

Genetic parameters for clutch and broodiness traits in turkeys (*Meleagris Gallopavo*) and their relationship with body weight and egg production

H. Emamgholi Begli,^{*,1} B. J. Wood,^{†,*} E. A. Abdalla,^{*} A. Balzani,^{*} O. Willems,[†] F. Schenkel,^{*} A. Harlander-Matauschek,[‡] and C. F. Baes^{*,§}

^{*}Centre for Genetic Improvement of Livestock, Department of Animal Biosciences, University of Guelph, Guelph, Ontario, N1G 2W1, Canada; [†]Hybrid Turkeys, A Hendrix Genetics Company, Kitchener, Ontario, N2K 3S2, Canada; [‡]Campbell Centre for the Study of Animal Welfare, Department of Animal Biosciences, University of Guelph, Guelph, Ontario, N1G 2W1, Canada; and [§]Institute of Genetics, Vetsuisse Faculty, University of Bern, Bern, 3001, Switzerland

ABSTRACT The objective of this study was to estimate phenotypic and genetic parameters for clutch and broodiness (BR) traits in turkeys and their relationship with body weight and egg production. Data on dam line hens was available and included: body weight at 18 wk of age (BW18), body weight at lighting (BWL, 29 to 33 wk), age at first egg (AFE), egg number (EN), rate of lay (RL), clutch length (CL), maximum clutch length (MCL), pause length (PL), maximum PL (MPL) and BR. BR was defined as the average number of consecutive pause days between clutches that was higher than the average PL per hen. Heritability estimates for BW18 and BWL were 0.50 and 0.53, respectively. The heritability for egg production, clutch, and pause traits varied from low (MPL = 0.15; BR = 0.15) to moderate (AFE = 0.22; EN = 0.28; RL = 0.29; CL = 0.21; MCL = 0.27; PL = 0.25). Genetic correlations were negative between body weight traits and

EN ($r_g(\text{BW18}, \text{EN}) = -0.27$; $r_g(\text{BWL}, \text{EN}) = -0.33$) and CL ($r_g(\text{BW18}, \text{CL}) = -0.40$; $r_g(\text{BWL}, \text{CL}) = -0.33$). BR was negatively genetically correlated with EN ($r_g(\text{BR}, \text{EN}) = -0.85$) and CL ($r_g(\text{BR}, \text{CL}) = -0.30$), and positively genetically correlated with PL ($r_g(\text{BR}, \text{PL}) = 0.93$) and AFE ($r_g(\text{BR}, \text{AFE}) = 0.21$). EN had a positive (0.73) and a negative (-0.84) genetic correlation with CL and PL, respectively. Overall, the results of this study confirmed the negative (unfavorable) correlations between egg production and body weight. Despite unfavorable genetic and phenotypic correlations between egg production traits and those relating to BR, the inclusion of BR in a selection program through incorporation of clutch length traits and pause length traits is feasible. Integration of either clutch length traits or pause length traits in a selection index is likely to increase egg number while decreasing broodiness.

Key words: genetic parameter, age at first egg, pause length, broodiness, egg production

2019 Poultry Science 0:1–7

<http://dx.doi.org/10.3382/ps/pez446>

INTRODUCTION

The turkey industry is characterized by primary breeders, who develop pure-bred male and female lines with specialized breeding objectives within each line. These specialized lines are selected and crossed in breeding programs tailored to meet the needs of different markets. While body weight remains a prominent trait for genetic selection due to its high economic impact and heritability, balanced selection for a multitude of traits (e.g., feed efficiency, locomotion, meat quality, reproduction) is required to ensure a sustainable equilibrium between animal health, welfare, productivity, and reproduction. Phenotypic and genetic relationships

between economic traits of interest may be favorable, such as those between body weight and breast yield, or negative, such as those between growth and reproductive efficiency.

Unfavorable genetic correlations between growth rate and reproduction have been observed in many species of livestock e.g., swine (Holm et al., 2004), dairy (Pryce et al., 2004), and sheep (Safari et al., 2007). Similar unfavorable genetic correlations between growth or body weight and reproductive efficiency in poultry are also well established (Rauw et al., 1998; Kranis et al., 2006; Jambui et al., 2017, etc.). Modern genetic selection programs are designed to balance these unfavorable correlations and allow balanced genetic gain across all traits. In the three and 4-way commercial turkey cross system, sire lines are mainly selected for meat production traits such as body weight, meat quality and feed efficiency, whereas selection is primarily focussed on growth and egg production traits in dam lines (Nestor et al., 2006).

© Crown copyright 2019.

