Veterinary Integrative Sciences 2027; 25(1): e2026003-1-13. DOI: 10.12982/VIS.2027.003

Veterinary Integrative Sciences
ISSN; 2629-9968 (online)



Research article

Association of prolactin gene polymorphisms and haplotypes with egg production traits in Vietnamese Tre chickens

Trang Thanh Gia[1], Nguyen Thiet[2] and Nguyen Trong Ngu[2,*]

[1] *Department of Molecular Biology, Institute of Food and Biotechnology, Can Tho University, Can Tho City 94000, Vietnam*
[2] *Faculty of Animal Sciences, College of Agriculture, Can Tho University, Can Tho City 94000, Vietnam*

Abstract

Improving egg production in Tre chickens through conventional selection is challenging because reproductive traits are expressed late and vary among individuals. This study evaluated two prolactin gene polymorphisms, PRL_Indel and PRL_*Alu*I, and their associations with egg production traits in a single evaluated population of 400 Tre hens monitored for 20 weeks; no independent validation population was included. Genotype, additive, dominance, and haplotype effects were analyzed using models adjusted for age and body weight at first egg. Hens reached sexual maturity at 131.7 days on average, and total egg production averaged 57.1 ± 23.1 eggs. PRL_Indel showed moderate genetic variation but was not significantly associated with the evaluated traits. In contrast, PRL_*Alu*I was associated with total egg production, laying rate, and peak production. TT hens showed higher adjusted means than CC hens, and contrast analysis indicated a mainly additive favorable effect of the T allele. Haplotype analysis was consistent with this pattern, with the I-C haplotype showing lower egg production and laying rate than the D-T reference haplotype. These findings represent population-specific statistical associations rather than evidence of direct causality. PRL_*Alu*I and related haplotype information may be considered candidate markers for egg production traits in Tre chickens, but validation in independent populations and functional studies are needed before routine breeding application.

Keywords: Egg production, Haplotype, PRL polymorphism, Prolactin, Tre chickens

*Corresponding author: Nguyen Trong Ngu, Faculty of Animal Sciences, College of Agriculture, Can Tho University, Can Tho City *94000*, Vietnam. E-mail: ntngu@ctu.edu.vn. Tel: +84 292 3831166.

Funding; *The authors sincerely acknowledge the Department of Science and Technology of Dong Thap Province for providing financial support for this study through the research project coded ĐTNN 09/23.*

Article history; *received manuscript: 10 June 2026,*
revised manuscript: 28 June 2026,
accepted manuscript: 30 July 2026,
published online: 25 August 2026,
Academic editor; *Korakot Nganvongpanit*

INTRODUCTION

Local chicken breeds are valuable genetic resources for sustainable poultry production because they are often well adapted to local environments, show good resilience under smallholder conditions, and possess meat quality traits preferred by consumers (Phuong et al., 2020). In Vietnam, Tre chickens are appreciated for their small body size, diverse plumage, and firm, flavorful meat (Hung et al., 2014; Phuong et al., 2020). With increasing consumer interest in specialty poultry products, the production of Tre chickens has gradually shifted from traditional backyard systems toward more intensive and market-oriented farming. However, the wider use of Tre chickens in commercial production is still limited by reproductive performance, particularly low egg yield, late or variable onset of lay, and broodiness-related interruptions in egg production (Phuong et al., 2018; Ngu et al., 2026).

Improving egg production in local chicken populations is not straightforward. Egg production is a sex-limited and complex trait, and its full expression can only be evaluated after hens reach reproductive age. In addition, reproductive traits are generally influenced by many genes and environmental factors, which makes progress through conventional phenotypic selection relatively slow, especially in less intensively selected populations (Fairfull and Gowe, 1990; Mackay, 2001; Dekkers, 2004). In this context, marker-assisted selection (MAS) may complement phenotypic selection by helping to identify birds carrying favorable genetic variants before complete laying records are available.

Among the candidate genes related to reproductive performance in chickens, the prolactin (PRL) gene has received considerable attention. Prolactin plays an important role in the regulation of incubation behavior, and elevated prolactin levels are closely associated with broodiness, suppression of ovarian activity, and temporary cessation of laying (Reddy et al., 2002; Jiang et al., 2005). Several polymorphisms have been reported within or near the avian PRL gene, including single nucleotide polymorphisms and insertion/deletion variants located in regulatory and transcribed regions (Cui et al., 2006). Two commonly studied variants are the 24-bp insertion/deletion in the promoter region, referred to as PRL_Indel, and the C-2402T substitution in the 5' flanking/promoter region, referred to as PRL_*Alu*I. The 24-bp insertion in the PRL promoter has been reported in relation to broody traits in chickens, supporting its potential relevance to reproductive regulation (Jiang et al., 2005). In addition, polymorphisms in the 5' regulatory region of PRL have been associated with egg production, egg quality traits, and prolactin expression in White Leghorn chickens (Bhattacharya et al., 2011). These findings suggest that regulatory variation in PRL may contribute to differences in laying performance, although the direction and magnitude of the effect may vary among populations.

