



## Genetic Parameters Estimated for Sexual Maturity and Weekly Live Weights of Japanese Quail (*Coturnix coturnix japonica*)

Metin Sezer\*

Gaziosmanpasa Universitesi, Ziraat Fakultesi, Zootečni Bolumu, 60200, Tokat, Turkey

**ABSTRACT :** Covariance components and genetic parameters of weekly live body weight from hatching to six weeks of age and age of sexual maturation were estimated in a laying type Japanese quail line. The univariate and bivariate animal model analysis included hatching group and sex as fixed effects. Each trait was analysed with animal as random effect to fit the additive direct effect. Additional random effects incorporated in the models were changed according to the trait examined. The best model for a trait was chosen based on a likelihood ratio test, comparing the models with and without maternal additive genetic and maternal permanent environmental effects. Heritability estimates of live-weight at hatch and one to six weeks of age with their standard errors were  $0.22 \pm 0.088$ ,  $0.39 \pm 0.099$ ,  $0.31 \pm 0.086$ ,  $0.38 \pm 0.056$ ,  $0.46 \pm 0.055$ ,  $0.50 \pm 0.059$ , and  $0.56 \pm 0.062$ , respectively. Direct heritability value of age of sexual maturation was moderate ( $0.24 \pm 0.055$ ). The variances due to permanent environmental effect of dam after one week of age and maternal genetic effect after two weeks of age were not important sources of variation. The correlations between direct and maternal genetic effects were negative and ranged from high to moderate values (-0.21 to -0.83). Among the weekly live weights, genetic correlations were generally high between not only successive but also early and late weightings. It suggests that selection for final weight may be based on early weight records. Genetic correlations between age of sexual maturation and live weights were low, favourable but had high standard errors. These results indicate that selection for high weight will potentially result in lower age of sexual maturation only with accurate determination of breeding values. (**Key Words :** Genetic Parameter, Maternal Effect, Japanese Quail, REML, Age at Sexual Maturity, Weekly Weights)

### INTRODUCTION

Selection studies of improved growth rate (Anthony et al., 1996; Marks, 1996; Aggrey et al., 2003) and egg production (Minvielle and Oguz, 2002) have been performed for Japanese quail to meet the demand for quail eggs and meat. Estimation of genetic parameters for Japanese quail mostly focused on the weekly live weight (Anthony et al., 1996; Marks, 1996; Saatci et al., 2003). On the other hand, early sexual maturity promotes poultry production by increasing laying performance of the females and reducing the cost to produce males for semen production. If there is a genetic correlation between characters under selection, the overall response to selection will change according to the heritability of the traits examined, and the strength and sign of the genetic covariance among them (Jensen et al., 2003). Hence, selection for highly heritable traits such as body weight and

breast muscle yield may be accompanied by a correlated genetic decline in the reproductive potential of the selected lines (Barbato, 1999; Reddish and Lilburn, 2004). In the case of an antagonistic relationship between quantitative traits, some sophisticated selection scheme (such as restricted selection or mate selection based on Best Linear Unbiased Prediction (BLUP) of breeding value) would need to be applied.

The additive genetic effect of the individuals for a maternally-influenced trait can be estimated more precisely with the animal models (Meyer, 1989), incorporating maternal genetic, maternal permanent environmental effects and several fixed effects such as hatchling group and sex (Aggrey and Cheng, 1994; Saatci et al., 2003). Although, published estimates of genetic parameters for Japanese quail exist, few are based on REML (Toelle et al., 1991; Aggrey and Cheng, 1994; Saatci et al., 2003), integrating maternal effects (Schüler et al., 1998) or enlighten the genetic parameters for sexual maturity (Koçak et al., 1995; Camci et al., 2002). The objectives of the current study were to estimate direct and maternal heritabilities for

\* Corresponding Author: Metin Sezer. Tel: +90-356-252-16-16, Fax: +90-356-252-14-89, E-mail: msezer@gop.edu.tr  
Received February 15, 2006, Accepted July 10, 2006

weekly live weights and age of sexual maturity in addition to determination of correlations among them for Japanese quail.

