T-Maze Behavior and Early Egg Production in Japanese Quail Selected for Contrasting Adrenocortical Responsiveness[1]

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ABSTRACT Broiler chicks that traverse a T-maze quickly to reinstate contact with their companions (HP, high performance) are known to grow faster, be more social, and exhibit a reduced plasma corticosterone (B) response to acute stress than slower (LP, low performance) chicks. Genetic lines of Japanese quail selected for reduced (LS, low stress) or exaggerated (HS, high stress) plasma B response to brief restraint also differ in sociality and performance. In the present study, we asked if divergence in early T-maze behavior was associated with differential attainment of puberty and early egg production in these lines. At 3 d of age, LS and HS quail were categorized as HP or LP birds based on running times in a T-maze. Thus, there were four treatment combinations: HP-LS, HP-HS, LP-LS, and LP-HS birds. Daily egg records were kept for 8 wk. The average ages at first egg lay (FIRST), at 25% egg production (A25%EP), and weekly and cumulative hen-day egg production (HDEP) where calculated. Daily egg weight (EWT) data were also collected, and BW measures were made at the end of the trial. Mean FIRST and A25%EP responses were lower ($P < 0.02$) and cumulative HDEP was greater ($P < 0.04$) in HP than in LP quail. Despite considerable numerical reductions in FIRST and A25%EP, as well as 5% elevation in cumulative HDEP in LS quail, line differences in these variables were not significant. On the other hand, FIRST and A25%EP were reduced ($P < 0.05$) in HP-LS quail when compared to LP-HS ones, whereas HP-HS and LP-LS quail showed intermediate and similar responses that did not differ from the other two treatment groups. Mean cumulative HDEP findings for the interactive effect of performance category with line mimicked these puberty findings. EWT and BW measures were not affected by any of the treatments or their interactions. Our results suggest that rapid negotiation of the T-maze by quail chicks is associated with accelerated puberty and increased HDEP in quail of two genetically diverse lines. This effect is particularly evident in quail selected for reduced adrenocortical responsiveness, suggesting possible additive effects.

(*Key words*: Japanese quail, T-maze behavior, stress responsiveness, puberty, egg production)

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INTRODUCTION

Coincident with selection for enhanced performance traits in commercial chicken stocks has been the alteration of many behavioral characteristics that vary substantially between and within genetic strains of modern egg- and meat-type chickens. These include differences in aggression, mating behavior, fearfulness, feather pecking, and sociality (Siegel, 1993; Jones et al., 1994; Jones, 1996; Muir, 1996; Craig and Muir, 1998; Faure and Mills, 1998; Jones and Hocking, 1999). Many of these traits influence bird abilities to adapt to their social and physical environment and, thereby, exert profound effects on the productivity and welfare of farmed poultry (Jones, 1996; Faure and Mills, 1998; Jones and Hocking, 1999). Further, because the behavioral traits identified above are extremely sensitive to genetic manipulation, establishment of selection programs for performance- and welfare-friendly characteristics is a distinct possibility (Jones, 1996; Jones and Hocking, 1999; Mench, 1992). Indeed, such genetic selection may be the quickest and most reliable method of eliminating harmful characteristics and promoting desirable ones.

Substantial individual variation is also evident in the T-maze responses of individually tested, 2-to-3-d-old

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Abbreviation Key: A25%EP = age at 25 % egg production; B = corticosterone; EWT = egg weight; FIRST = age at first egg lay; G_x = generation; **[AUTH QUERY: G OK as defined?]** HDEP = hen-day egg production; HP = high performance; HS = high-stress line; LP = low performance; LS = low-stress line.