Received March 15, 2019.

Accepted August 7, 2019.

¹Corresponding author: hemamgho@uoguelph.ca

A number of egg production traits are commonly recorded for use in commercial turkey breeding programs, including age at first egg (**AFE**), egg number (**EN**), and rate of lay (**RL**). Clutch traits, such as clutch length (**CL**) and the interval between clutches (pause length), may provide additional information on laying characteristics, where clutch refers to the number of eggs laid in a single brood by a bird. Birds with longer CL (oviposition sequence) and shorter intersequence pauses are likely to also have more stable egg production throughout lay. These birds are also expected to express less broodiness (**BR**), which is the behavioral tendency to sit on a clutch of eggs to incubate them. Bird BR is a specific behavioral trait characteristic of precocial birds that is triggered to protect chicks from predators (Ohkubo, 2017). This intrinsic desire to incubate eggs is expressed by behavioral and physiological states associated with maternal care of the unhatched eggs (incubation behavior). BR is associated with persistent nesting behavior, reduced feed and water intake, cessation of egg laying, and ovarian regression, resulting in economic losses for the poultry industry (El Halawani and Rozenboim, 1993; Romanov et al., 2002).

In commercial turkey flocks, a number of prevention and control strategies to reduce BR are incorporated into management strategies, such as frequent floor egg collection, provision of uniform lighting systems that discourages nesting in dim corners, and moving broody hens to different surroundings or less comfortable areas without nests. These management strategies are costly, time consuming, and impede some birds' natural instincts to brood, which can be more or less pronounced in individual birds. One possible strategy to reduce the frequency of broody behavior is to harness the genetic variation within turkey populations and genetically select for birds with a less pronounced requirement to express broody behavior (Muir and Cheng, 2014).

Several approaches have been developed in order to better understand the physiology in broody birds, and to define a quantitative measure for BR which could be used in breeding programmes. Hormone levels have been investigated in an attempt to measure and explain the physiological variation between birds, as some birds express no BR, and others express extreme BR (Saeki and Tanabe, 1955; Opel and Proudman, 1980). Data collection of this kind, however, is impossible in large numbers of birds. Behavioral observations as described by Romanov et al. (2002) could provide a method to identify and describe broody bird behavior, however, large-scale trait collection is not feasible, thus prevention methods continue to be a costly problem for turkey breeders.

The use of indicator traits can be helpful in cases when traits are difficult to measure, such as in the case of BR. Nestor (1980) described an indicator trait for BR in which broody periods were defined as five or more consecutive non-production days during lay. With this definition, the realized heritability for total days broody was 0.31 ± 0.12 (Nestor, 1980), indicating that a sub-

stantial amount of additive genetic variance could be harnessed by including BR in a genetic selection strategy. However, due to the favorable correlation between egg production and BR (Nestor, 1971), egg production is selected for directly, whereas BR is not commonly included in the selection index. By splitting the selection pressure between egg production and BR, it may be possible to further increase egg production while reducing the need for prevention and control strategies required as a result of broody behavior.

When considering additional traits in a breeding program, it is of fundamental importance to investigate the genetic and phenotypic parameters of the various traits under consideration. The objective of this present study was therefore to estimate genetic parameters for clutch and BR traits, and to investigate their relationship with body weight and other conventional egg production traits in a female turkey line.

MATERIALS AND METHODS

Data was available on dam line hens collected over 9 generations. The pedigree used included a total of 19,159 birds. Hens were fed a standard commercial diet, and dietary energy, protein and other essential nutrient levels were adjusted according to age requirements. Birds were fed starter diets (27.5% CP and 2850 ME/Kg) ad libitum until the 17th wk of age. After the 18th wk of age, a restricted diet with less CP and more dietary energy (17% and 3520 ME/Kg) was fed. Until 18 wk of age, the birds were exposed to a daily photoperiod of 12 h light, with an intensity of 107 lx. From 18 to 30 wk of age, the photoperiod was modified to 6 h of restricted light and 18 h of light with an intensity of approximately 88 lx.

Measured Traits

Body weight and egg production traits were collected as part of a commercial breeding program. Body weights were recorded at 18 wk of age (**BW18**) and at lighting date (**BWL**, approximately 29 to 33 wk).

