Ontogeny of the Cloacal Gland in Male Japanese Quail Classified in a T-Maze[1]

M. C. Lábaque,* D. G. Satterlee,† D. A. Guzman,* and R. H. Marin*[2]

*Consejo Nacional de Investigaciones Científicas y Técnicas–Instituto de Ciencia y Tecnología de los Alimentos, Edificio de Investigaciones Biológicas y Tecnológicas, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, 5016, Argentina; and †Applied Animal Biotechnology Laboratories, Department of Animal Sciences, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, Louisiana State University, Baton Rouge, 70803

ABSTRACT Broiler chicks that traverse a T-maze quickly to reinstate contact with their companions (HP, high performers) are known to grow faster, are more social, and have a reduced plasma corticosterone response to acute stress than slower chicks (LP, low performers). High-performing quail from a line selected for reduced rather than exaggerated (high-stress) adrenocortical stress responsiveness also show enhanced female reproductive performance when compared with LP–high-stress quail. Herein, time courses of male sexual development were evaluated in genetically unremarkable quail that were categorized at 2 d of age as HP or LP in the T-maze. Body weight, cloacal gland volume (CVOL), proportion of individuals that produced cloacal gland foam, intensity of foam production, and CVOL relative to BW (RCVOL) were determined weekly from 4 to 10 wk of age, and again at 22 wk, along with absolute and BW-adjusted testes weight. Although CVOL and RCVOL were initially similar in both T-maze groups, both variables were greater ($P < 0.05$) in HP than in LP quail between 6 and 10 wk of age. High-performing birds also showed a trend ($P < 0.1$) of greater cloacal gland foam than their LP counterparts from 5 to 7 wk. From 8 wk on, all birds were in foam production. Intensity of foam production results generally mimicked those found for CVOL and RCVOL. Body weights were higher ($P < 0.05$) in HP than LP quail from 5 to 7 wk. No T-maze group differences were found in any of the variables at 22 wk of age. The results suggest that rapid negotiation of the T-maze is associated with accelerated growth and puberty in male quail, although the enhanced reproductive development of HP males does not remain extant in aged adults.

Key words: T-maze, cloacal gland, corticosterone, Japanese quail

2007 Poultry Science 86:2013–2019

INTRODUCTION

Selective reproduction, commonly known as genetic selection, is probably the quickest and most reliable method of promoting desirable characteristics and eliminating harmful ones in poultry and other farm animals (Craig and Swanson, 1994; Jones, 1996; Jones and Hocking, 1999). The substantial variation in behavioral characteristics that exists within, as well as between, populations of poultry provides considerable scope for selective breeding (Jones et al., 1991; Jones, 1997; Faure and Mills, 1998).

Substantial individual variation is also evident in the T-maze responses of individually tested, 2- to 3-d-old broiler chicks (Marin and Arce, 1996; Marin et al., 1997b; Jones et al., 1999; Marin et al., 2002). 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 1 of 2 categories: those that performed the task in a short time are classified as high-performance (**HP**) birds, and those that performed the task in a long time as low-performance (**LP**) birds. Broiler chicks classified as HP are known to grow faster (Marin et al., 1997a, 1999, 2003), show greater sociality (Jones et al., 1999; Marin et al., 2003), and, in response to an acute stressor, have a higher number of benzodiazepine γ-aminobutyric acid receptors (Marin and Arce, 1996) and a lower adrenocortical responsiveness (Marin and Jones, 1999) than their slower LP counterparts. Furthermore, broiler chick sex does not affect T-maze solution times (Marin and Arce, 1996). These findings suggest that T-maze behavior, if found to be a

Received March 23, 2007.
Accepted May 24, 2007.
[1]Approved for publication by the director of the Louisiana Agricultural Experiment Station as manuscript number 07-18-0121.
[2]Corresponding author: rmarin@efn.uncor.edu

heritable trait, might be a useful selection criterion for poultry breeding programs intended to improve the birds' productivity and welfare.