broiler chicks (Marin and Arce, 1996; Marin et al., 1997b; Jones et al., 1999). The T-maze test combines elements of fear and social stress, both of which can damage productivity (Jones, 1996). The test involves measuring the time taken by the chick to leave an isolation chamber, traverse a short corridor and a perpendicular arm, and reinstate visual contact with its companions in a nearby enclosure. Chicks are then assigned to one of three categories: those that performed the task in a short, moderate, or long time are classified as high (HP), medium (MP), or low (LP) performance birds, respectively. HP birds grow faster in the laboratory (Marin et al., 1997a) and at a farm (Marin et al., 1999) and they show greater sociality (Jones et al., 1999), more benzodiazepine/GABA receptors (Marin and Arce, 1996), and lower adrenocortical responses (Marin and Jones, 1999) to an acute stressor than their slower LP counterparts. These findings suggest that T-maze behavior, if found to be a heritable trait, might be a useful selection criterion for poultry breeding programs intended to improve bird productivity and welfare.

The Japanese quail is an important agricultural species for meat and egg production in many countries (Caron et al., 1990; Baumgartner, 1994; Jones, 1996) as well as a useful model for the extrapolation of data to chickens and other commercially important poultry species (Padgett and Ivey, 1959; Wilson et al., 1961; Kovach, 1974; Mills and Faure, 1992; Jones, 1996). Genetically selected lines of quail are valuable tools for studying physiological and behavioral traits influencing performance and welfare. For example, quail selected for reduced (low stress, LS) rather than exaggerated (high stress, HS) plasma corticosterone (B. Kendall, 1941) response to brief mechanical restraint (Satterlee and Johnson, 1988) show less fearfulness, a non-specific reduction in stress responsiveness, less developmental instability, and greater sociality (Satterlee and Johnson, 1985; Jones et al., 1992a,b, 1994, 1999, 2000, 2001; Jones and Satterlee, 1996; Satterlee et al., 2000). Fear and distress exert many deleterious effects on the welfare and productivity of fowl (Jones, 1996; Faure and Mills, 1998; Jones and Hocking, 1999). Therefore, the LS and HS quail lines are particularly useful for studying the relationships between behavior, stress, welfare, and production performance. However, apart from reports that body and liver weights are lower in HS than LS quail (Satterlee and Johnson, 1985), that bone strength is less severely compromised in LS than HS birds after sequential exposure to stressors (Satterlee and Roberts, 1990), and that puberty is delayed in HS males (Satterlee et al., 2002), these lines have not been extensively characterized for differences in production performance traits.

Herein, we compared the attainment of puberty and rate of early egg production in LS and HS quail categorized as HP or LP chicks in the T-maze. This comparison enabled us to address two main questions: 1) is early T-maze behavior indicative of egg production in Japanese quail, and if so, 2) does egg production of HP and LP quail depend upon genetic differences in their stress responsiveness?

MATERIALS AND METHODS

Genetic Stocks and Husbandry

Japanese quail (*Coturnix japonica*) from the LS and HS lines of Satterlee and Johnson (1988) were used in the present study. The lines' intermediate and recent genetic histories, from Generation 13 (G_{13}) **[AUTH QUERY: G OK as defined?]** to G_{24} and up to G_{29}, respectively, are discussed in detail elsewhere (Satterlee et al., 2000, 2002). Divergent adrenocortical responsiveness to the genetic selection stressor has been maintained.

The quail used here were offspring of G_{29} (see above) and were taken from a larger population of an approximately 1,200-bird hatch. Egg incubation procedures were identical to those described by Jones and Satterlee (1996). At hatch, 400 chicks were leg-banded and housed in mixed-line groups of 80 birds (40 LS + 40 HS) per compartment in each of five compartments (102 × 64 × 20 cm, length × width × height) of a Model 2S-D, six-deck Petersime brooder battery[3] modified for quail. At 3 d of age, chicks of each line were categorized as HP or LP birds according to their performance in a T-maze (see T-maze testing, below) and returned to the battery. Brooding temperature was 37.8 C during the first week of life, with a weekly decline of 2.8 C until room temperature (23.9 to 26.7 C) was achieved. A quail starter diet (28% CP; 2,800 kcal ME/kg) and water were provided ad libitum. Juveniles were exposed to continuous dim light (22 lx) with a 14-h light (280 to 300 lx):10-h dark override. Leg bands were replaced by wing bands at 21 d of age.