Previous studies have suggested that PRL polymorphisms may be associated with egg production and broodiness-related traits, but the reported effects are not always consistent across chicken populations. For example, in the White Leghorn population investigated by Cui et al. (2006), the 24-bp insertion allele was reported at a very high frequency and was discussed in relation to reduced broodiness and improved laying performance. Similarly, associations involving PRL_*Alu*I have been reported in different indigenous chicken populations. However, the favorable allele or genotype may differ among breeds, and some studies have reported neutral or even contrasting effects depending on the population examined. These differences suggest that the usefulness of PRL markers may depend on the genetic background, breeding history, and linkage phase within each target population.

Although PRL polymorphisms have been investigated in several chicken populations, their relationship with egg production traits in Tre chickens has not been well documented. Recent related work has examined candidate gene polymorphisms associated with reproductive traits in Ac chickens, including

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INHA/*Pst*I and VIPR1/*Hha*I variants (Phuong et al., 2023). In comparison with these previous studies, the novelty of the present work is its focus on Vietnamese Tre chickens and on the combined evaluation of PRL_Indel, PRL_*Alu*I, additive/dominance effects, and PRL haplotypes in a 400-hen population. It is also unclear whether PRL_Indel and PRL_*Alu*I act independently or whether their combined haplotype background is related to egg production in this breed. Therefore, the present study was conducted to evaluate the genetic variation of these two PRL polymorphisms and to examine their associations with egg production traits in Vietnamese Tre chickens. Single-locus genotype effects, additive and dominance effects, and haplotype associations were also examined to better describe how PRL variation is related to egg production traits in this local chicken population.

MATERIALS AND METHODS

Experimental birds and trait measurements

All chicken care and experimental procedures were conducted in accordance with institutional guidelines for the care and use of experimental animals. The study protocol was reviewed and approved by the Animal Ethics Committee of Can Tho University under approval number CTU-AEC24032.

A total of 400 Tre laying hens were used in this study. The birds were selected based on breed-specific phenotypic standards and reared at an experimental farm in Dong Thap province, southern Vietnam (10.3541° N, 106.3985° E). The hens represented a single evaluated Tre chicken flock maintained under the same farm conditions. Sampling was based on breed-specific phenotypic standards and flock availability rather than a pedigree-based random design. Detailed pedigree or genomic relationship information was not available; therefore, potential relatedness among hens could not be explicitly modeled. This area is characterized by a tropical monsoon climate with two distinct seasons: a rainy season generally occurring from May to November and a dry season generally extending from December to April. The hens were of the same age and were housed in an open-sided poultry house, with each hen kept in an individual cage to allow accurate recording of egg production traits.

Throughout the experimental period, the hens were managed under the same environmental, nutritional, and veterinary conditions. They were provided with a commercial complete layer diet and water *ad libitum*. The diet was formulated for laying hens from 19 weeks of age and contained 17% crude protein, 2,700 kcal/kg metabolizable energy, 3.4-4.8% calcium, 0.4-1.0% total phosphorus, 0.7% lysine, and 0.6% methionine plus cystine. The lighting program was maintained at approximately 14-16 h of light per day. Routine farm veterinary care, vaccination, and biosecurity practices were applied during the study.

Egg production was recorded daily for each hen over a 20-week evaluation period. The recording period started when the flock reached an overall laying rate of 5%, and this point was defined as week 1 of the laying performance evaluation. The recorded traits included age at first egg (AFE, days), body weight at first egg (BWFE, kg), and egg production in five consecutive four-week intervals: weeks 1-4, 5-8, 9-12, 13-16, and 17-20.

Total egg production was calculated as the cumulative number of eggs produced by each hen during the 20-week period. Overall laying rate was calculated as: Laying rate (%) = (total egg production during 20 weeks / 140) × 100, where 140 represents the total number of observation days. Peak production was defined as the highest number of eggs produced by an individual hen in any four-week interval during the 20-week evaluation period.

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DNA extraction and genotyping

Feather follicle samples were collected from each hen at 20 weeks of age. The samples were temporarily stored in iceboxes for a short period after collection and then preserved at -20°C until DNA extraction.

Genomic DNA was extracted using the standard phenol-chloroform method. The quality and integrity of extracted DNA were checked by electrophoresis on 1% agarose gel. DNA concentration and purity were assessed using spectrophotometry at 260/280 nm. Only DNA samples with acceptable concentration and purity were used for subsequent PCR amplification. The DNA samples were diluted to a working concentration of 50 ng/μL before genotyping.

Two polymorphisms in the prolactin gene were genotyped: PRL_Indel, a 24-bp insertion/deletion polymorphism at position -358 in the promoter region, and PRL_*Alu*I, a C-2402T substitution in the 5' flanking/promoter region. The PRL_Indel locus was genotyped by direct PCR followed by agarose gel electrophoresis, whereas the PRL_*Alu*I locus was genotyped using PCR-restriction fragment length polymorphism (PCR-RFLP). Primer sequences, annealing temperatures, genotyping methods, expected product sizes, and references are shown in Table 1.