Interestingly, in Japanese quail, the ability to negotiate a T-maze has recently been shown to interact with genetic propensity to react to stress. Specifically, Marin et al. (2002) found that HP quail chicks from a line selected for reduced (low stress; **LS**) rather than exaggerated (high stress; **HS**) adrenocortical responsiveness (HP-LS quail) matured sooner and had a higher early hen-day egg production rate than LP-HS quail. In that study, HP-HS and LP-LS quail showed intermediate female reproductive performance. These findings suggest yet another advantage of using T-maze performance in selection programs: the potential to improve female reproduction. It should be noted here that Japanese quail are not only considered to be a useful model for the extrapolation of data to chickens and other commercially important poultry species (Kovach, 1974; Mills and Faure, 1992; Jones, 1996), but, in many countries, they are also an important agricultural species for meat and egg production (Caron et al., 1990; Baumgartner, 1994; Jones, 1996) as well.

Because of the numerous links between T-maze performance and the other behavioral, physiological, somatic growth, and female reproductive development and performance responses cited above, it is conceivable that T-maze-classified quail may differ in their male reproductive characteristics as well. In Japanese quail, cloacal gland (**CG**) hypertrophy and foam production are well known to be androgen dependent and highly positively correlated with testes size as well as with sexual activity (Coil and Wetherbee, 1959; McFarland et al., 1968; Sachs, 1969; Siopes and Wilson, 1975; Oishi and Konishi, 1983; Delville et al., 1984). Thus, measurement of CG size and expression of CG foam are considered to be excellent nondestructive indicators of male gonadal and general reproductive development. Therefore, in the present study, the ontogeny of male reproductive development in HP and LP T-maze-classified quail chicks was evaluated by studying temporal differences in various parameters that reflect CG size and foam production. The study was conducted over a range of time that spanned ages during which growing, photostimulated quail would be expected to have no CG development and foam production (i.e., all birds being prepubescent), rapidly developing CG growth and foam production, and full development of the CG with all birds in foam production (i.e., 100% of birds having reached puberty).

MATERIALS AND METHODS

Animals and Husbandry

Genetically unremarkable male Japanese quail (*Coturnix coturnix japonica*) were used in the present study. The birds evaluated (see below) were taken from a population of a single 432-bird hatch. Egg incubation, chick brooding, and lighting procedures were similar to those described elsewhere (Jones and Satterlee, 1996), with the exception that chicks were brooded from d 1 in mixed-sex groups of 36 within each of 12 brooder cages, each measuring 85 × 45 × 50 cm (length × width × height). Upon hatching, birds were leg banded to maintain the identity of each bird. At 2 d of age, all birds were categorized as HP or LP birds according to the time they took to traverse a T-maze to reinstate contact with their companions (see below). At 21 d of age, leg bands were replaced with wing bands of the same color and number to maintain permanent bird identity. Quail were sexed by plumage coloration at 28 d of age, at which time 44 HP and 44 LP males were randomly and individually housed into the cages of two 5-tier cage batteries, each battery comprising 50 cages. Each cage measured 45 × 20 × 25 cm (length × width × height).

From hatch to 4 wk of age, birds were fed a starter ration (28% CP; 2,800 kcal of ME/kg) and water ad libitum. From 4 wk on, birds were switched to a breeder ration (21% CP; 2,750 kcal of ME/kg) with feed and water continuing ad libitum. Birds were subjected to a daily photoperiod cycle of 14L:10D. Light intensity was approximately 350 lx during the lighted portion of the day, with lights-on occurring at 0600 h daily. Daily maintenance and feeding chores were done at the same time each day (0900 h). During the trial, 2 birds that died and a bird that escaped were not replaced. Thus, 42 HP and 43 LP males were considered for statistical analyses at the end of the study.