At 4 wk of age, birds were sexed by plumage coloration and randomly caged in same-line, same-category pairs of one male and one female. Thus, there were four treatment combinations (cage replicated) as follows: 19 HP-LS, 21 HP-HS, 23 LP-LS, and 24 LP-HS pairs. Cages measuring 50.8 × 15.2 × 26.7 cm (length × width × height) were located within two four-tier cage batteries, each battery comprising 48 cages. Coincident with placement in laying cages, birds were given a laying ration (21% protein, 2,750 kcal ME/kg) and water ad libitum and were subjected to a daily cycle of 14 h light (280 to 300 lx):10 h dark until the end of the study (at 14 wk of age).

T-Maze Testing

The T-maze used here was a smaller version of the one used for domestic chicks (Marin et al., 1997a). It consisted of an isolation chamber (12.5 × 12.5 cm, length × width) leading to a 15 cm long × 5 cm wide corridor that ended in two 5 × 5 cm perpendicular arms (top of the T). A 10 × 10 cm (length × width) mirror was situated at the junction of the corridor with the perpendicular wings to facilitate movement of the chick toward this point. The T-maze apparatus was painted white. It was placed in a 25 × 40

[3]Petersime Incubator Co., Gettysburg, OH.

cm (length × width) section of a 60 × 40 cm wooden brooder box also painted white. Hardware cloth wire was used to separate the area within the brooder box containing the T-maze apparatus from a 35 × 40 cm (length × width) brood area containing 20 quail. Exit from the arm nearest the brood area by the test chick allowed visual contact with its companions. Food and water were freely available in the brood area and an overhead lamp provided light for the whole apparatus. The apparatus was situated in a separate room (3 × 3 m) where the ambient temperature and illumination were similar to those of the room containing the brooder batteries.

The T-maze responses of 400 quail were measured at 3 d of age. Prior to testing, groups of chicks (n = 20 mixed-line birds) were placed in the brood areas of each of four identical T-mazes. Birds were allowed 10 min acclimation before testing began (at 0830 h). This procedure allowed four experimenters to simultaneously test four individuals and it was continued until all 20 chicks had been tested. At test, a quail was removed from the brood area and placed in the center of the isolation chamber facing away from the entrance to the T corridor. We then recorded the time it took to exit from the arm of the T-maze facing the brood area. The floor of the apparatus was wiped clean after each test. Tested birds were lightly marked on the head with a fast-drying color marker to prevent re-testing. When all quail within each experimenter's brood area were tested, the entire group was returned to the battery brooder. The procedures described above were repeated with new (untested) groups of quail until 200 HS and 200 LS quail had been tested. Quail that negotiated the maze in less than 25 s were categorized as high performance (HP) chicks, whereas those that took longer than 100 s were classified as low performance (LP) birds.

Variables Measured

Daily egg production was recorded for 8 wk beginning with the day on which the first bird laid an egg; this occurred at 41 d of age and was considered Day 1 of lay. During the laying period, any bird that naturally succumbed, escaped, or was removed for health reasons was not replaced, and the data from such affected cages were not included in the analyses. To assess the onset of puberty, the average ages (d) at first egg lay (FIRST) and at 25% egg production (A25%EP) were calculated for each of the four treatment groups. Hen-day egg production (HDEP) was determined weekly and a cumulative HDEP (full 8 wk of lay) was also calculated. Egg weight (EWT) data were collected daily except during the sixth week of lay. The BW of each hen was measured at the end of the trial (following 8 wk of lay or at 14 wk of age).