Table 1 Primer sequences and PCR conditions for PRL gene polymorphism genotyping

Primer	Sequence (5'-3')	Tm (°C)	Restriction enzyme/ genotyping method	Product size (bp)	Ref.
PRL_Indel_F	TTTAATATTGGTGGGTGAAGAGACA	54	Indel (24 bp)	154/130	Xu et al. (2011)
PRL_Indel_R	ATGCCACTGATCCTCGAAAACTC				
PRL_*Alu*I_F	AGAGGCAGCCCAGGCATTTTAC	62	*Alu*I	439	Bora et al. (2021)
PRL_*Alu*I_R	CCTGGGTCTGGTTTGGAAATTG				

The PCR amplification was performed in a final reaction volume of 10 μL. Each reaction contained 5.0 μL of 2× PCR Master Mix (Phu Sa Genomics, Vietnam), 0.20 μL of forward primer (10 pmol/μL), 0.20 μL of reverse primer (10 pmol/μL), 2.0 μL of genomic DNA template, corresponding to approximately 100 ng of DNA per reaction, and 2.60 μL of nuclease-free water.

For the PRL_Indel locus, PCR amplification was performed under the following cycling conditions: initial denaturation at 94°C for 4 min; 35 cycles of denaturation at 94°C for 30 s, annealing at 54°C for 35 s, and extension at 72°C for 35 s; followed by a final extension at 72°C for 7 min. Because PRL_Indel is a 24-bp insertion/deletion polymorphism, PCR products were directly separated on 2.5% agarose gel at 70 V for 25 min. The I allele was identified by a 154-bp fragment, whereas the D allele was identified by a 130-bp fragment. Accordingly, the II genotype showed a single 154-bp band, the DD genotype showed a single 130-bp band, and the ID genotype showed both 154-bp and 130-bp bands.

For the PRL_*Alu*I locus, PCR amplification was performed using the following cycling conditions: initial denaturation at 95°C for 5 min; 35 cycles of denaturation at 95°C for 45 s, annealing at 62°C for 45 s, and extension at 72°C for 45 s; followed by a final extension at 72°C for 5 min. The PCR product size was 439 bp. The PCR products were digested with *Alu*I restriction enzyme (Thermo Fisher Scientific, USA) according to the manufacturer's instructions and incubated at 37°C for 8 h. The digested products were separated on 2.5% agarose gel and visualized under UV light after staining with Gelred (ABT, Vietnam).

The PRL_*Alu*I genotypes were determined based on restriction fragment patterns after *Alu*I digestion of the 439-bp PCR product. The TT genotype produced fragments of 304, 81, and 54 bp; the CC genotype produced fragments of 160, 144, 81, and 54 bp; and the TC genotype produced fragments of 304, 160, 144, 81, and 54 bp. Because the 81-bp and 54-bp fragments are relatively small, genotype identification was primarily based on the diagnostic 304-bp fragment for

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the T allele and the 160/144-bp fragments for the C allele. Genotype quality control was based on DNA quality assessment and clear diagnostic banding patterns. For genotyping quality control, selected PCR products representing the observed genotypes at the PRL_Indel and PRL_*Alu*I loci were confirmed by Sanger sequencing. The obtained sequences were checked and aligned with the chicken PRL reference sequence. Sequencing results confirmed the 24-bp insertion/deletion at PRL_Indel and the C-2402T substitution at PRL_*Alu*I, supporting the PCR and PCR-RFLP genotype calls.

Statistical analysis

All statistical analyses were performed using R software (R Core Team, 2024). Genotype and allele frequencies were calculated for the PRL_Indel and PRL_*Alu*I loci. Genetic diversity at each locus was assessed using observed heterozygosity (Ho), expected heterozygosity (He), and polymorphism information content (PIC). Departure from Hardy-Weinberg equilibrium (HWE) was tested using a chi-square test.

Descriptive statistics were calculated for all recorded traits, including mean, standard deviation, minimum, maximum, and coefficient of variation. The association between PRL genotypes and egg production traits was evaluated using adjusted linear models. Genotype was included as a fixed effect, while age at first egg and body weight at first egg were included as covariates for egg production traits to reduce potential bias related to variation in sexual maturity and body weight. The model was defined as follows: $Y_{ij} = \mu + G_i + \beta_1(AFE_{ij}) + \beta_2(BWFE_{ij}) + e_{ij}$; where Y_{ij} is the observed value of the trait for the j-th hen within the i-th genotype group; μ is the overall mean; G_i is the fixed effect of the i-th genotype; AFE_{ij} and $BWFE_{ij}$ are age at first egg and body weight at first egg, respectively; β_1 and β_2 are the corresponding regression coefficients; and e_{ij} is the residual error.

Adjusted least-square means and standard errors were estimated for each genotype group using the emmeans package in R. Pairwise comparisons among genotypes were performed using Tukey's post-hoc test. For the PRL_*Alu*I locus, additive and dominance effects were estimated using linear contrasts based on adjusted least-square means. The additive effect was calculated as: a = (TT - CC)/2 and the dominance effect was calculated as: d = TC - (CC + TT)/2; where CC, TC, and TT represent the adjusted least-square means of the corresponding genotypes.