T-Maze Testing

The T-maze used was a smaller version of the one described by Marin et al., (1997b) for domestic chicks. It consisted of an isolation chamber (12.5 × 12.5 cm, length × width) leading to a 15 × 5 cm (length × width) 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 arms to facilitate movement of the chick toward this point. The T-maze apparatus was made of wood and painted white. It was placed in a 25 × 40 cm (length × width) section of a larger (60 × 40 cm) wooden brooder box, also painted white. Hardware cloth wire was used to separate the area within the box that contained the T-maze apparatus from a separate 35 × 40 cm (length × width) brooder box area that contained 17 or 18 quail on wood shavings litter (see below). Food and water were freely available in the brood area and an overhead lamp provided light for the entire apparatus. The T-maze apparatus was situated in a separate room from the room containing the brooder batteries. Ambient temperature and light intensity were similar between the 2 rooms.

The T-maze responses of 424 quail were measured at 2 d of age. Prior to testing, groups of chicks (n = 17 or 18) were placed in the brood areas of each of 4 identical T-maze apparatuses. Birds were allowed a 10-min acclimation period before testing began (at 0830 h). This arrangement allowed 4 experimenters to simultaneously test 4 individuals. 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. The time it took to exit from the arm of the T-maze facing the brood area was then recorded. Exit from the T-maze arm nearest the brood area allowed a test chick visual contact with its companions. The floor of the T-maze apparatus was wiped clean after each test. Tested birds were lightly marked on the head with a fast-drying non-toxic color marker before being returned to the brood area to prevent retesting. The procedures thus far were repeated by each experimenter until all quail within a given experimenter's brood area were tested. When this occurred, the entire groups of tested quail were returned to their brooders. The procedures described above were then repeated with new (untested) groups of quail (n = 17 or 18) until all 424 quail had been tested. Quail that negotiated (successfully completed) the maze in less than 20 s were categorized as HP chicks, whereas those that took longer than 100 s were classified as LP birds. These time intervals were chosen to include only those individuals that occupied the top and bottom quartile of the T-maze performance distribution. Birds with intermediate time scores (medium performers) were not included in the present study.

Traits Measured

Cloacal gland size measurements, length (mm) and width (mm), were made by using a digital calliper. Cloacal gland volume (**CVOL**) was calculated from these measurements according to the formula proposed by Chaturvedi et al. (1993):

$$4/3 \times 3.5414 \times a \times b^2,$$

where a is 0.5 times the long axis and b is 0.5 times the short axis. In addition, 2 measures of CG foam production (**CFP**) were made: proportion of individuals that produced CG foam (**PICF**) and intensity of CFP. Cloacal gland foam production was quantified by subjective scaling of the amount of foam ejected upon manual expression (squeezing) of the foam gland by using a scale of 1 (no foam expressed) to 5 (maximum amount of foam expression).

Cloacal gland volume, PICF, CFP, and BW measurements were made in all HP and LP quail at 4, 5, 6, 7, 8, 9, 10, and 22 wk of age. After the last measurement, all birds from each T-maze category were killed by cervical dislocation and their testes were removed by blunt dissection to determine testes weight (**TW**). Each individual's TW, CVOL, and BW were used to calculate TW relative to BW (**RTW**) and CVOL relative to BW (**RCVOL**).

Statistical Analyses

Cloacal gland volume, CFP, BW, and RCVOL were subjected to repeated-measures ANOVA that examined the main effects of T-maze category (HP and LP), time of sampling (4, 5, 6, 7, 8, 9, 10, and 22 wk of age; the repeated measure), and their interaction. To better fit the assumptions of the ANOVA, CFP values were transformed to ranks (Shirley, 1987). Testes weights and RTW data (measured only at 22 wk of age) were subjected to 1-way ANOVA that examined the main effect of T-maze category. Where appropriate, Fisher's least significant difference tests were used for post hoc comparisons of means. To evaluate T-maze category differences in PICF, the proportion test (Analytical Software, 2000) was used. This test compared the number of birds that were producing foam (successes) as a proportion of the sample size. To further examine the association between CVOL and TW and between RCVOL and RTW, Spearman rank correlations were also performed. A P-value of <0.05 was considered to represent significant differences.