Statistical Analyses

A two-way ANOVA with a 2 × 2 factorial arrangement of treatments (T-maze performance categories, HP vs. LP and quail lines, HS vs. LS) was used to assess differences in puberty (FIRST and A25%EP) and BW. Treatment differences in HDEP and EWT were detected by a split-plot ANOVA that incorporated the same 2 × 2 factorial arrangement described above on the main plot with weeks of lay (repeated measure) and the appropriate performance category, line, and time interactions considered on the split. An EWT observation within each of the four main treatment groups was considered to be the average of all the eggs laid by a given hen for a given week. Posthoc treatment group comparisons were conducted using the least significant differences test. $P < 0.05$ was indicative of significant differences.

TABLE 1. Mean (± SE) age at first egg lay (d) in low stress (LS) and high stress (HS) quail categorized as high (HP) or low (LP) performers in a T-maze at 3 d of age

	T-maze performance category		
Line	HP	LP	Marginal mean
LS	53.8 ± 1.1[b]	59.1 ± 2.1[ab]	56.6 ± 1.3
HS	56.4 ± 2.2[ab]	61.5 ± 2.4[a]	59.4 ± 1.7
Marginal mean	55.1 ± 1.2[y]	60.4 ± 1.6[z]	

[a,b]Means without a common letter differ ($P < 0.05$).

[y,z]Marginal means without a common letter differ ($P < 0.02$).

RESULTS

High performance quail matured earlier than LP quail as evidenced by a marked reduction in both indices of puberty ($P < 0.02$; FIRST, Table 1; A25%EP, Table 2). On average, egg lay was initiated more than 5 d earlier and 25% egg production was achieved nearly 8 d sooner in HP quail than in LP ones. Although the influence of line on the onset of puberty was not statistically significant, on average, egg lay was initiated earlier (by nearly 3 d, Table 1) and 25% egg production was reached sooner (by slightly more than 2 d, Table 2) in LS hens. T-maze performance category × line effects on puberty measures showed that mean FIRST and A25%EP were reduced ($P < 0.05$) in HP-LS quail when compared to LP-HS quail, whereas HP-HS and LP-LS quail showed intermediate and similar responses that did not differ from the other two treatment groups (Tables 1 and 2).

The HDEP data supported the FIRST and A25%EP findings. Cumulative HDEP (full 8 wk of lay) was markedly greater (> 11%, $P < 0.04$) in HP than LP quail (Table

TABLE 2. Mean (± SE) age at 25% egg production (d) in low stress (LS) and high stress (HS) quail categorized as high (HP) or low (LP) performers in a T-maze at 3 d of age

	T-maze performance category		
Line	HP	LP	Marginal mean
LS	57.7 ± 2.8[b]	66.2 ± 2.9[ab]	62.3 ± 2.1
HS	60.5 ± 3.2[ab]	67.8 ± 3.1[a]	64.5 ± 2.3
Marginal mean	59.1 ± 2.1[y]	67.0 ± 2.1[z]	

[a,b]Means without a common letter differ significantly ($P < 0.05$).

[y,z]Marginal means without a common letter differ significantly ($P < 0.02$).

TABLE 3. Mean (± SE) cumulative (8 wk of lay) hen day egg production (%) in low stress (LS) and high stress (HS) quail categorized as high (HP) or low (LP) performers in a T-maze at 3 d of age

Line	T-maze performance category HP	LP	Marginal mean
LS	72.8 ± 4.0[a]	59.7 ± 3.4[ab]	66.2 ± 2.6
HS	65.9 ± 6.6[ab]	56.6 ± 5.7[b]	61.3 ± 5.2
Marginal mean	69.4 ± 3.8[y]	58.2 ± 3.3[z]	

[a,b]Means without a common letter differ significantly ($P < 0.03$).

[y,z]Marginal means without a common letter differ significantly ($P < 0.04$).

3). Again, albeit non-significant, a considerable increase (nearly 5%) in cumulative HDEP was also observed in LS quail when compared to their HS counterparts. HDEP was also higher ($P < 0.03$) in HP-LS quail than LP-HS ones (Table 3), whereas HP-HS and LP-LS quail showed intermediate and similar HDEP responses that were not different from either of the other treatment groups.