Haplotype frequencies for the PRL_Indel and PRL_*Alu*I loci were inferred from unphased genotype data using the expectation-maximization algorithm implemented in the haplo.stats package. Haplotype association analysis was performed for selected egg production traits using haplotype-based linear models adjusted for age at first egg and body weight at first egg. The most frequent haplotype was used as the reference haplotype. Based on the observed haplotype distribution, the D-T haplotype was used as the reference in the final analysis. Haplotype effects were reported as regression coefficients relative to this reference haplotype.

Statistical significance was declared at $P < 0.05$. Results with $0.05 <= P < 0.10$ were considered as trends and interpreted cautiously where relevant.

RESULTS

Genetic diversity of PRL_Indel and PRL_*Alu*I polymorphisms

Genotype and allele frequencies of the two PRL polymorphisms are presented in Table 2. At the PRL_Indel locus, the DD genotype was the most frequent (n = 182; 45.50%), followed by ID (n = 163; 40.75%) and II (n = 55; 13.75%); the D allele was more common than the I allele (0.659 vs. 0.341). At the

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PRL_*Alu*I locus, the TT genotype predominated (n = 224; 56.00%), followed by TC (n = 134; 33.50%) and CC (n = 42; 10.50%); the T allele showed a higher frequency than the C allele (0.728 vs. 0.272).

Table 2 Genotype and allele frequencies, genetic diversity indices, and Hardy–Weinberg equilibrium of PRL polymorphisms

Locus	G	n	F (%)	All	All-F	Ho	He	PIC	HWE (χ^2)	P
PRL_Indel	DD	182	45.50	D	0.659	0.408	0.449	0.348	3.51	0.061
	ID	163	40.75	I	0.341					
	II	55	13.75							
PRL_*Alu*I	CC	42	10.50	C	0.272	0.335	0.396	0.318	9.643	0.002
	TC	134	33.50	T	0.728					
	TT	224	56.00							

All: Allele; F: Frequency; G: Genotype; Ho: observed heterozygosity; He: expected heterozygosity; PIC: polymorphism information content; HWE: Hardy–Weinberg equilibrium.

Both loci showed moderate genetic variation, with PIC values of 0.348 for PRL_Indel and 0.318 for PRL_*Alu*I. The PRL_Indel genotype distribution did not deviate significantly from Hardy-Weinberg equilibrium, although the value was close to the threshold of significance (P = 0.061). In contrast, PRL_*Alu*I showed a significant deviation from Hardy-Weinberg equilibrium (P = 0.002).

Descriptive statistics of egg production traits

Descriptive statistics for age at first egg, body weight at first egg, and egg production traits are shown in Table 3. The hens reached sexual maturity at an average age of 131.7 ± 12.0 days, with relatively low variation among individuals (CV = 9.1%). Body weight at first egg followed a similar pattern, averaging 1.34 ± 0.13 kg (CV = 9.7%).

Table 3 Descriptive statistics of egg production traits and onset-related traits

Trait	N	Mean ± SD	Min	Max	CV (%)
Age at first egg (days)	400	131.7 ± 12.0	110.0	175.0	9.1
Body weight at first egg (kg)	400	1.34 ± 0.13	1.05	1.72	9.7
Egg production from weeks 1-4	400	8.9 ± 7.5	0.0	25.0	84.2
Egg production from weeks 5-8	400	14.8 ± 6.4	0.0	28.0	43.2
Egg production from weeks 9-12	400	11.4 ± 6.6	0.0	26.0	57.8
Egg production from weeks 13-16	400	10.7 ± 6.4	0.0	26.0	59.6
Egg production from weeks 17-20	400	11.3 ± 6.7	0.0	25.0	59.0
Total egg production	400	57.1 ± 23.1	1.0	113.0	40.4
Laying rate (%)	400	40.8 ± 16.5	0.7	80.7	40.4
Peak production	400	17.7 ± 5.1	1.0	28.0	28.7

CV: coefficient of variation.

In contrast, egg production varied more widely among hens. Total egg production averaged 57.1 ± 23.1 eggs over the 20-week evaluation period, ranging from 1 to 113 eggs, while the laying rate averaged 40.8 ± 16.5%. These results indicate clear individual differences in laying performance within the evaluated population.

Association between PRL_Indel genotypes and egg production traits

The association between PRL_Indel genotypes and egg production traits is shown in Table 4. No significant differences were detected among the DD, ID, and II genotypes for egg production across the five four-week intervals, total egg production, laying rate, or peak production (P > 0.05).

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Table 4 Effects of PRL_Indel genotypes on egg production traits

Trait	DD	ID	II	P-value
Egg production from weeks 1-4	8.6 ± 0.3	9.2 ± 0.3	9.0 ± 0.5	0.380
Egg production from weeks 5-8	15.1 ± 0.4	15.1 ± 0.5	13.0 ± 0.8	0.055
Egg production from weeks 9-12	11.5 ± 0.5	11.5 ± 0.5	10.3 ± 0.9	0.444
Egg production from weeks 13-16	11.1 ± 0.5	10.7 ± 0.5	9.5 ± 0.9	0.257
Egg production from weeks 17-20	11.8 ± 0.5	10.8 ± 0.5	11.0 ± 0.9	0.323
Total egg production	58.2 ± 1.5	57.3 ± 1.6	52.8 ± 2.8	0.225
Laying rate (%)	41.6 ± 1.1	40.9 ± 1.1	37.7 ± 2.0	0.225
Peak production	17.9 ± 0.3	17.9 ± 0.4	17.0 ± 0.6	0.434

Values are presented as least-square means ± SE.