Egg production traits were recorded for a 180 d from the beginning of the lighting date. AFE was recorded and was defined as the age of the hen on the day of the first egg laid. Individual daily egg records were analyzed to investigate laying patterns and to measure BR. EN was also recorded during the 180 d. RL was determined individually and defined as the number of eggs laid divided by the length of the laying period. Laying period was defined as the number of days in which a hen layed during the recording period. To describe the cyclical laying process, clutch traits were defined as: CL expressed as the average number of days in a clutch per hen; maximum CL (**MCL**) expressed as the maximum number of days in a clutch per hen; pause length between clutches (**PL**) expressed as the average number of days between clutches per hen, and maximum pause length (**MPL**) expressed as the maximum number of

days between clutches per hen. Finally, consideration of bird physiology which varies between birds and their reproductive status, a novel BR trait was expressed as the average number of consecutive pause days between clutches that was higher than the average pause length per hen.

Statistical Analyses

Descriptive statistics of the data were calculated using R software (version 3.4.1). All studied traits were analyzed with the following animal model:

$$y_{ij} = \mu + hw_i + a_j + e_{ij} \quad (1)$$

where y_{ij} = the trait observation of the j^{th} hen in the i^{th} hatch-week, μ = mean of the population, hw_i = the fixed effect of hatch-week i , a_j = the random direct additive genetic effect of hen j , and e_{ij} = the random residual error.

Variance-covariance components were estimated using a multivariate animal model with restricted maximum likelihood. The same model was used for all traits under investigation. Multivariate analyses were used to estimate genetic and phenotypic parameters. The genetic and environmental variance estimates from univariate analysis were set as initial values for multivariate analysis. Parameter estimates were obtained using DMU (Madsen and Jensen, 2010). In addition, for PL, MPL, and BR traits, Box-Cox transformation was performed to improve normality (Box and Cox, 1964).

RESULTS AND DISCUSSION

In this study, genetic parameters for clutch and BR traits were estimated and their relationship with body weight and other conventional egg production traits in a female turkey line were investigated. Descriptive statistics of the recorded traits are shown in Table 1.

Table 1. Descriptive statistics for body weight and egg production traits in turkeys.

TRAITS ¹	Number of records	Least square mean (SE)
BW18 (kg)	82,033	10.75 (0.002)
BWL (kg)	2972	14.75 (0.01)
AFE (d)	5538	230.11 (0.11)
EN (d)	5538	78.53 (0.29)
RL (%)	5538	52.28 (0.14)
CL (d)	5327	3.27 (0.01)
MCL (d)	5327	5.01 (0.03)
PL (d)	5538	1.83 (0.01)
MPL (d)	5538	8.15 (0.08)
BR (d)	5480	3.86 (0.03)

¹BW18 = body weight at 18 wk; BWL = body weight at lighting date; AFE = age at first egg; EN = egg number; RL = rate of lay; CL = clutch length; MCL = maximum clutch length; PL = pause length; MPL = maximum pause length; BR = the average number of consecutive pause days between clutches that were higher than the average pause length per hen.

Heritability Estimates of Body Weight, Egg Production, Clutch, and BR Traits

The estimates of genetic and phenotypic parameters of body weight and egg production traits are shown in Table 2. Body weight at 18 wk and body weight at lighting (approximately 29 to 33 wk) were used to characterize the growth of each turkey, the heritability estimates for these traits were 0.50 ± 0.05 and 0.53 ± 0.01 , respectively. The heritabilities were found to be higher than those previously reported of 0.34 and 0.43 for body weight at 19 wk in UK and USA dam-line turkeys, respectively, using a multivariate animal model (Kranis et al., 2006). Willems et al. (2014) reported heritability of 0.48 for 18-wk body weight in a bronze dam line, which was a little lower than our estimate. Nestor et al. (2008) indicated that the magnitude of genetic relationships between different age groups and correlated traits change with selection; more intense selection decreases heritability over time. Finally, heritabilities were estimated in different lines, which may also affect estimates. Because the female line investigated here has not been heavily selected for body weight, and only egg-producing birds were used in the analysis, we could expect higher heritability for body weight traits in our study than in those previously published.

With regards to conventional egg production traits, AFE had a moderate heritability of 0.22 ± 0.03 . Previous studies in chickens reported higher heritability estimates, ranging from 0.37 to 0.55 in hybrid and purebred lines (Wolc et al., 2012; Tongsiri et al., 2015), although these differences may be because those studies were carried out in another species. EN and RL were moderately heritable (0.28 ± 0.03 ; 0.29 ± 0.03 , respectively), which are similar estimates to those found in three other selected turkey lines (Chapuis et al., 1996; Kranis et al., 2006).