## MATERIAL AND METHODS

The data used in this study were collected from the Japanese quail population (*Coturnix coturnix japonica*) at the Quail Breeding Unit of Gaziosmanpasa University, Tokat, Turkey. For accurate pedigree identification females were housed in individual stainless steel wire mesh cages. Each male was mated with two females, allowing each male to stay with a female for a day. Analyses were carried out with the records of 1,644 quail (861 males and 783 females), progeny of 162 sires and 251 dams in 11 hatching groups (generations). Parents of the next generation were chosen without selection for the traits examined in this study. Special care was taken to avoid inbreeding.

Egg collection for artificial incubation was started one week after the beginning of the mating. Collected eggs were recorded with their sire and dam number. When the chicks hatched, they were labelled with wing-rings and randomly placed in quail battery brooders. Birds were housed for the first three weeks at 24 h lighting, with the following weeks at 16:8 light:dark cycle. The initial temperature was 36°C, and was decreased by 3°C every week until it reached 24°C. Birds were allowed *ad libitum* access to food and water. They were fed with starter diet containing 240 g/kg crude protein (CP) and 13.39 MJ ME/kg for 21 days, grower diet containing 190 g/kg CP and 12.55 MJ ME/kg between 22 and 35 days of age, and thereafter a breeder diet containing 170 g/kg CP and 11.50 MJ ME/kg.

Birds were weighed every week from hatching (HW) to six weeks of age (W6) with a 0.01 g sensitivity electronic balance. Records from quail that died before 21 days of age were removed from the data set, because the sex of the bird is determined correctly by the plumage coloration between 15 and 21 days of age. The foam produced by the cloacal gland is an androgen dependent secondary sex character in the male Japanese quail and could be used as an external index of sexual maturity (Siopes and Wilson, 1980; Adkins-Regan, 1999; Mohan et al., 2002; Marin and Satterlee, 2004). Males were inspected daily (after 25 days of age), to determine the day of cloacal gland foam production, and this day was recorded as the age of sexual maturity (ASM) for males. After the last weighing, females were transferred to individual cages. The day of laying the first egg was recorded as the ASM for females. Although ASM was measured differently for male and female, both methods reliably determine the time of sexual maturation for each gender. Like most of farm animals, differences in weekly live-weight and onset of sexual maturation between male and female quail (sexual dimorphism) are marked, but the

REML procedure allows incorporation of the sexual differences as fixed effect in the models.

Covariance components and genetic parameters were estimated using restricted maximum likelihood (REML) procedures (ASREML software; Gilmour et al., 2000). The univariate animal model analysis included hatching group and sex as fixed effects. Each trait was analysed with animal as a random effect to fit the additive direct effect. Additional random effects incorporated in the models were changed according to the trait examined. The statistical significance of random effects was determined for each trait using likelihood ratio tests (Meyer, 1992; Morrell, 1998). Models were compared with -2 times the difference in log-likelihood scores being distributed as  $\chi^2$  with 1 degree of freedom for each additional covariance component in the more complex model. Genetic and phenotypic correlations between traits were estimated using bivariate analyses, fitting significant fixed and random effects for each trait independently. The ASREML program returns standard errors for combined parameter estimates (i.e., heritability, genetic correlations and maternal effects). Estimated parameters were considered to be significant if the component divided by its standard error was greater than the corresponding value of the standard normal distribution (Tosh and Kemp, 1994; Gilmour et al., 2000).

For W3, W4, W5, W6 and ASM, the model (1) incorporating animal as the only random factor was the best one. For W2, dam was added into the model (2) as a second random effect allowing estimation of maternal additive genetic effect. For HW and W1, permanent environmental effect of dam was fitted as an additional random effect uncorrelated with all other effects in the model (3). The models used were:

$$Y_{ikl} = \mu + a_i + h_k + s_l + hs_{kl} + e \quad (1)$$

$$Y_{ijkl} = \mu + a_i + m_j + h_k + s_l + hs_{kl} + e \quad (2)$$

$$Y_{yikl} = \mu + a_i + m_j + (mh)_{jk} + h_k + s_l + hs_{kl} + e \quad (3)$$

where  $Y$  = is the observation of animal weight (HW-W6) or age of sexual maturation,  $\mu$  is the population mean,  $a_i$  is the animal additive genetic effect,  $m_j$  is the additive maternal genetic effect,  $(mh)_{jk}$  is the permanent environmental effect common to full-sibs of a hatch from a given dam,  $h_k$  is the effect of hatching group,  $s_l$  is the effect of sex,  $hs_{kl}$  is the interaction between hatching group and sex,  $e$  is the residual error.