Although DD and ID hens showed numerically higher total egg production than II hens, the difference was not significant. Total egg production was 58.2 ± 1.5 eggs for DD, 57.3 ± 1.6 eggs for ID, and 52.8 ± 2.8 eggs for II hens (P = 0.225). A similar tendency was observed during weeks 5-8, where DD and ID hens both averaged 15.1 eggs compared with 13.0 eggs in II hens, but this difference only approached statistical significance (P = 0.055). Taken together, PRL_Indel did not show a clear independent association with egg production traits in this population.

Association between PRL_*Alu*I genotypes and egg production traits

The PRL_*Alu*I locus was significantly associated with several egg production traits (Table 5). Hens carrying the TT genotype generally showed better laying performance than those carrying the CC genotype, while TC hens tended to show intermediate values.

Table 5 Effects of PRL_*Alu*I genotypes on egg production traits

Trait	CC	TC	TT	P-value
Egg production from weeks 1-4	9.2 ± 0.6	8.3 ± 0.3	9.3 ± 0.3	0.067
Egg production from weeks 5-8	12.8^{a} ± 0.9	14.5^{ab} ± 0.5	15.4^{b} ± 0.4	0.028
Egg production from weeks 9-12	9.5 ± 1.0	11.3 ± 0.6	11.7 ± 0.4	0.136
Egg production from weeks 13-16	8.9 ± 1.0	10.4 ± 0.5	11.3 ± 0.4	0.071
Egg production from weeks 17-20	9.2^{a} ± 1.0	10.8^{ab} ± 0.6	12.0^{b} ± 0.4	0.025
Total egg production	49.7^{a} ± 3.1	55.3^{ab} ± 1.7	59.6^{b} ± 1.3	0.006
Laying rate (%)	35.5^{a} ± 2.2	39.5^{ab} ± 1.2	42.6^{b} ± 1.0	0.006
Peak production	15.8^{a} ± 0.7	17.9^{b} ± 0.4	18.0^{b} ± 0.3	0.014

Values are presented as least-square means ± SE. Means within a row with different superscripts differ significantly at P < 0.05.

Total egg production differed significantly among genotypes, with TT hens producing 59.6 ± 1.3 eggs compared with 49.7 ± 3.1 eggs in CC hens (P = 0.006). The same pattern was observed for laying rate, which was higher in TT hens than in CC hens (P = 0.006). Peak production was also affected by PRL_*Alu*I, with TT and TC hens showing higher values than CC hens (P = 0.014).

Across the four-week intervals, significant genotype effects were observed during weeks 5-8 and weeks 17-20. During weeks 5-8, TT hens produced 15.4 ± 0.4 eggs compared with 12.8 ± 0.9 eggs in CC hens (P = 0.028). During weeks 17-20, TT hens produced 12.0 ± 0.4 eggs compared with 9.2 ± 1.0 eggs in CC hens (P = 0.025). Similar tendencies were also observed during weeks 1-4 (P = 0.067) and weeks 13-16 (P = 0.071), although these differences did not reach statistical significance. These results indicate a consistent pattern in which the TT genotype showed higher laying performance than the CC genotype.

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Additive and dominance effects of PRL_*Alu*I

Estimated additive and dominance effects of PRL_*Alu*I are presented in Table 6. The additive effect was positive for most egg production traits, supporting a favorable contribution of the T allele to laying performance. The strongest additive effects were observed for total egg production and laying rate, with estimated values of 4.95 and 3.53, respectively, both of which were statistically significant (P = 0.004).

Table 6 Estimated additive and dominance effects of PRL_*Alu*I on egg production traits

Trait	CC	TC	TT	Additive effect (a) ± SE	P-value for a	Dominance effect (d) ± SE	P-value for d
Egg production from weeks 1-4	9.2	8.3	9.3	0.02 ± 0.34	0.942	-0.98 ± 0.49	0.045
Egg production from weeks 5-8	12.8	14.5	15.4	1.27 ± 0.50	0.011	0.36 ± 0.71	0.611
Egg production from weeks 9-12	9.5	11.3	11.7	1.10 ± 0.55	0.046	0.71 ± 0.79	0.370
Egg production from weeks 13-16	8.9	10.4	11.3	1.17 ± 0.53	0.029	0.32 ± 0.76	0.675
Egg production from weeks 17-20	9.2	10.8	12.0	1.38 ± 0.55	0.012	0.23 ± 0.79	0.767
Total egg production	49.7	55.3	59.6	4.95 ± 1.69	0.004	0.65 ± 2.43	0.788
Laying rate (%)	35.5	39.5	42.6	3.53 ± 1.21	0.004	0.47 ± 1.73	0.788
Peak production	15.8	17.9	18.0	1.12 ± 0.39	0.004	0.99 ± 0.55	0.074

Values are presented as least-square means ± SE.