The heritability of CL was estimated to be 0.21 ± 0.03 and is consistent with estimates obtained with different models in laying hens (Akbas et al., 2002). Heritability for maximum CL was higher (0.27 ± 0.02) than that estimated for average CL and is similar to that found in previous research in laying hens (Wolc et al., 2010). Nestor (1971) reported a higher heritability estimate (0.47) for maximum CL in turkeys using a simple method of regression of daughters on dams. In this study, restricted maximum likelihood methodology was used, which may affect on the magnitude of the estimated parameters.

In the current study, heritability estimates for pause length and MPL were 0.25 ± 0.03 and 0.15 ± 0.03 for non-transformed data, and 0.19 ± 0.03 and 0.16 ± 0.02 for transformed data respectively. The transformation aimed at improving the normality of traits did not change the estimated heritabilities for MPL and BR traits, which is consistent with the study of Anang et al. (2000). However, the heritability for PL increased, which indicates that transformation can improve the statistical properties of a trait depending on its original

Table 2. Heritabilities (diagonal, bold), genetic (above diagonal), and phenotypic (below diagonal) correlations with standard errors for body weight and egg production traits.¹

Traits ¹	BW18	BWL	AFE	EN	RL	CL	MCL	PL	MPL	BR	TPL	TMPL	TBR
BW18	0.50 ± 0.05	0.91 ± 0.02	0.13 ± 0.04	-0.27 ± 0.04	-0.32 ± 0.04	-0.40 ± 0.04	-0.38 ± 0.04	0.12 ± 0.04	0.27 ± 0.06	0.07 ± 0.05	0.19 ± 0.10	0.23 ± 0.14	0.14 ± 0.12
BWL	0.72 ± 0.05	0.53 ± 0.01	0.03 ± 0.01	-0.33 ± 0.06	-0.34 ± 0.06	-0.33 ± 0.07	-0.36 ± 0.07	0.25 ± 0.08	0.20 ± 0.09	0.16 ± 0.10	0.21 ± 0.11	0.17 ± 0.09	0.12 ± 0.12
AFE	0.04 ± 0.03	0.01 ± 0.01	0.22 ± 0.03	-0.42 ± 0.07	-0.25 ± 0.07	-0.39 ± 0.08	-0.44 ± 0.07	0.22 ± 0.09	0.16 ± 0.09	0.21 ± 0.10	0.19 ± 0.12	0.12 ± 0.14	0.20 ± 0.11
EN	-0.18 ± 0.03	-0.15 ± 0.03	-0.24 ± 0.04	0.28 ± 0.03	0.96 ± 0.01	0.73 ± 0.05	0.78 ± 0.03	-0.84 ± 0.05	-0.87 ± 0.03	-0.85 ± 0.04	-0.85 ± 0.03	-0.91 ± 0.05	-0.94 ± 0.03
RL	-0.18 ± 0.03	-0.18 ± 0.05	-0.12 ± 0.03	0.75 ± 0.02	0.29 ± 0.03	0.68 ± 0.05	0.76 ± 0.03	-0.89 ± 0.01	-0.85 ± 0.03	-0.85 ± 0.03	-0.88 ± 0.02	-0.91 ± 0.04	-0.93 ± 0.03
CL	-0.16 ± 0.03	-0.14 ± 0.05	-0.10 ± 0.04	0.43 ± 0.03	0.37 ± 0.03	0.21 ± 0.03	0.96 ± 0.02	-0.37 ± 0.08	-0.39 ± 0.08	-0.30 ± 0.10	-0.32 ± 0.10	-0.48 ± 0.11	-0.35 ± 0.10
MCL	-0.15 ± 0.02	-0.15 ± 0.06	-0.15 ± 0.04	0.48 ± 0.03	0.48 ± 0.03	0.92 ± 0.01	0.27 ± 0.03	-0.49 ± 0.07	-0.48 ± 0.07	-0.41 ± 0.09	-0.45 ± 0.10	-0.53 ± 0.11	-0.45 ± 0.10
PL	0.11 ± 0.03	0.10 ± 0.04	0.08 ± 0.04	-0.69 ± 0.03	-0.85 ± 0.01	-0.15 ± 0.03	-0.26 ± 0.04	0.25 ± 0.03	0.80 ± 0.04	0.93 ± 0.02	NA	NA	NA
MPL	0.12 ± 0.02	0.08 ± 0.05	0.04 ± 0.03	-0.52 ± 0.03	-0.67 ± 0.03	-0.12 ± 0.03	-0.20 ± 0.03	0.71 ± 0.02	0.15 ± 0.03	0.96 ± 0.01	NA	NA	NA
BR	0.06 ± 0.05	0.06 ± 0.04	0.07 ± 0.03	-0.60 ± 0.03	-0.67 ± 0.03	-0.11 ± 0.03	-0.20 ± 0.03	0.81 ± 0.01	0.83 ± 0.01	0.15 ± 0.03	NA	NA	NA
TPL	0.13 ± 0.03	0.13 ± 0.04	0.09 ± 0.03	-0.81 ± 0.01	-0.90 ± 0.01	-0.23 ± 0.03	-0.31 ± 0.02	NA	NA	NA	0.19 ± 0.03	0.94 ± 0.02	0.96 ± 0.01
TMPL	0.10 ± 0.03	0.13 ± 0.05	0.06 ± 0.03	-0.66 ± 0.01	-0.77 ± 0.02	-0.22 ± 0.02	-0.24 ± 0.01	NA	NA	NA	0.83 ± 0.05	0.16 ± 0.02	0.97 ± 0.01
TBR	0.10 ± 0.04	0.11 ± 0.04	0.11 ± 0.04	-0.75 ± 0.01	-0.82 ± 0.02	-0.23 ± 0.03	-0.30 ± 0.02	NA	NA	NA	0.87 ± 0.02	0.91 ± 0.03	0.16 ± 0.03