## RESULTS AND DISCUSSION

The statistical description of weekly live weight and age

**Table 1.** Number of observations, mean and standard error of mean, minimum and maximum values, and the result of analysis of variance of weekly live weight (g) and age of sexual maturation (d) for Japanese quail

	N	Mean	SE	Min	Max	Sex effect <sup>1</sup>	Hatch <sup>2</sup>
HW	1,644	8.2	0.02	5.0	10.80	NS	**
W1	1,636	23.8	0.12	10.10	42.80	0,80*	**
W2	1,640	54.9	0.25	20.30	89.90	1,60**	**
W3	1,642	97.3	0.36	43.30	152.20	3,10**	**
W4	1,636	134.5	0.44	58.70	194.90	4,80**	**
W5	1,595	169.3	0.48	103.20	246.90	12,20**	**
W6	1,472	192.3	0.58	128.70	289.90	21,00**	**
ASM	1,259	39.7	0.23	25.00	69.00	12,80**	**

HW = Hatchling weight; W1 to W6 = Weight at one to six weeks of age; ASM = Age of sexual maturation.

N = Number of observation; SE = Standard error of mean; Min = Minimum values; Max = Maximum values.

<sup>1</sup> Estimates of deviation from male sex.

<sup>2</sup> Because of the high number of hatchling group (generation), only the significance of this effect was shown.

\*  $p \leq 0.05$ . \*\*  $p \leq 0.01$ .

**Table 2.** Estimates of covariance components and genetic parameters for weekly live weight and age of sexual maturation

	HW	W1	W2	W3	W4	W5	W6	ASM
$\sigma^2_A$	0.13±2.44	8.34±3.70	27.53±3.40	79.21±5.58	133.99±6.44	152.33±6.45	202.84±6.56	4.27±3.95
$\sigma^2_M$	0.08±1.32	4.57±2.53	13.70±2.81					
$\sigma_{AM}$	-0.02±0.55	-5.12±3.03	-12.25±2.16					
$\Sigma^2_C$	0.20±4.16	2.48±2.29						
$\Sigma^2_E$	0.20±6.97	10.91±8.82	59.60±12.12	132.01±14.02	158.99±12.46	152.95±10.98	162.03±9.12	13.73±15.29
$\sigma^2_p$	0.59	21.17	88.58	211.22	292.98	305.28	364.87	18.00
$h^2$	0.22±0.088	0.39±0.099	0.31±0.086	0.38±0.056	0.46±0.055	0.50±0.059	0.56±0.062	0.24±0.055
$m^2$	0.14±0.061	0.22±0.083	0.15±0.053					
$c^2$	0.34±0.081	0.12±0.051						
$r_{AM}$	-0.21±0.323	-0.83±0.118	-0.63±0.152					
$h^2_T$	0.24	0.14	0.18					

HW = Hatchling weight; W1 to W6 = Weight at one to six weeks of age; ASM = Age of sexual maturation;  $\sigma^2_A$  = Direct additive genetic variance;  $\sigma^2_M$  = Maternal additive genetic variance;  $\sigma_{AM}$  = Direct-maternal genetic covariance;  $\Sigma^2_C$  = Maternal permanent environmental variance;  $\Sigma^2_E$  = Error variance;  $\sigma^2_p$  = Phenotypic variance;  $h^2$  = Direct heritability;  $m^2$  = Maternal heritability;  $c^2$  = The permanent environmental variance due to the dam as a proportion of the phenotypic variance;  $r_{AM}$  = Direct-maternal genetic correlation;  $h^2_T$  = Total heritability ( $h^2_T = (\sigma^2_A + 0.5 \sigma^2_M + 1.5 \sigma_{AM}) / \sigma^2_p$ ) (Willham, 1972).