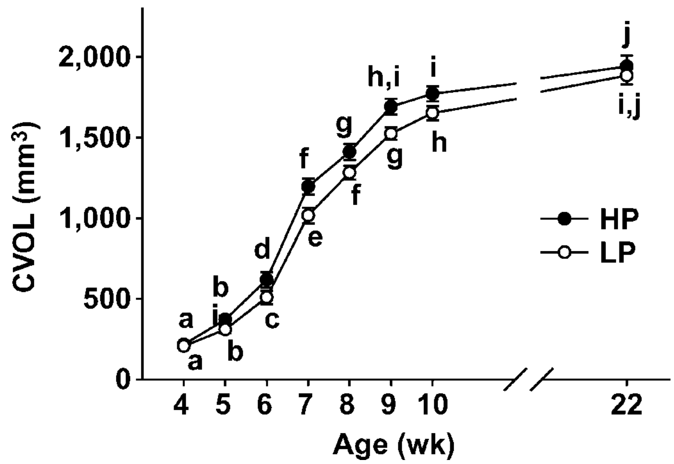

Figure 1. Mean (±SE, error bars) cloacal gland volume (CVOL) in Japanese quail categorized as high (HP) or low (LP) performers in a T-maze at 2 d of age. [a–j]Means with no common letter differ (P < 0.05).

RESULTS

Figure 1 depicts the mean (±SE) CVOL of HP and LP quail at 4, 5, 6, 7, 8, 9, 10, and 22 wk of age. Cloacal gland volume was significantly affected by T-maze category (HP > LP; $F_{1,83}$ = 5.86; P < 0.02) and quail age (CVOL increasing in time; $F_{7,581}$ = 789.28; P < 0.001), but these treatments did not interact (P = 0.15) to affect CVOL. Post hoc least significant difference tests showed that mean CVOL were similar in HP and LP quail initially (at 4 and 5 wk of age) and by the end of the study (at 22 wk). However, HP quail showed a significantly greater (P < 0.05) weekly CVOL than LP birds from 6 to 10 wk of age. Mean RCVOL (CVOL relative to BW) was also affected by T-maze category (HP > LP; $F_{1,83}$ = 3.96; P < 0.05) and quail age (increasing in time; $F_{7,581}$ = 611.41; P < 0.001). Similar to CVOL results, post hoc tests showed a higher (P < 0.03) RCVOL in HP birds than in LP birds only from 6 to 10 wk of age (data not shown).

No birds were in foam production at 4 wk of age. At 5 wk, about 32% of the birds began producing CG foam. A trend for a greater PICF in HP than in LP birds was detected at 5 (P < 0.10), 6 (P = 0.09), and 7 (P < 0.08) wk

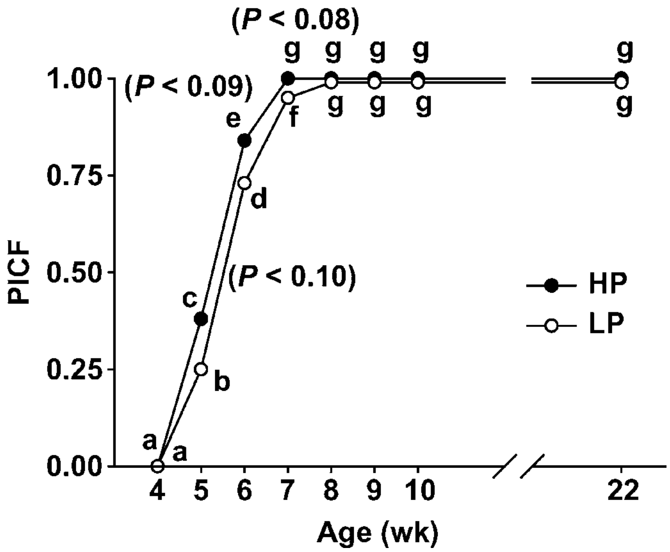

Figure 2. Proportion of individuals producing cloacal gland foam (PICF) in Japanese quail categorized as high (HP) or low (LP) performers in a T-maze at 2 d of age. [a–g]Proportions with no common letter differ ($P < 0.05$), unless otherwise indicated on the graph.

of age (Figure 2). Beginning at 8 wk and thereafter, all birds were in foam production.