¹BW18 = body weight at 18 wk; BWL = body weight at lighting date; AFE = age at first egg; EN = egg number; RL = rate of lay, CL = clutch length, MCL = maximum clutch length; PL = pause length; MPL = maximum pause length; BR = the average number of consecutive pause days between clutches that were higher than the average pause length per hen. TPL, TMPL and TBR = pause length, maximum pause length and broodiness using transformed data, respectively.

distribution. Skewness coefficients of PL were higher compared to those of MPL and BR.

There is limited genetic information regarding pause traits in turkeys. However, a low estimated heritability (0.12) in laying hens has been reported (Akbas et al., 2002).

Heritability for BR by using non-transformed and transformed data was relatively low in the current study (0.15 ± 0.03 and 0.16 ± 0.03). Nestor (1972) estimated the heritability of BR to be moderate at 0.31, the difference in the heritability could be partially explained by using a different definition of BR, however he strongly recommended direct selection on egg production as opposed to including BR as an indicator trait, reasoning that BR would decrease indirectly. Housing and production systems, however, have changed dramatically over the past 50 yr, and the prevention and control strategies required as a result of broody behavior now pose significant problems for both birds and producers. Even though response to selection for clutch or BR traits could be limited due to low/moderate heritability, more comprehensive genetic improvement could be achieved through their inclusion in a selection index. With the larger size of modern flocks, the more intense production systems, and the increasing pressure from consumers and public to ensure high welfare standards in food production animals, the inclusion of behavioral traits such as BR in current selection indices may be timely. However, there is evidence indicating that making hens lay for long periods of time is the most reasonable method to efficiently use resources, having both environmental and economic benefits (Bain et al., 2016).

Correlations

The correlation between traits is important when considering which traits to include in a genetic selection program, as intense selection for one economic trait of interest often affects multiple traits either favourably or unfavourably. Understanding the relationship between traits of interest, thereby harnessing those relationships to maximize overall response to selection, is a characteristic intrinsic to balanced overall breeding objectives.

The high positive genetic correlation of 0.91 for body weight at 18 wk of age and body weight at lighting date traits suggests that these traits are genetically similar. This genetic correlation for body weight was close to prior estimates in turkeys (Aslam et al., 2011). Several studies have shown that body weight affects the onset of sexual maturity (Eitan and Soller, 2001, 2009), however the results of the current study revealed only low positive genetic correlations (0.13 to 0.03) between AFE and body weight at 18 wk of age and body weight at lighting date, respectively. Nestor et al. (2008) studied the response to selection of over 40 generations for increased body weight in turkeys and showed no change in AFE after 10 generations. These results support the relatively low correlation between body weight and AFE traits in the current study.

Negative genetic correlations between body weight and egg production traits were observed ($r_{g(BW18, EN)} = -0.27 \pm 0.04$; $r_{g(BWL, EN)} = -0.33 \pm 0.06$) and are in agreement with previous findings obtained in both chickens and turkeys (Nestor et al., 2000; Niknafs et al., 2012; Jambui et al., 2017). Nestor (1984) found that selection for increased body weight resulted in decreased EN and RL in turkeys, supporting those correlations found in the current investigation. Physiological studies reported that increases in body weight are negatively associated with factors affecting egg production, such as incidence of multiple ovulations, erratic ovipositions, shell defects, and follicular collapse (Hocking et al., 1989; Hocking, 1993). These findings clearly show the need to include both growth or body weight traits as well as egg production traits in breeding programs to obtain prolific, fast-growing birds.