of sexual maturation is summarized Table 1. The effect of sex was significant for all traits (except hatchling weight). The mean values of all traits were higher in males than in females. Hatchling group (generation) also affected quail weight and ASM ( $p < 0.01$ ). Significant effect of rearing group was reported as a common phenomenon in the literature (Michalska 1992; Aggrey and Cheng, 1994; Brah et al., 1997; Saatci et al., 2003). This effect did not show any trend throughout the study. Hence the effect of generation might be caused by the genetic structure of the parents used in each generation. The effect of interaction between sex and generation was significant for W5, W6 and ASM. Live weights of Japanese quail from hatching to 6 week of age were similar to the reports in literature (for review, see Saatci et al., 2003). Age of sexual maturation for females ( $45.9 \pm 0.23$ ) and males ( $33.1 \pm 0.18$ ) determined in this study were within the range reported in previous research (Siopes and Wilson, 1980; Thomas and Ahuja, 1988; Camci et al., 2002; Reddish et al., 2003; Satterlee, 2004).

Heritability estimates and variance components are

presented in Table 2. Estimated direct heritability of live weights was significant and became the lowest at HW ( $0.22 \pm 0.088$ ), afterwards increasing steadily. The heritability estimates in this study were similar to those reported by Michalska (1994), Marks (1996), Schüller et al. (1998), and Resende et al. (2005) but were higher than those reported by Aggrey and Cheng (1994) and Saatci et al. (2003). Reports of a heritability trend for body weight with age are controversial in the literature. While Saatci et al. (2003) reported a decrease with age in heritability of weekly live weights of Japanese quail, an increase was noted by Resende et al. (2005) for Japanese quail and by Chambers (1990) for broilers, whereas not even a trend was noticed by others (Sefton and Siegel, 1974; Aggrey and Cheng, 1994). Differences in heritability estimates could be qualified by the method of estimation, population, sample size and environmental effects.

Maternal effects may be caused by the genes that a mother is carrying and by the environment she provided for her offspring. In the former case, such maternal genetic effects will represent a heritable source of phenotypic

**Table 3.** Genetic and phenotypic correlations estimated between weekly live weights and age of sexual maturation for Japanese quail

	HW	W1	W2	W3	W4	W5	W6	ASM
HW		0.32±0.21	0.89±0.05	0.27±0.17	0.18±0.16	0.33±0.16	0.33±0.15	-0.13±0.21
W1	0.44±0.07		0.89±0.05	0.78±0.08	0.65±0.09	0.65±0.10	0.51±0.11	-0.23±0.18
W2	0.94±0.06	0.94±0.06		0.94±0.03	0.87±0.04	0.83±0.06	0.69±0.09	-0.21±0.17
W3	0.19±0.03	0.64±0.02	0.87±0.01		0.93±0.02	0.87±0.03	0.77±0.05	-0.23±0.15
W4	0.17±0.03	0.55±0.02	0.78±0.01	0.90±0.01		0.92±0.02	0.85±0.04	-0.26±0.13
W5	0.19±0.03	0.46±0.03	0.64±0.02	0.77±0.01	0.84±0.01		0.96±0.02	-0.14±0.14
W6	0.19±0.03	0.35±0.03	0.50±0.02	0.62±0.02	0.68±0.02	0.81±0.01		-0.04±0.14
ASM	-0.06±0.03	-0.23±0.03	-0.28±0.03	-0.30±0.03	-0.27±0.03	-0.25±0.03	-0.17±0.03	

Genetic correlations above and phenotypic correlations below the diagonal with their standard errors.

HW = Hatchling weight; W1 to W6 = Weight at one to six weeks of age; ASM = Age of sexual maturation.

variance. The presence of maternal effects in the models reduces the variance of direct genetic effects (Meyer, 1992). Application of REML in animal models using pedigree records allowed investigation of additional random effects. Since maternal effects would bias the direct heritability estimate upwards (Clement et al., 2001), the phenotypic variances were partitioned into direct and maternal components. The permanent environmental variance due to the dam as a proportion of the phenotypic variance ( $c^2$ ) was high at HW (0.34±0.081) and continued to be significant ( $p < 0.01$ ) at W1 (0.12±0.051). The  $c^2$  estimates include influence of egg size, egg weight, shell quality and yolk composition (Aggrey and Cheng 1994; Hartmann et al., 2003). Because quail were raised in battery brooders, the post-hatch maternal influence on bird growth was not an important source of variation. In poultry, most of the variation in chick weight at hatch could be explained by egg weight, yolk/albumen ratio, and weight loss during incubation (Tullett and Burton, 1982; Burke, 1992). Similar to the trend in this study, it was reported that maternal environmental variance proportions of the phenotypic variance were 0.50, 0.11 and 0.07 for HW, W1 and W2, respectively (Resende et al., 2005). The results illustrated that maternal permanent environmental effects made large contributions to the variability of HW. This situation implies that qualities of incubated eggs are very important determinants of early live weight of chicks. It is therefore desirable to separate maternal permanent environmental effect from heritability estimates.