Cloacal gland foam production results generally mimicked those found for CVOL (i.e., higher CFP was observed in HP than LP quail beginning at 6 wk of age and ending at 10 wk of age), although these group differences were statistically significant ($P < 0.02$) only at 7 wk of age (Figure 3). At 6, 9, and 10 wk, T-maze group differences (HP > LP) narrowly failed to reach significance ($P < 0.07$ in all 3 cases). Mean (±SE) BW of HP and LP quail at each of the 8 age intervals of measurement are shown in Figure 4. Body weights were significantly higher ($P < 0.05$) in HP quail compared with LP quail at 5, 6, and 7 wk of age.

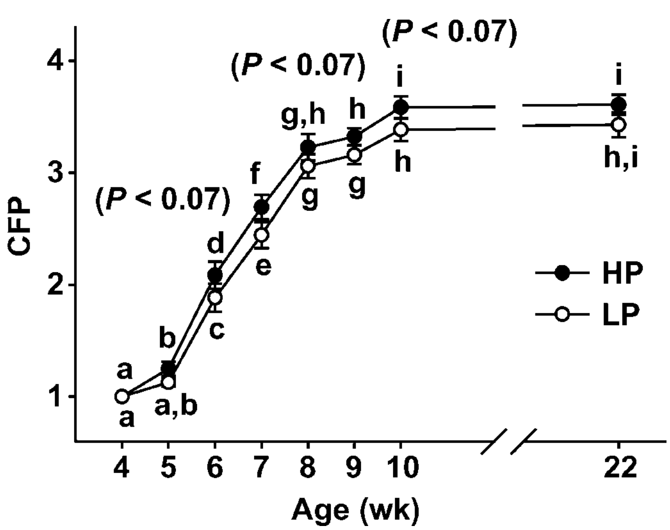

Figure 3. Mean (±SE, error bars) cloacal gland foam production (CFP) in Japanese quail categorized as high (HP) or low (LP) performers in a T-maze at 2 d of age. [a–i]Means with no common letter differ ($P < 0.05$), unless otherwise indicated on the graph.

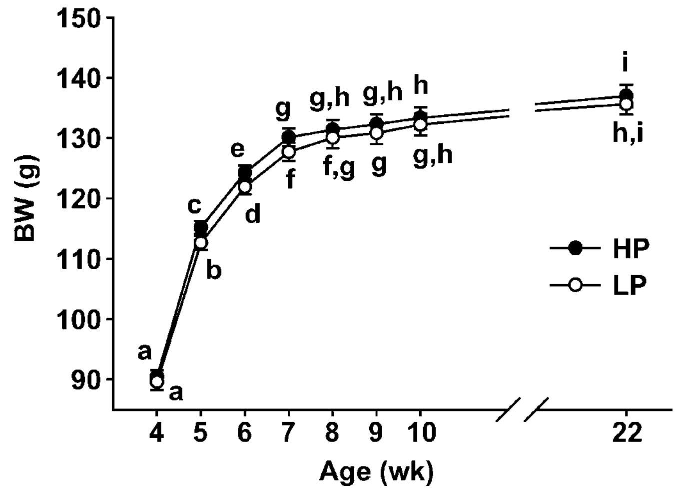

Figure 4. Mean (±SE, error bars) BW in Japanese quail categorized as high (HP) or low (LP) performers in a T-maze at 2 d of age. [a–i]Means with no common letter differ ($P < 0.05$).

Mean (±SE) TW and RTW measured at the end of the experiment (22 wk of age) did not differ between HP (2.282 ± 0.065 g and 0.017 ± 0.0005 g, respectively) and LP (2.234 ± 0.057 g and 0.016 ± 0.0004 g, respectively) quail. Spearman rank correlations from combined data of all HP and LP birds showed a positive significant relationship between CVOL and TW ($R_S = 0.32$; $P < 0.003$) and between RCVOL and RTW ($R_S = 0.36$; $P < 0.001$).

