EBV) based on BLUP and ssGBLUP, respectively.

Accuracy and Bias of Prediction for Pendulous Crop

To assess the predictive ability of each model, the following procedure was performed. For both BLUP and ssGBLUP, the first 12 generations (N = 245,783 birds) were used to train the models, whereas birds from the 13th generation (N = 17,561) composed the validation subset (Table 3). This procedure was considered to mimic what would happen in practice, where young animals without phenotypes would be selected based on pedigree and marker effects predicted on older animals. The numbers of genotyped animals were 31,991 and 4,839 in training and validation subsets, respectively. Furthermore, adjusted-to-fixed effects phenotypes ($\mathrm{y_{adj}}$) for birds in the validation group were obtained from each model. For BLUP, the Pearson correlation coefficient between $\mathrm{y_{adj}}$ and EBV divided by square root of heritability and the regression coefficient of $\mathrm{y_{adj}}$ on EBV were the measures of prediction accuracy and bias, respectively (Wolc et al., 2011; Putz et al., 2018). The same procedure was performed to evaluate the accuracy and bias for ssGBLUP, but with using the respective $\mathrm{y_{adj}}$ and (G)EBV. Genetic parameters were estimated using AIREMLF90 software, while $\mathrm{y_{adj}}$ obtained using PREDICTF90 (Misztal et al., 2014).

RESULTS AND DISCUSSION

The overall prevalence rate of PC in this studied turkey population was 2.5%. Willems et al. (2014) reported prevalence rates that ranged between 1.52 and 2.96% and higher rates of PC ranging from 5 to 15% were previously indicated by Steimling (2014). As our data was collected from a pure turkey line, the incidence could be different than that observed at the commercial level. van Staaveren et al. (2020) conducted a cross-sectional survey in which they asked farmers to indicate the main perceived reasons for culling in their flock. Approximately 25% of farmers noted PC as one of the main reasons for culling; while this does not give any indication on prevalence of PC in turkey flocks, it does highlight

Table 3. Number of turkeys used for training (generations 1 to 12) and validation (the 13th generation) datasets for each model as well as the number of birds affected by pendulous crop (PC) in each group.

	Training (genotyped)		Validation (genotyped)		Total (genotyped)	
Model	Total	Affected with PC	Total	Affected with PC	Total	Affected with PC
BLUP model	245,783	5,804 (3)	17,561	741 (1)	263,344	6,545 (4)
ssGBLUP model[1]	245,783 (31,991)	5,804 (3)	17,561 (4,839)	741 (1)	263,344 (36,830)	6,545 (4)

Table 4. Genetic variance, residual variance, heritability (h2) ± standard error (SE), prediction accuracy and prediction bias for pendulous crop (PC) incidence based on BLUP or ssGBLUP models in a purebred turkey line.

Model	Genetic variance	Residual variance	$h^2 \pm SE$	Prediction accuracy	Prediction bias
BLUP	0.004	0.023	0.16 ± 0.00	0.35	0.30 ± 0.08
ssGBLUP	0.005	0.023	0.17 ± 0.00	0.51	0.33 ± 0.05

that the farmers' main method of intervening is the quick culling of these birds. Thus, PC remains a serious welfare issue in turkey flocks requiring early identification and on-farm euthanasia by trained personnel which also has implications for the welfare of farm staff (Turner and Doonan, 2010; National Farm Animal Care Council, 2016).