Positive additive effects were also observed across most laying intervals and for peak production. In contrast, dominance effects were generally smaller and not significant for most traits, except for egg production from weeks 1-4 (P = 0.045). The results indicate that the favorable effect of PRL_*Alu*I on laying performance was mainly additive.

Haplotype frequency and haplotype association analysis

Estimated haplotype frequencies are shown in Table 7, and haplotype associations with selected egg production traits are presented in Table 8. Four haplotypes were inferred from PRL_Indel and PRL_*Alu*I: D-T, I-T, D-C, and I-C. The D-T haplotype was the most frequent, accounting for 52.1% of the estimated haplotypes, followed by I-T at 20.7%, D-C at 13.8%, and I-C at 13.4%.

Table 7 Estimated haplotype frequencies of PRL_Indel and PRL_*Alu*I loci

Haplotype	PRL_Indel	PRL_*Alu*I	Frequency	Frequency (%)
D-T	D	T	0.5206	52.06
I-T	I	T	0.2069	20.69
D-C	D	C	0.1381	13.81
I-C	I	C	0.1344	13.44

Haplotypes were estimated from unphased genotype data using the expectation-maximization algorithm.

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Table 8 Association of estimated PRL haplotypes with selected egg production traits in Tre chickens

Trait	Haplotype	Effect vs D-T ± SE	P-value
Egg production from weeks 5–8	D-C	-1.40 ± 0.65	0.032
	I-C	-1.43 ± 0.63	0.024
	I-T	-0.86 ± 0.55	0.121
Egg production from weeks 17–20	D-C	-0.09 ± 0.69	0.892
	I-C	-2.31 ± 0.69	<0.001
	I-T	0.48 ± 0.59	0.419
Total egg production	D-C	-3.47 ± 2.19	0.114
	I-C	-6.57 ± 2.15	0.002
	I-T	-0.74 ± 1.87	0.691
Laying rate (%)	D-C	-2.48 ± 1.57	0.114
	I-C	-4.69 ± 1.54	0.002
	I-T	-0.53 ± 1.34	0.691
Peak production	D-C	-0.78 ± 0.48	0.108
	I-C	-0.93 ± 0.48	0.055
	I-T	-0.21 ± 0.42	0.620

Values are regression coefficients ± SE relative to the reference haplotype D-T. Haplotype effects were estimated using haplotype-based linear models adjusted for age at first egg and body weight at first egg. These estimates represent relative haplotype effects rather than haplotype-specific means.

Because D-T was the most frequent haplotype, it was used as the reference in the association analysis (Table 8). Compared with D-T, the I-C haplotype was associated with lower total egg production and laying rate, with estimated effects of -6.57 (P = 0.002) and -4.69 (P = 0.002), respectively. The I-C haplotype was also associated with reduced egg production during weeks 5-8 (effect = -1.43, P = 0.024) and weeks 17-20 (effect = -2.31, P < 0.001). The D-C haplotype showed a negative effect during weeks 5-8 (effect = -1.40, P = 0.032), whereas I-T did not differ significantly from D-T for the analyzed traits (P > 0.05).

The haplotype analysis was consistent with the single-locus results for PRL_*Alu*I, showing lower performance mainly for the I-C haplotype relative to the D-T reference haplotype.

DISCUSSION

This study examined two PRL polymorphisms in relation to egg production traits in Vietnamese Tre chickens. The results showed that PRL_Indel was polymorphic but not significantly associated with the evaluated traits, whereas PRL_*Alu*I was more consistently associated with total egg production, laying rate, and peak production. The additive and haplotype analyses were broadly consistent with the PRL_*Alu*I result. Because the study was conducted in a single evaluated population, we interpret these findings as population-specific statistical associations that require confirmation in independent flocks before breeding application.

The moderate PIC values observed for both PRL_Indel and PRL_*Alu*I indicate that these loci retained sufficient genetic variation for association analysis. The presence of polymorphism at both loci also means that these markers could be evaluated for association with laying traits in this population. At the PRL_Indel locus, the D allele was more frequent than the I allele. This pattern is similar to that reported in Vietnamese Lien Minh chickens, where the D allele was also predominant (Nguyen et al., 2018a; Nguyen et al., 2018b), but differs from some other populations, such as Mazandaran chickens, in which the I allele was reported at a higher frequency (Rashidi et al., 2012). This pattern also differs from the White Leghorn population examined by Cui et al. (2006), in which the 24-bp insertion allele was reported at a very high frequency. These differences suggest that allele

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frequencies at the PRL locus can vary considerably among breeds and may reflect differences in breeding history, selection pressure, and genetic background.

At the PRL_*Alu*I locus, the T allele and TT genotype were predominant in the evaluated Tre chickens. The significant deviation from Hardy-Weinberg equilibrium at this locus requires cautious interpretation. In the present population, observed heterozygosity was lower than expected heterozygosity, suggesting a possible heterozygote deficiency. This deviation may be explained by several factors, including population structure, non-random mating, sampling effects, previous selection, or technical factors related to genotyping. Because Tre chickens used in this study were sampled from an evaluated breeding population rather than a randomly mating natural population, some degree of deviation from Hardy-Weinberg equilibrium is not unexpected. Such deviation may also indicate underlying population stratification, which could potentially influence genotype-trait association results if genotype frequencies and laying performance differ among subgroups. Therefore, the association observed for PRL_*Alu*I is best interpreted as population-specific and requires validation in additional flocks or generations. Although the high frequency of the T allele is consistent with the favorable association observed in this study, it should not be considered direct evidence of directional selection without additional population-level or pedigree-based analyses.