DISCUSSION

Cloacal gland size and foam production in photostimulated male Japanese quail are well known to increase with increasing age (Siopes and Wilson, 1975; Chaturvedi et al., 1993; Marin and Satterlee, 2004). Thus, the continual temporal increases in all of the CG measurements, CVOL, PICF and CFP, in birds of both T-maze chick groups of the present study were expected outcomes.

At 4 or 5 wk of age, no differences in CVOL or CFP were observed between HP and LP quail, suggesting that T-maze classification did not alter CG size or the gland's ability to produce foam at these very early ages. However, CVOL and CFP were greater from 6 to 10 wk of age in HP quail than in LP quail. These results suggest that sexual development is accelerated in birds of the HP category. Furthermore, because similar HP > LP temporal developmental differences were also found in RCVOL during the same time frame of 6 to 10 wk of age, these findings collectively suggest that the enhanced CG size and foam production in HP chicks during this time is likely a direct function of an altered endocrinology (see below) and is independent of somatic growth (i.e., concurrent changes in BW; see below). The HP > LP CG size and CFP differences detected at these earlier ages were lost by 22 wk of age, further indicating that the augmented reproductive development in HP males is not maintained in aged adults.

Interestingly, the PICF measure may have been even slightly more sensitive in first detecting HP > LP develop-

mental reproductive differences. Beginning at 5 wk of age, 1 and 2 wk earlier than what was found for the significant T-maze group differences in CVOL and CFP, respectively (see above), a higher number of HP than LP birds had begun foam production, although this difference was only of marginal statistical relevance ($P = 0.10$). Perhaps a larger number of observations would have allowed detection of PICF T-maze group differences at this very early age. Nevertheless, the greater HP PICF at 5 wk, a trend that continued at 6 ($P = 0.09$) and 7 ($P = 0.08$) wk of age, well supported our thesis that the onset of puberty (preciousness) was advanced in birds that more quickly traversed the T-maze.

Even though CVOL and CFP were still rising differently by T-maze group (HP > LP) beyond 7 wk of age, at 8 wk of age and thereafter, all birds were producing at least some CG foam, regardless of their T-maze category. This is not surprising because eventually all birds should begin to produce some foam (i.e., reach a recognizable state of puberty) or they would be considered sexually dysfunctional adults. Collectively, the findings of our former study of the interactive effects of T-maze-classified LS and HS chicks on female quail sexual maturation and early egg lay (see the introduction section and Marin et al., 2002) and the present male findings suggest that a quail chick's ability to rapidly negotiate a T-maze is associated with accelerated puberty in both quail sexes.

Cloacal gland hypertrophy and foam production are known to be androgen dependent and highly positively correlated with testes size as well as sexual activity (see the introduction section). Thus, because of the HP > LP differences in CVOL, CFP, and PICF between 6 to 10 wk of age, we hypothesized that HP quail likely also possess both higher TW and blood levels of testosterone during these intermediate ages. Unfortunately, we did not measure TW during this pubertal development period because doing so would have required killing birds, and thus not allowing any further repeated measures on the temporally sampled birds (i.e., a habitual loss of n and power of statistical testing with increasing time). Likewise, we decided not to sample blood for testosterone measurements at each of these ages to avoid adding any further stressors beyond the unavoidable stressors that likely accompanied the collection of the 7 repeated weekly (4 to 10 wk of age) CG measurements. Thus, TW and RTW were determined only at the end of the study (22 wk). Although TW and RTW were similar between the HP and LP groups by this time (i.e., in aged adults), we nevertheless found moderate but highly significant positive relationships between CVOL and TW and between RCVOL and RTW at this age when all data were combined. This result suggests that CG hypertrophy may even somewhat reflect testicular size in aged birds that are no longer sexually developing.