Heritability and Genetic Correlations

Heritability estimates of PC incidence and its genetic correlations with the other 5 traits are presented in Table 4. The genetic parameters, including estimates of heritability and genetic correlation for BW, WS, BMY, FCR, and RFI were reported in Abdalla et. al. (2019). The estimated heritability for PC based on BLUP was moderate at 0.16 ± 0.00 indicating a considerable genetic component underlying the incidence of this disease in turkeys. In 2011, Quinton et al. (2011) observed a heritability of 0.12 ± 0.00 for PC incidence and an estimate of 0.15 ± 0.00 was reported by Willems et al. (2014). This is an indication that selection for higher resistance to PC is feasible and may ultimately assist in alleviating the detrimental effect of this disease. Table 4 also shows the estimate of heritability when genomic data were incorporated, which was slightly higher at 0.17 ± 0.00. We could not compare this heritability to previous estimates in the literature because, to our best knowledge, all reported estimates are based on pedigree relationships only. However, the use of genomic data is generally expected to increase heritability due to the improvement in predicting the kinship between individuals based on genomic markers rather than probabilities (Aguilar et al., 2010; Christensen et al., 2012). The increase in heritability with genomic data has been also observed by Abdalla et al. (2019) for BW, WS, BMY, FCR, and RFI in turkey, and a similar trend appears to be maintained for PC in the current study. It is noteworthy that the number of genotyped and PC-affected birds was 4; however, one of the substantial advantages of ss-GBLUP is improving the genetic predictions through enhancing genetic relationships between individuals in the numerator relationship matrix (Aguilar et al., 2010; Christensen et al., 2012).

Although the decrease in susceptibility to PC through genetic and genomic selection would be small for each generation, the improvement is cumulative and permanent. Additionally, reducing susceptibility to diseases using genetics is generally desirable for several reasons. For example, birds can be selected as early as the day of hatch and those with a high probability to be infected can be removed at that point. This procedure reduces the number of birds that may suffer from the disease in future. Moreover, breeding for reduced susceptibility does not require the exposure of animals to pathogenic agents through experiments, which from an animal welfare standpoint may raise ethical questions (Gibbs and Wooley, 2003; Blanco et al., 2018).

Genetic and residual correlations for PC with the other studied traits are shown in Table 5. PC incidence was observed to have a low positive correlation with BW at 0.12 ± 0.02 and 0.14 ± 0.03 for BLUP and ssGBLUP, respectively. Similar but slightly larger estimates were reported by Willems et al. (2014), with a correlation of 0.16 ± 0.02 for sire and 0.18 ± 0.02 for dam lines using BLUP. In addition, BMY was found to have a positive genetic correlation with PC, and the estimates for this correlation from both models were similar at 0.24. Since the genetic correlation between BMY and PC was not previously reported in the literature, we could not find estimates to compare with those obtained in this study. The highest genetic correlation was the negative correlation between PC and RFI, which was −0.33 ± 0.07 with BLUP and −0.28 ± 0.06 with ssGBLUP. These correlations were higher than those reported by Willems et al. (2014), which was estimated to be −0.22 ± 0.06. PC was not genetically correlated with either WS (−0.09 ± 0.03 and −0.08 ± 0.03 for BLUP and ssGBLUP, respectively) or FCR (−0.01 ± 0.07 and 0.07 ± 0.07 for BLUP and ssGBLUP, respectively).

Defining genetic correlations between economically important traits is essential for designing selection objectives and developing more comprehensive selection indexes. The results of this study indicate that selection

Table 5. Genetic and residual correlations of pendulous crop (PC) incidence with body weight, breast meat yield, walking score, residual feed intake, and feed conversion ratio based on BLUP or ssGBLUP models in a purebred turkey line.

	BLUP		ssGBLUP	
Trait	Genetic	Residual	Genetic	Residual
Body weight	0.12 ± 0.02	0.03 ± 0.00	0.14 ± 0.03	0.03 ± 0.00
Breast meat yield	0.24 ± 0.06	0.31 ± 0.07	0.24 ± 0.06	0.31 ± 0.07
Walking score	−0.09 ± 0.03	0.05 ± 0.01	−0.08 ± 0.03	0.05 ± 0.01
Residual feed intake	−0.33 ± 0.07	−0.12 ± 0.09	−0.28 ± 0.06	−0.12 ± 0.08
Feed conversion ratio	−0.01 ± 0.07	−0.06 ± 0.00	0.07 ± 0.07	−0.06 ± 0.00