The phenotypic results provide a useful background for interpreting the genetic associations. Tre chickens in this study reached sexual maturity relatively early and uniformly, as shown by the low coefficient of variation for age at first egg. However, egg production traits showed much wider variation among individuals. This contrast suggests that, although the onset of lay was relatively synchronized, the capacity to sustain egg production differed considerably among hens. Similar challenges have been reported in local chicken populations, where reproductive traits are often variable and improvement through conventional phenotypic selection can be slow because these traits are sex-limited, expressed later in life, and influenced by many genes and environmental factors (Fairfull and Gowe, 1990; Dekkers, 2004). In this context, molecular markers may provide useful support for identifying hens with favorable genetic potential, provided that marker effects are validated within the target population.

The lack of a significant association between PRL_Indel and laying performance is an important finding. Previous studies have often highlighted the 24-bp insertion/deletion in the promoter region of PRL because of its possible role in transcriptional regulation and broodiness-related traits (Jiang et al., 2005; Cui et al., 2006). In some populations, the insertion allele or genotypes carrying this allele have been associated with improved reproductive performance or reduced broodiness. For example, favorable effects of PRL_Indel have been reported in commercial or indigenous chicken populations, although the direction and strength of association have not always been consistent across studies (Cui et al., 2006; Rashidi et al., 2012; Nguyen et al., 2018a; Nguyen et al., 2018b). Similar population-dependent results have also been reported in Silkie chickens, where PRL and DRD2 Indel polymorphisms were evaluated for reproductive traits, further supporting the view that reproductive marker effects should be validated within each target population (Tu et al., 2023). In the present study, however, PRL_Indel showed no clear independent effect on total egg production, laying rate, or peak production. This may indicate that the 24-bp indel is not a major marker for laying performance in these Tre chickens, or that its effect depends on other loci and the broader genetic background.

One possible explanation for the neutral effect of PRL_Indel is that the linkage phase between this marker and nearby functional variants may differ among chicken populations (Falconer and Mackay, 1996; Hartl and Clark, 2007). A marker that is useful in one breed may not show the same association in another if recombination, selection history, or founder effects have altered the relationship between the marker and the causal variant. Another possibility is that PRL_Indel

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influences reproductive traits related more directly to broodiness or PRL expression, as previously suggested for PRL-related polymorphisms in chickens (Jiang et al., 2005), but not strongly enough to affect egg production under the conditions evaluated in this study. Because broodiness behavior and PRL expression were not directly measured here, this interpretation remains tentative. Therefore, while PRL_Indel remains biologically relevant, the present results suggest that it should not be used as a standalone marker for improving egg production in Tre chickens without further supporting evidence.

In contrast, PRL_*Alu*I showed a clearer association with egg production traits. Hens carrying the TT genotype had higher total egg production, laying rate, and peak production than those carrying the CC genotype, while the TC genotype generally showed intermediate values. This pattern is consistent with the positive additive effect estimated for the T allele. The biological relevance of this locus is plausible because PRL_*Alu*I corresponds to the C-2402T substitution in the 5' flanking/promoter region of the PRL gene, where sequence variation may influence transcriptional activity. Previous work has shown that polymorphisms in the regulatory region of PRL can be associated with egg production, egg quality traits, and PRL expression in chickens (Bhattacharya et al., 2011). In addition, PRL is closely involved in incubation behavior, and elevated prolactin levels are associated with broodiness, suppression of ovarian activity, and interruption of laying (Reddy et al., 2002; Jiang et al., 2005). In Tre chickens, variation within or near PRL may therefore contribute to differences in laying persistency, total egg production, and laying rate by modifying PRL regulation or by being linked to functional variants affecting this pathway. However, this biological explanation remains hypothetical because PRL expression, circulating prolactin levels, broodiness behavior, and functional assays were not examined in the present study. Thus, the observed PRL_*Alu*I association is best interpreted as a statistical association rather than evidence that the C-2402T substitution itself is causal. The effect may also reflect linkage disequilibrium with nearby functional variants within or around the PRL region.

The additive and dominance analyses provided further insight into the genetic action of PRL_*Alu*I. The positive additive effects observed for total egg production, laying rate, and most laying intervals suggest that the T allele, or a linked functional variant, may contribute additively to egg production traits in this population. This is relevant from a breeding perspective because additive effects are more predictable across generations than dominance effects and are therefore more directly related to selection response (Falconer and Mackay, 1996). In practical terms, TT hens produced approximately 9.9 more eggs over the 20-week evaluation period than CC hens, corresponding to a 7.1 percentage-point higher laying rate, and the estimated additive effect of the T allele was approximately 4.95 eggs over 20 weeks. Although these effects are moderate at the individual level, they may be meaningful in a local chicken population with relatively low and variable egg production, especially when marker information is used together with phenotypic records. Nevertheless, PRL_*Alu*I is best viewed as a supporting candidate marker rather than a confirmed quantitative trait nucleotide.