The maternal heritability was estimated for HW, W1 and W2 as 0.14±0.061, 0.22±0.083 and 0.15±0.053, respectively. The variance due to maternal additive genetic effect was negligible for W3 and thereafter. Narayan (1976) studied the contribution of the maternal effect to live weight and growth rate and concluded that it was remarkable on hatchling weight, and then declined as the chicks grew. Because of observed possible antagonism between direct and maternal effects, knowledge of the maternal influence on examined traits and the correlation between these effects is essential for achieving unbiased heritability estimates. The model allowing for a direct maternal covariance

yielded significant negative estimates of  $r_{AM}$  and  $\sigma_{AM}$  for W1 and W2. Subsequently, total estimated heritability ( $h^2_T$ ) was lower than the direct heritability. It has therefore been suggested that in the presence of maternal effects, total heritability will be a more complete measure of a trait's potential to respond to selection than the direct heritability (Willham, 1972). Negative correlation between the additive direct and maternal genetic effect has also been observed in some other livestock species (Diop and Van Vleck, 1998; Hartmann et al., 2003; Hassen et al., 2003). This negative covariance between the additive direct and maternal genetic effect might occur not only from genetic antagonism, but sometimes also from additional sire or sire×year variation or negative dam offspring covariances (Robinson, 1996). Maternal effect on ASM was insignificant and direct heritability for ASM was moderate (0.24±0.055). The current results indicate that individual selection (based on BLUP) will be effective in improving both weekly live weight and ASM.

Estimated genetic and phenotypic correlations of the weekly live weights and ASM are presented in Table 3. Generally, high genetic correlations were observed among weekly live weights. Genetic correlations between HW and weight at most of the other ages ranged from low to moderate. These relatively low estimated genetic correlations may arise from controlling of HW by maternal permanent environmental effects (i.e. egg weight or egg composition) rather than direct genetic effect. The genetic and phenotypic correlations among live weights decreased as the time interval between them increased. Among the successive live weights, the lowest genetic (0.32±0.21) and phenotypic (0.44±0.07) correlation was detected between HW and W1. The genetic correlation (0.69±0.09) between W2 and W6 estimated in this study was high, similar to previous reports (Aggrey and Cheng, 1994; Brah et al., 1997; Saatci et al., 2003).

The current estimates indicate that ASM is favourably associated with weekly live weight, but estimated genetic correlations were generally not different from zero. In any case, genetic correlations among weekly live weight and age of sexual maturation showed that selection for one of

these traits would not have any adverse effects on the other traits. Reports of correlation between age of sexual maturity and live weight vary from moderately positive to moderately negative (Kocak et al., 1995; Liu et al., 1995; Camci et al., 2002). The effects of chronological age, body weight and body composition on sexual maturity were studied in detail and it was concluded that interaction between them for the onset of sexual maturity was generally inseparable (Siegel and Dunnigton, 1985; Oruwari and Brody, 1988; Reddish et al., 2003). Another explanation for such a low correlation between live weight and ASM includes the multiple thresholds concept in which body weight and a selected aspect of body composition must exceed a threshold value in order for sexual development to proceed (Reddish et al., 2003).