A negative genetic correlations between body weight and CL traits ($r_{g(BW18, CL)} = -0.40 \pm 0.04$; $r_{g(BW18, MCL)} = -0.38 \pm 0.04$; $r_{g(BWL, CL)} = -0.33 \pm 0.07$; $r_{g(BWL, MCL)} = -0.36 \pm 0.07$) are in line with correlations found between body weight and egg production; heavier birds tend to produce smaller clutches. The results also confirm those reported by Nestor (1971). Subsequently, moderate positive genetic correlations were observed for body weight traits and pause traits ($r_{g(BW18, PL)} = 0.12 \pm 0.04$; $r_{g(BW18, MPL)} = 0.27 \pm 0.06$; $r_{g(BWL, PL)} = 0.25 \pm 0.08$; $r_{g(BWL, MPL)} = 0.20 \pm 0.09$), indicating that heavier birds have longer pauses between clutches. In a long-term selection experiment, body weight was not associated with genetic increases in EN, however EN was negatively associated with BR in early generations; in later generations, body weight decreased when the number of egg and CL increased and no significant change in BR were reported (Nestor, 1971; Nestor et al., 2000, 2008). Overall, results of these studies and the current study showed that the negative association of body weight and egg production is mediated through the CL and RL, however further studies may help to clarify the relationship between these traits and identify causal pathways.

Negative genetic correlation was recorded between AFE and EN ($r_{g(AFE, EN)} = -0.42 \pm 0.07$), which can be considered favorable, as early-maturing birds produce more eggs. Similar estimates were observed for CL ($r_{g(AFE, CL)} = -0.39 \pm 0.08$ and $r_{g(AFE, MCL)} = -0.44 \pm 0.07$). Positive genetic correlations were found between AFE, pause length ($r_{g(AFE, PL)} = 0.22 \pm 0.09$; $r_{g(AFE, MPL)} = 0.16 \pm 0.09$) and BR ($r_{g(AFE, BR)} = 0.21 \pm 0.10$), which are also favorable. These outcomes are in agreement with estimates reported by Harper (1949) who stated that turkey selection for early sexual maturity naturally results in fewer pauses and increased EN. Long term selection for age at sexual maturity, however, may have detrimental physiological effects (Kamali et al., 2007) and should be further investigated before implemented in breeding programs.

The phenotypic correlations in Table 2 show similar trends to those of the genetic correlations, albeit at

a lower magnitude. Standard errors were also slightly lower overall. The strongest phenotypic correlation observed was between pause length and RL ($r_p(PL, RL) = -0.85 \pm 0.01$, -0.90 ± 0.01 with transformed and non-transformed data), respectively.

Overall, heritabilities for the traits examined ranged from low to moderate, and correlations between body weight traits, conventional egg production traits, and clutch traits were in agreement with those previously published. The most important results of this study were the parameters estimated for BR and its relationship to other economically important traits in a female line. Due to the complexity of detecting BR, the risk of frustrated birds, and the expense incurred through management practices to mitigate broody behavior, genetic selection for less broody birds could provide a means for cumulative and long-term improvement in turkey breeding programs. In particular, the moderate heritability estimates of clutch traits combined with their correlation to BR and their favorable relationship with egg production traits make them possible candidates for inclusion in a selection index.

Chen and Tixier-Boichard (2003) supported the inclusion of clutch traits in dwarf laying hens breeding goals to increase EN. The same conclusion has been made by Wolc et al. (2010) to enhance genetic improvement of egg production persistence in hens.

The findings of the current study confirmed the strong negative correlations between body weight and EN, as previously reported, and presented new correlation estimates between CL, pause length, and BR in a female commercial turkey line. This important new knowledge could be used to select for animals more suitable for current housing and management systems, which express less broody behavior. Incorporation of additional traits in a selection index could be used to optimize selection for a broader genetic gain while managing the unfavorable genetic correlation of egg production traits with body weight.

CONCLUSION

In the present study, genetic parameters for body weight, egg production, clutch and pause traits, as well as BR were estimated to determine their importance in a breeding program for a female commercial line of turkeys. Mixed model methodologies were used to benchmark current genetic parameters compared to those in the literature. Furthermore, the development of a novel BR trait was presented, and its relationship to clutch and pause traits was investigated.

The results of this study confirmed the negative (unfavorable) correlations between egg production and body weight previously described in the literature. Despite unfavorable genetic and phenotypic correlations between egg production traits and those relating to BR, the inclusion of BR in a selection program through incorporation of CL traits and/or pause length traits is

feasible. Integration of either CL traits or pause length traits in a selection index is likely to increase EN while decreasing BR.