It has been proposed that full spermatogenesis occurs in the *Coturnix* when a left and right TW of 500 mg is achieved (Mather and Wilson, 1964; Purcell and Wilson, 1975). Although daily sperm production was not measured in the present study, at 22 wk of age, all birds were in foam production of an apparently maximal amount, as expected, and they had greatly exceeded (range: 5.3- to 14.5-fold; data not shown) this 500-mg TW threshold. Therefore, it is highly likely that full spermatogenesis was extant in both HP and LP quail at this late age. The finding of similar TW and RTW in both HP and LP quail at 22 wk of age is also not surprising because male quail of that age would be about 11 to 13 wk beyond their sexual peak. However, it would be interesting to determine whether T-maze category differences reemerge in very aged quail when blood levels of testosterone and sexual senescence are known to occur (Ottinger et al., 1997).

Of particular relevance to the present study, male quail selected for a reduced (LS) rather than exaggerated (HS) plasma corticosterone response to brief restraint, similar to HP males in the present study, have an accelerated onset of puberty (Satterlee et al., 2002; Marin and Satterlee, 2004; Satterlee and Marin, 2004; Satterlee et al., 2007a,b). Quail from the LS line have also been shown to possess lower fearfulness, a nonspecific reduction in stress responsiveness, less developmental instability, and greater sociality than HS quail (Satterlee and Johnson, 1985; Jones et al., 1992a,b, 1994, 2000, 2002; Jones and Satterlee, 1996; Satterlee et al., 2000). In avians, the administration of corticosterone or adrenocorticotrophin, as well as activation of the hypothalamic-pituitary-adrenal axis by various nonspecific systemic stressors, is associated with depression in the hypothalamic-pituitary-testicular axis (Deviche et al., 1982; Deviche, 1983; Edens, 1987; Joseph and Ramachandran, 1993). Thus, we have proposed that the negative relationships between corticosterone and male reproductive function reported in the literature may reflect corticosterone-induced alterations of pituitary gonadotrophic hormone release, Leydig cell apoptosois, or both—phenomena that may underlie the compromised reproductive functioning found in HS quail when compared with LS birds (Satterlee et al., 2000, 2002, 2006, 2007b; Marin and Satterlee, 2004; Satterlee and Marin, 2004). Interestingly, plasma corticosterone responses to a partial water immersion stressor were lower in HP than LP chicks (Marin and Jones, 1999), indicating a differential susceptibility to stressful stimulation in T-maze categorized birds. Therefore, because adrenocortical stress responses are classically considered to be nonspecific in terms of the stressors that induce such responsiveness, it is conceivable that HP quail may be less sensitive to other stressors as well. Therefore, in the present study, although the quail were not intentionally exposed to stressors, it may well be that periodic differential adrenocortical responses in the direction of HP < LP may have occurred during daily routine maintenance chores and during the unavoidable stress associated with bird capture, transport, and handling for the purposes of hatching, leg and wing banding, housing, and collection of the CG measurements. Thus, the etiology of the accelerated reproductive development found in HP quail in the present study may have stemmed from a decreased adrenocortical responsiveness.

In addition to the differences in stress susceptibility between the HP and LP broiler chicks mentioned above, HP chicks are known to grow faster under different rearing conditions (Marin et al., 1997a, 1999, 2003) and show greater sociality (Jones et al., 1999; Marin et al., 2003). Given the demonstrated negative effects of corticosterone on BW (Bartov, 1982; Satterlee and Johnson, 1985; Puvadolpirod and Thaxton, 2000), Marin et al. (2003) proposed that the superior growth rates found in the more sociable HP birds may simply reflect the possibility that they can devote more of their feed and bodily resources to growth rather than using energy to respond to social or other stressors. These authors further suggested that HP-type birds may be better suited to being reared in very large, high-density (crowded) groups. Interestingly, beginning at 4 wk of age, quail in this study were reared in isolation, where the more sociable HP birds would have been expected to be more ill-suited. However, birds from the HP category still showed a significantly higher BW from 5 to 7 wk of age than their LP counterparts. The present results also suggest that the phenomenon of better growth rate in HP birds can be generalized to include another poultry species (*Coturnix*). Comparisons of growth rates and circulating levels of corticosterone in HP and LP quail reared at different densities may help further elucidate the mechanisms that underpin rapid growth in HP individuals.