### IMPLICATIONS

The variance due to maternal additive and common environmental effects of dam disappears as the chicks grow older. Therefore, a simple animal model is suitable for genetic parameter estimates only after two weeks of age in Japanese quail. High genetic correlations among younger and older age live weights support the general view of possibility of selection in Japanese quail based on early body weight. However, estimated antagonism between the additive direct and maternal genetic effect for HW, W1 and W2 indicates that application of sophisticated selection criterion should be undertaken for an increased final weight based on early growth. Estimated genetic correlations between weekly live weight and age of sexual maturation were essentially negligible and ranged from negatively low to relatively high values. Hence, selection based on BLUP generated estimated breeding values would be more powerful than phenotypic selection to improve both live weight and age of sexual maturation.

### REFERENCES

- Adkins-Regan, E. 1999. Foam produced by male Coturnix quail: What is its function? *Auk* 116:184-193.
- Aggrey, S. E., G. A. Ankra-Badu and H. L. Marks. 2003. Effect of long-term divergent selection on growth characteristics in Japanese quail. *Poult. Sci.* 82:538-542.
- Aggrey, S. A. and K. M. Cheng. 1994. Animal model analysis of genetic (co)variances for growth traits in Japanese quail. *Poult. Sci.* 73:1822-1828.
- Anthony, N. B., K. E. Nestor and H. L. Marks. 1996. Short-term selection for four-week body weight in Japanese quail. *Poult. Sci.* 75:1192-1197.
- Barbato, G. F. 1999. Genetic relationships between selection for growth and reproductive effectiveness. *Poult. Sci.* 78:444-452.
- Brah, G. S., M. L. Chaudhary and J. S. Sandhu. 1997. Genetic analyses of body weight in three lines of Japanese quail. *Ind. J. Poult. Sci.* 32:242-248.
- Camci, Ö., C. Erensayin and S. Aktan. 2002. Relations between age at sexual maturity and some production characteristics in quails. *Arch. Geflügelk.* 66:280-282.
- Chambers, J. R. 1990. Genetics of growth and meat production in chickens. In: *Quantitative Genetic and Selection* (Ed. R. D. Crawford). *Poult. Breed. Genetic*, Elsevier, Amsterdam, pp. 559-643.
- Clement, V., B. Bibe, E. Verrier, J. M. Elsen, E. Manfredi, J. Bouix and E. Hanocq. 2001. Simulation analysis to test the influence of model adequacy and data structure on the estimation of genetic parameters for traits with direct and maternal effects. *Genet. Sel. Evol.* 33:369-395.
- Diop, M. and L. D. Van Vleck. 1998. Estimates of genetic parameters for growth traits of Gobra cattle. *J. Anim. Sci.* 66:349-355.
- Gilmour, A. R., B. R. Cullis, S. J. Welham and R. Thompson. 2000. *ASREML*. NSW Agriculture, Orange, Australia.
- Hartmann, C., K. Johansson, E. Strandberg and L. Rydhmer. 2003. Genetic correlations between the maternal genetic effect on chick weight and the direct genetic effects on egg composition traits in a white leghorn line. *Poult. Sci.* 82:1-8.
- Hassen, Y., B. Fuerst-Waldt and J. Sölkner. 2003. Genetic parameter estimates for birth weight, weaning weight and average daily gain in pure and crossbred sheep in Ethiopia. *J. Anim. Breed. Genet.* 120:29-38.
- Jensen, H., B. E. Saether, T. H. Ringsby, J. Tufto, S. C. Griffith and H. Ellegren. 2003. Sexual variation in heritability and genetic correlations of morphological traits in house sparrow (*Passer domesticus*). *J. Evol. Biol.* 16:1296-1307.
- Kocak, Ç., Ö. Altan and Y. Akbas. 1995. Japon bildirenlerinin çeşitli verim Özellikleri Üzerinde araştırmalar. *Turkish J. Vet. Anim. Sci.* 19:65-71.
- Liu, G., E. A. Dunnigton and P. B. Diegel. 1995. Correlated responses to long-term divergent selection for eight-week body weight in chickens: growth, sexual maturity, and egg production. *Poult. Sci.* 74:1259-1268.
- Marin, R. H. and D. G. Satterlee. 2004. Cloacal gland and testes development in male Japanese quail selected for divergent adrenocortical responsiveness. *Poult. Sci.* 83:1028-1034.
- Marks, H. L. 1996. Long-term selection for body weight in Japanese quail under different environments. *Poult. Sci.* 75:1198-1203.
- Mayer, K. 1989. Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. *Genetique, Selection et Evolution.* 21:317-340.
- Michalska, E. 1994. Direct and correlated response to the index with constraints in selection for body weight and feed conversion ratio in Japanese quail. *Proc. 5<sup>th</sup> WCGALP*, Uni. of Guelph, Ontario, Canada, 19:103-106.
- Minvielle, F. and Y. Oguz. 2002. Effects of genetic and breeding on egg quality of Japanese quail. *World's Poult. Sci. J.* 58:291-295.
- Mohan, J., R. P. Moudgal, K. Venkata, H. Sastry, J. Tyagi and R. Singh. 2002. Effects of hemicastration and castration on foam production and its relationship with fertility in male Japanese quail. *Theriogenol.* 58:29-39.