Ethics Statement

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

ACKNOWLEDGEMENTS

The authors extend their gratitude to the managers and personnel of the Hybrid Turkeys pedigree farm (Kitchener, Canada) for collecting and providing data used in this study. This study was part of the project entitled "Application of genomic selection in turkeys for health, welfare, efficiency and production traits" funded by the government of Canada through the Genome Canada Genomic Application Partnership Program and administered by Ontario Genomics (recipients: B.J. Wood (Industry) and C.F. Baes (Academic)). The authors are grateful to Ryley Vanderhout for proofreading the manuscript.

REFERENCES

- Akbas, Y., Y. Unver, I. Oguz, and O. Altan. 2002. Comparison of different variance component estimation methods for genetic parameters of clutch pattern in laying hens. *Eur. Poult. Sci.* 66:232–236.
- Anang, A., N. Mielenz, and L. Schuler. 2000. Genetic and phenotypic parameters for monthly egg production in White Leghorn hens. *J. Anim. Breed. Genet.* 117:407–415.
- Aslam, M. L., J. W. Bastiaansen, R. P. Crooijmans, B. J. Ducro, A. Vereijken, and M. A. Groenen. 2011. Genetic variances, heritabilities and maternal effects on body weight, breast meat yield, meat quality traits and the shape of the growth curve in turkey birds. *BMC Genet.* 12: 14.
- Bain, M. M., Y. Nys, and I. C. Dunn. 2016. Increasing persistency in lay and stabilising egg quality in longer laying cycles. What are the challenges? *Br. Poult. Sci.* 57:330–338.
- Box, G. P. E., and D. R. Cox. 1964. An analysis of transformations. *J. R. Stat. Soc.* 26:211–243.
- Chapuis, H., M. Tixier-Boichard, Y. Delabrosse, and V. Ducrocq. 1996. Multivariate restricted maximum likelihood estimation of genetic parameters for production traits in three selected turkey strains. *Genet. Sel. Evol.* 28:299–317.
- Chen, C. F., and M. Tixier-Boichard. 2003. Estimation of genetic variability and selection response for clutch length in dwarf brown-egg layers carrying or not the naked neck gene. *Genet. Sel. Evol.* 35:219–238.
- Eitan, Y., and M. Soller. 2001. Effect of photoperiod and quantitative feed restriction in a broiler strain on onset of lay in females and onset of semen production in males: a genetic hypothesis. *Worlds Poult. Sci. J.* 80:1397–1405.
- Eitan, Y., and M. Soller. 2009. Problems associated with broiler breeder entry into lay: a review and hypothesis. *Worlds Poult. Sci. J.* 65:641–648.
- El Halawani, E. M., and I. Rozenboim. 1993. The ontogeny and control of incubation behavior in turkeys. *Poult. Sci.* 72:906–911.
- Harper, J. A. 1949. The rate of response of turkey hens to artificial light as related to reproduction. *Poult. Sci.* 28:312–314.
- Hocking, P. M., D. Waddington, M. A. Walker, and A. B. Gilbert. 1989. Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by food restriction during rearing. *Br. Poult. Sci.* 30:161–174.
- Hocking, P. M. 1993. Effects of body weight at sexual maturity and the degree and age of restriction during rearing on the ovarian follicular hierarchy of broiler breeder females. *Br. Poult. Sci.* 34:793–801.
- Holm, B., M. Bakken, G. Klemetsdal, and O. Vangen. 2004. Genetic correlations between reproduction and production traits in swine. *J. Anim. Sci.* 82:3458–3464.
- Jambui, M., C. F. Honaker, and P. B. Siegel. 2017. Correlated responses to long-term divergent selection for 8-week body weight in female White Plymouth Rock chickens: sexual maturity. *Poult. Sci.* 96:3844–3851.
- Kamali, M. A., S. H. Ghorbani, M. Moradi Sharbabak, and M. J. Zamiri. 2007. Heritabilities and genetic correlations of economic traits in Iranian native fowl and estimated genetic trend and in-breeding coefficients. *Br. Poult. Sci.* 48:443–448.
- Kranis, A., P. M. Hocking, W. G. Hill, and J. A. Woolliams. 2006. Genetic parameters for a heavy female turkey line: impact of simultaneous selection for body weight and total egg number. *Br. Poult. Sci.* 47:685–693.