The haplotype analysis was useful for examining whether the two PRL loci showed a combined association with egg production traits. The D-T haplotype was the most frequent and was used as the reference haplotype. Compared with D-T, the I-C haplotype was associated with lower total egg production and laying rate, while I-T did not differ significantly from D-T. These results support the single-locus PRL_*Alu*I finding and suggest that the haplotype analysis mainly provides additional context rather than strong evidence for an independent haplotype effect. The lower performance associated with the I-C haplotype relative to D-T may partly reflect the PRL_*Alu*I C allele background or linkage with nearby functional variants within the PRL region. Because detailed linkage disequilibrium analysis was not performed, and because functional validation was not included, it would be

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premature to conclude that the two loci have a true independent or synergistic haplotype effect.

These results are relevant to ongoing efforts to identify genetic markers for reproductive traits in local poultry. Recent work reported associations of INHA/*Pst*I and VIPR1/*Hha*I polymorphisms with reproductive traits in Ac chickens (Phuong et al., 2023), whereas previous studies in Vietnamese local chickens have examined other candidate markers associated with egg production traits (Ngu et al., 2015; Phuong and Thuy, 2025). The present study adds population-specific information for Tre chickens by focusing on PRL_Indel, PRL_*Alu*I, and PRL haplotypes. Recent poultry genomics studies further show that egg production traits are polygenic and involve multiple genomic regions and reproductive regulatory networks. For example, whole-genome sequencing-based GWAS in Shuanglian and Laiwu Black chickens identified multiple loci and candidate genes for egg number and related traits (Fu et al., 2023; Lei et al., 2024), while multi-omics analysis has highlighted coordinated regulation across the hypothalamic-pituitary-ovarian axis and peripheral tissues (Wang et al., 2024). Therefore, PRL markers are best interpreted within a broader polygenic background and used only as supporting information together with phenotypic selection, not as standalone determinants of egg production.

Although the present study provides useful evidence for the association between PRL polymorphisms and egg production traits in Tre chickens, several statistical and biological limitations warrant consideration. Egg production across the five four-week intervals was analyzed as separate traits, and within-hen correlations among repeated laying intervals were not explicitly modeled. Therefore, interval-specific results warrant cautious interpretation and are best viewed as supportive of the overall pattern rather than independent confirmation. In addition, the statistical models did not include random hen effects, and multiple egg production traits and time intervals were tested without formal correction for multiple testing, which may increase the risk of false-positive findings. The analysis was conducted in a single evaluated population; therefore, the observed associations are best regarded as population-specific at this stage. Further validation in independent flocks, additional Tre chicken populations, or subsequent generations would help confirm the stability of these marker effects. PRL expression, circulating prolactin levels, and broodiness behavior were not assessed; therefore, the biological mechanism and direct functional relevance of the studied polymorphisms remain to be clarified. Finally, because this was a candidate gene association study, PRL_*Alu*I and related haplotype information are best regarded as promising candidate markers rather than confirmed causal variants.

Overall, PRL_*Alu*I appeared to be more closely related to egg production traits than PRL_Indel in this Tre chicken population. The TT genotype, the positive additive effect of the T allele, and the lower performance of the I-C haplotype relative to D-T showed a consistent pattern. Even so, PRL_*Alu*I remains a candidate marker rather than a confirmed causal variant, and its practical value needs to be validated before routine use in breeding programs.

CONCLUSIONS

The present study showed that PRL_Indel was not significantly associated with the evaluated egg production traits, whereas PRL_*Alu*I was associated with total egg production, laying rate, and peak production in the evaluated Tre chicken population. Hens with the TT genotype showed higher adjusted means than CC hens, and the T allele showed a positive additive effect. Haplotype analysis was broadly consistent with the PRL_*Alu*I result, with lower performance observed for the I-C haplotype relative to the D-T reference haplotype. These findings represent population-specific statistical associations rather than evidence of direct causality.

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PRL_*Alu*I and related haplotype information may be considered candidate markers to support, but not replace, phenotypic selection. Validation in independent populations or subsequent generations, together with functional studies, is needed before routine breeding application.

CONFLICT OF INTEREST

The authors declare no financial or personal conflicts of interest. ChatGPT (OpenAI) was used during manuscript preparation and revision to assist with English-language editing, improve clarity and readability, and restructure selected passages. All AI-assisted outputs were critically reviewed and revised by the authors, who take full responsibility for the accuracy and integrity of the final manuscript.

AUTHOR CONTRIBUTIONS

Trang Thanh Gia: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Visualization, Writing - original draft.
Nguyen Thiet: Investigation, Data curation, Formal analysis, Writing - original draft.
Nguyen Trong Ngu: Conceptualization, Methodology, Supervision, Project administration, Funding acquisition, Writing - review and editing.
All authors read and approved the final version of the manuscript.

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How to cite this article;
Trang Thanh Gia, Nguyen Thiet and Nguyen Trong Ngu. Association of prolactin gene polymorphisms and haplotypes with egg production traits in Vietnamese Tre chickens. Veterinary Integrative Sciences. 2027; 25(1): e2026003-1-13.

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