Not surprisingly, the split plot ANOVA for HDEP detected a significant ($P < 0.04$) interaction between T-maze performance category, line, and week of lay (depicted in Figure 1). The general superiority of HP-LS quail in HDEP was particularly evident during Weeks 2, 3, 4, and 5 of lay. Although measurements of the incidences of misshapen, checked, membrane, and double-yolk eggs were not made, our subjective impression was that such variables did not differ across treatments.

Mean EWT was not affected by the main treatments (Table 4) but, as expected, EWT increased ($P < 0.05$) with time after initiation of lay (data not shown). BW at the end of the trial was also similar across treatments.

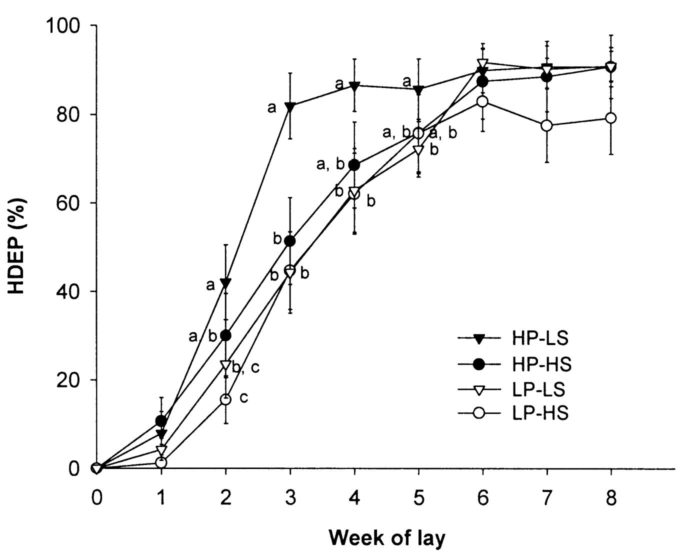

FIGURE 1. Weekly mean hen-day egg production (HDEP) in low stress (LS) and high stress (HS) quail categorized as high (HP) or low (LP) performers in a T-maze at 3 d of age. [a-c]Within each week, HDEP means with no common letter differ significantly ($P < 0.05$).

TABLE 4. Mean (± SE) egg weight (EWT) and BW (g) in low stress (LS) and high stress (HS) quail categorized as high (HP) or low (LP) performers in a T-maze at 3 d of age

	HP		LP	
Line	LS	HS	LS	HS
EWT (g)	9.7 ± 0.2	9.8 ± 0.2	9.4 ± 0.3	9.5 ± 0.2
BWT (g)	172.6 ± 3.4	169.1 ± 2.1	174.6 ± 2.4	170.6 ± 3.4

DISCUSSION

In the present study, Japanese quail chicks from the LS and HS lines were categorized as HP or LP based on their running times in a T-maze. The HP birds initiated egg lay earlier, reached A25%EP sooner, and laid more eggs during the first 8 wk of lay than did LP quail. Collectively, these findings suggest that, irrespective of the birds' markedly different genetic backgrounds of stress responsiveness, a quail chick's ability to rapidly negotiate a T-maze is associated with accelerated puberty and increased egg production. The significant performance category × line × laying period interaction showed that most of this favorable reproductive response was attributable to the HP chicks from the LS line (i.e., HP-LS individuals). HP broiler chicks showed a reduced adrenocortical response to an acute stressor (Marin and Jones, 1999). Therefore, although LS quail are already genetically predisposed to reduced adrenocortical responsiveness (see Introduction), it is conceivable that those that run the T-maze quickly may be even less sensitive to non-specific systemic stressors.