- Madsen, P., and J. Jensen. 2010. A User's Guide to DMU. Danish Inst. Agric. Sci., Res. Centre, Centre, Foulum, Denmark.
- Muir, W. M., and H. W. Cheng. 2014. Genetics and the Behavior of Domestic Animals. Second Edition. Elsevier Inc.
- Nestor, K. E. 1971. Genetics of growth and reproduction in the turkey. 3. Further selection for increased egg production. *Poult. Sci.* 50:1672–1682.
- Nestor, K. E. 1972. Broodiness, intensity of lay and total egg production of turkeys. *Poult. Sci.* 51:86–92.
- Nestor, K. E. 1980. Genetics of growth and reproduction in the turkey. 7. Relationship of total egg production, intensity of lay, broodiness, and body weight. *Poult. Sci.* 59:1385–1394.
- Nestor, K. E. 1984. Genetics of growth and reproduction in the turkey. 9. Long-term selection for increased 16-week body weight. *Poult. Sci.* 63:2114–2122.
- Nestor, K. E., J. W. Anderson, and R. A. Patterson. 2000. Genetics of growth and reproduction in the turkey. 14. Changes in genetic parameters over thirty generations of selection for increased body weight. *Poult. Sci.* 79:445–452.
- Nestor, K. E., J. W. Anderson, R. A. Patterson, and S. G. Velleman. 2006. Genetics of growth and reproduction in the turkey. 16. Effect of repeated backcrossing of an egg line to a commercial sire line. *Poult. Sci.* 85:1550–1554.
- Nestor, K. E., J. W. Anderson, R. A. Patterson, and S. G. Velleman. 2008. Genetics of growth and reproduction in the turkey. 17. changes in genetic parameters over forty generations of selection for increased sixteen-week body weight. *Poult. Sci.* 87:1971–1979.
- Niknafs, S., A. Nejati-Javaremi, H. Mehrabani-Yeganeh, and S. A. Fatemi. 2012. Estimation of genetic parameters for body weight and egg production traits in Mazandaran native chicken. *Trop. Anim. Health Prod.* 44:1437–1443.
- Ohkubo, T. 2017. Neuroendocrine control of broodiness. *Avian Reproduction, Advances in Experimental Medicine and Biology*. Springer, Singapore. 151–171.
- Opel, H., and J. A. Proudman. 1980. Failure of mammalian prolactin to induce incubation behavior in chickens and turkeys. *Poult. Sci.* 59:2550–2558.
- Pryce, J. E., M. D. Royal, P. C. Garnsworthy, and I. L. Mao. 2004. Fertility in the high-producing dairy cow. *Livest. Prod. Sci.* 86:125–135.
- Rauw, W. M., E. Kanis, E. N. Noordhuizen-Stassen, and F. J. Grommers. 1998. Undesirable side effects of selection for high production efficiency in farm animals: a review. *Livest. Prod. Sci.* 56:15–33.
- Romanov, M. N., R. T. Talbot, P. W. Wilson, and P. J. Sharp. 2002. Genetic control of incubation behavior in the domestic hen. *Poult. Sci.* 81:928–931.
- Saeki, Y., and Y. Tanabe. 1955. Changes in prolactin content of fowl pituitary during broody periods and some experiments on the induction of broodiness. *Poult. Sci.* 34:909–919.
- Safari, E., N. M. Fogarty, A. R. Gilmour, K. D. Atkins, S. I. Mortimer, A. A. Swan, F. D. Brien, J. C. Greeff, and J. H. J. Van Der Werf. 2007. Genetic Correlations among and between wool, growth, and reproduction traits in Merino Sheep. *J. Anim. Breed. Gen.* 124:65–72.

- Tongsiri, S., M. G. Jeyaruban, and J. H. J. Van Der Werf. 2015. Genetic parameters for egg production traits in purebred and hybrid chicken in a tropical environment. *Br. Poult. Sci.* 56: 613–620.
- Willems, O. W., N. J. H., and B. J. Wood, 2014. Genetic analysis of production and feed efficiency traits in an Orlopp turkey line (*Meleagris gallopavo*). *Bri. Poult. Sci.* 55:715–719.
- Wolc, A., M. Bednarczyk, M. Lisowski, and T. Szwaczkowski. 2010. Genetic relationships among time of egg formation, clutch traits and traditional selection traits in laying hens. *J. Anim. Feed Sci.* 19:452–459.
- Wolc, A., J. Arango, P. Settar, N. P. O'Sullivan, V. E. Olori, I. M. S. White, W. G. Hill, and J. C. M. Dekkers. 2012. Genetic parameters of egg defects and egg quality in layer chickens. *Poult. Sci.* 91:1292–1298.