- Morrell, C. H. 1998. Likelihood ratio testing of variance components in the linear mixed effects model using restricted maximum likelihood. *Biometrics* 54:1560-1568.
- Narayan, A. D. 1976. Inbreeding components of body weight and growth rate in Japanese quail. *Br. Poult. Sci.* 17(2):513-517.
- Oruwari, B. M. and T. Brody. 1988. Roles of age, body weight, and composition in the initiation of sexual maturation of Japanese quail (*Coturnix coturnix Japonica*). *Br. Poult. Sci.* 29: 481-488.
- Reddish, J. M. and M. S. Lilburn. 2004. A comparison of growth and development patterns in diverse genotypes of broilers. 2. Pullet growth. *Poult. Sci.* 83:1072-1076.
- Reddish, J. M., K. E. Nestor and M. S. Lilburn. 2003. Effect of selection for growth on onset of sexual maturity in randombred and growth-selected lines of Japanese quail. *Poult. Sci.* 82: 187-191.
- Resende, R. O., E. N. Martins, P. C. Georg, E. Paiva, A. C. M. Conti, A. I. Santos, E. S. Sakaguti and A. E. Murakami. 2005. Variance components for body weight in Japanese quails (*Coturnix japonica*). *Brazilian J. Poult. Sci.* 7:23-25.
- Robinson, D. L. 1996. Models which might explain negative correlations between direct and maternal genetic effects. *Livest. Prod. Sci.* 45:111-122.
- Saatci, M., I. Ap Dewi and A. R. Aksoy. 2003. Application of REML Procedure to estimate the genetic parameters of weekly liveweights in one-to-one sire and dam pedigree recorded Japanese quail. *J. Anim. Bred. Genet.* 120:23-28.
- Schüller, L., N. Mielenz and S. Hempel. 1998. Asymmetry of the selection responses in performance traits of Japanese quails. *Proc. 6<sup>th</sup> WCGALP, Uni. of New England, Armidale, Australia.* 26:101-104.
- Sefton, A. E. and P. B. Siegel. 1974. Inheritance of body weight in Japanese quail. *Poult. Sci.* 53:1597-1603.
- Siegel, P. B. and E. A. Dunnington. 1985. Reproductive complications associated with selection for broiler growth (Ed. W. G. Hill, J. M. Manson, D. Hewitt) In: *Poultry Genetics and Breeding* Longman Group Limited: Harlow, pp. 59-72.
- Siopes, T. D. and W. O. Wilson. 1980. Participation of the eyes in the photosexual response of Japanese quail (*Coturnix coturnix japon*). *Biol. Reprod.* 23:352-357.
- Thomas, P. C. and S. D. Ahuja. 1988. Improvement of broiler quails of Cari through selective breeding. *Poult. Guide* 25:45-47.
- Toelle, V. D., G. B. Havenstein, K. E. Nestor and W. R. Harvey. 1991. Genetic and phenotypic relationships in Japanese quail: I. Body weight, carcass, and organ measurements. *Poult. Sci.* 70(8):1679-1688.
- Tosh, J. J. and R. A. Kemp. 1994. Estimation of Variance Components for Lamb Weights in Three Sheep Populations. *J. Anim. Sci.* 72:1184-1190.
- Tullett, S. G. and G. F. Burton. 1982. Factors affecting the weight and water status of the chick at hatch. *Br. Poult. Sci.* 23:361-369.
- Willham, R. L. 1972. The role of maternal effects in animal breeding. III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35:1288-1293.