It is important to note that, herein, quail of the divergent lines were not intentionally exposed to any stressors. Nevertheless, we would expect differential adrenocortical responses consistent with the genetic background of each line to have occurred. For example, non-specific systemic stress responses were anticipated: 1) during routine maintenance chores (e.g., daily manual feed replenishment, removal, and scraping of droppings pans, etc.), 2) during bird capture, crating, transport, and handling for the purposes of hatching, leg- and wing-banding, and housing, and 3) as a result of placement into novel environments and groups (e.g., housing at hatching, brooding, and laying) with the attendant modification of social structures. Thus, the etiology of the superior female reproductive performance found in HP-LS hens might have stemmed from an augmented sociality or decreased adrenocortical responsiveness expected in HP and LS birds (Satterlee and Johnson, 1988; Jones et al., 1994, 1999, 2000; Marin and Jones, 1999) as well as contributions from other known behavioral differences, e.g., LS quail are less fearful than HS ones (Jones et al., 1992a,b, 1994, 1999).

Adrenocortical activity is thought to serve as a timer of the onset of puberty in rats because adrenalectomy delays puberty (an age-dependent effect), whereas corticoid replacement therapy restores its normal length, exogenous corticoids or stressors that activate the adrenal axis delay the onset of puberty, and delayed and precocious puberty are associated with disruptions in the timing of the daily adrenal rhythm (Ramaley, 1974, 1978). In birds, although the influence of adrenocortical activity on sexual maturation has not been studied, challenge with corticosterone (B), depending upon dose and stage of the ovulatory cycle, can inhibit or induce ovulation in adult domestic fowl (Etches and Croze, 1983; Rzasa et al., 1983; Pettite and Etches, 1991). The induction of ovulation by B treatment is typically demonstrated only when a well-developed pre-ovulatory follicle is present in the ovary, whereas chronic B administration seems to be clearly linked to the cessation of egg lay. Thus, delayed puberty and reduced egg production may be an expected consequence of selection for hypercorticalism (HS line).

Although HS quail showed a marked delay in puberty and 5% reduction in HDEP in the present study, these effects failed to reach significance, perhaps due to low sample size (approximately 40 hens/line), low stocking density (two birds/cage), reduced sex ratio (female:male, 1:1), or omission of quail that ran the maze in 26 to 99 s. Indeed, in a larger (n = 120 hens/line) and longer (10 wk of lay) experiment that involved no T-maze categorization and housing in groups of 10 hens with five males, LS quail showed a significant acceleration in puberty when compared to HS ones (Marin and Satterlee, 2001, unpublished observations). It should be added that, in the present study, HDEP during Weeks 7 and 8 in the LP-HS birds appeared to wane in comparison to the other treatment groups (Figure 1), suggesting that an extended study would have revealed divergence in HDEP between LS and HS quail.

In view of substantial individual variation in the T-maze behavior of chickens from commercial stocks (see Introduction) and the positive relationships observed between T-maze performance and body weight, sociality, and favorable physiological responses (Marin et al., 1997a; Jones et al., 1999; Marin and Jones 1999; Marin et al., 1999), rapidity in traversing the T-maze was proposed as a potential selection criterion for future breeding programs. Furthermore, we have also suggested that selection for decreased adrenocortical responsiveness is likely to reduce the incidence of stress-induced behavioral, physiological, and morphological responses that are associated with decreased welfare and productivity in commercially important poultry species (Jones, 1996; Jones and Hocking, 1999; Jones et al., 2000; Satterlee et al., 2000, 2002). Indeed, LS quail show lower levels of underlying fearfulness as well as reduced adrenal stress responsiveness to a wide variety of stressors (see Introduction). Additionally, LS males show an increase in cloacal gland area and foam production at 42 d of age (Satterlee et al., 2002), variables that reflect testis development and sexual activity (Siopes and Wilson, 1975; Oishi and Konishi, 1983; Delville et al., 1984). The present observation of enhanced female reproductive performance without alteration of egg size or hen body weight in HP quail, an effect most evident in HP-LS individuals, strengthens each of the above proposals and further suggests that a strategy incorporating physiological (reduced adrenocortical responsiveness) and behavioral (high performance in a T-maze) selection criteria may be even more advantageous.

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