for higher BW and BMY may partially increase the occurrence of PC. The negative genetic correlation between RFI and PC suggests that improving RFI (lower value) is expected to increase the incidence of PC in turkey flocks. The other feed efficiency trait (**FC**R) had almost zero genetic correlation with PC. FCR and RFI are moderately genetically correlated (Abdalla et al., 2019,2021) and both are used in turkey selection indexes (Case et al., 2012). However, RFI is advantageous because it is independent of other production traits. The antagonistic relationship that can exist between production traits and diseases has been demonstrated in poultry as well as in other species (e.g., Quinton et al., 2011; Hocking, 2014; Abdalla et al., 2016). Improving BW and feed efficiency traits are generally among the most important goals of turkey breeding programs, however these traits all have an unfavorable genetic correlation with the occurrence of PC. However, such correlations should be carefully further investigated using recursive models to explore the cause-and-effect mechanisms that underlie interrelationships among environmental factors, management practices, and the genetic component of the animals (Abdalla et al., 2021).

Accuracy and Bias

Accuracies of EBV for PC incidence estimated using the ssGBLUP and the BLUP methods are presented in Table 4. The ssGBLUP generated a higher accuracy (0.51) compared to the BLUP (0.35). In other words, incorporating genomic data in the numerator relationship matrix had led to an increase in the accuracy of predicting the genetic merit for the candidates of the next generation by approximately 50%. One of the most cited advantages of ssGBLUP over BLUP is that information of genotyped and non-genotyped animals are used simultaneously (e.g., Aguilar et al., 2010) leading to higher accuracy in predicting the genetic merit for selection candidates. Recently, Abdalla et al. (2019) showed that ssGBLUP yielded a higher predictive ability than BLUP for BW, WS, BMY, RFI, and FCR traits in turkeys. The outperformance of the ssGBLUP over traditional genetic evaluation has been also reported in several studies in different species (e.g., Daetwyler et al., 2007; Hayes et al., 2010; Guarini et al., 2019). The Mendelian inheritance through markers included in ssGBLUP provides more accurate modelling, and has now been shown for PC in the current study. Interestingly, even for non-genotyped animals, ssGBLUP may produce more accurate EBV than BLUP (Christensen et al., 2012). Thus, it can be concluded that pedigree-marker-based methods (i.e., ssGBLUP) may replace the pedigree-based method (i.e., BLUP) in the turkey genetic evaluation system.

Although both modelling approaches showed inflated predictions, ssGBLUP had a slightly higher regression coefficient of corrected phenotypes on (G)EBV (0.33 ± 0.05) than BLUP (0.30 ± 0.08), as shown in Table 4. Both regression coefficients are lower than the expected value of 1, suggesting that EBV and (G)EBV overestimated differences in phenotypes of progeny. PC incidence is a binary trait (affected or not affected), hence the assumption of normality for genotypic values may not be valid, which could be the reason for the substantial bias observed in predicting EBV and (G)EBV for selection candidates. If proven and young candidates are expected to be simultaneously selected, it is important to apply appropriate bias correction methods (Patry and Ducrocq, 2011). It is worth mentioning that current turkey breeding systems do not allow for simultaneous selection for proven and young candidates.

CONCLUSIONS

We estimated a moderate heritability for PC disease in a turkey population using BLUP and ssGBLUP. These results show promise in reducing susceptibility to PC through genetics in purebred turkeys, however correlations with other traits should be taken into account. PC incidence had low unfavourable genetic correlations with BW, BMY and RFI. Compared to the pedigree-based approach, incorporating genomic data improved the predictions of genetic merit for the selection candidates by about 50%, while at the same time reducing the bias of these predictions The results suggest that the ssGBLUP method is an appealing approach for practical genomic prediction for PC incidence in turkeys and may play an important role in enhancing the breeding systems in this species while improving welfare.

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Ethics statement: No Animal Care Committee approval was necessary for the purposes of this study, as all information required was obtained from existing databases.

DISCLOSURES

All authors declare no conflict of interest.

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