In conclusion, the present findings not only confirm previous studies that showed better growth rates in HP birds, but they also provide evidence of yet another intuitively desirable reproductive outcome associated with HP in the T-maze, which augments the previously documented female precociousness and heightened egg lay: accelerated male puberty. Because of the positive relationships between CG development, testicular size, and spermatozoa production (Siopes and Wilson, 1975; Kirby et al., 1996; Amann, 1999), retention of HP males in breeding programs or selection for this trait may allow males to successfully breed at an earlier age and thus reduce the costs associated with male maintenance. A study of male reproductive behavior of T-maze-classified birds is currently underway. Preliminary results indicate that a higher number of HP than LP male quail are able to successfully copulate at an earlier age (Marin and Labaque, unpublished data).

It has been proposed (Jones, 1996; Jones and Hocking, 1999; Jones et al., 2000; Satterlee et al., 2000) that selection for reduced adrenocortical responsiveness, reduced fearfulness, heightened sociality, or their combination may be worthwhile in ameliorating the incidence of stress-induced behavioral, physiological, and morphological responses that are associated with decreased animal welfare and productivity in commercially important poultry species. Two of these traits (reduced adrenocortical responsiveness and increased sociality) are apparent in HP birds as well. Thus, assuming that HP behavior is sufficiently heritable, early-age T-maze testing may provide yet another useful tool as an alternative to poultry breeders interested in identifying genotypes that possess significant potential for improved productivity and animal welfare.

ACKNOWLEDGMENTS

This research was supported by grants from Agencia Nacional de Promoción Científíca y Tecnológica; Secretaría de Ciencia y Tecnológia, Universidad Nacional de Córdoba (SECyT UNC), and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina. RHM is a career member of CONICET, Argentina. MCL and DAG hold research fellowships from CONICET and SECyT UNC, respectively.

REFERENCES

Amann, R. P. 1999. Symposium: Managing poultry reproduction to satisfy market demands. Lessons for the poultry industry gleaned from experiences with other commodity species. Poult. Sci. 78:419–427.

Analytical Software. 2000. Statistix7: A User's Manual. Version 7. Analytical Software, Tallahassee, FL.

Bartov, I. 1982. Corticosterone and fat deposition in broiler chicks: Effect of injection time, breed, sex and age. Br. Poult. Sci. 23:161–170.

Baumgartner, J. 1994. Japanese quail production, breeding and genetics. World's Poult. Sci. J. 50:227–235.

Caron, N., F. Minvielle, M. Desmarais, and L. M. Poste. 1990. Mass selection for 45-day body weight in Japanese quail: Selection response, carcass composition, cooking properties, and sensory characteristics. Poult. Sci. 69:1037–1045.

Chaturvedi, C. M., R. Bhatt, and D. Phillips. 1993. Photoperiodism in Japanese quail (*Coturnix coturnix japonica*) with special reference to relative refractoriness. Ind. J. Exp. Biol. 31:417–421.

Coil, W. H., and D. K. Wetherbee. 1959. Observations on the cloacal gland of the Eurasian quail *Coturnix coturnix*. Ohio J. Sci. 59:268–270.

Craig, J. V., and J. C. Swanson. 1994. Welfare perspectives on hens kept for egg production. Poult. Sci. 73:921–938.

Delville, Y., J. C. Hendrick, J. Sulon, and J. Balthazart, 1984. Testosterone metabolism and testosterone-dependent characteristics in Japanese quail. Physiol. Behav. 33:817–823.

Deviche, P. 1983. Interaction between adrenal function and reproduction in male birds. Pages 243–254 in Avian Endocrinology: Environmental and Ecological Perspectives. S. Mikami, ed. Springer-Verlag, Berlin, Germany.

Deviche, P., R. Massa, L. Bottoni, and J. Hendrick. 1982. Effect of corticosterone on the hypothalamic-pituitary-gonadal system of male Japanese quail exposed to either short or long photoperiods. J. Endocrinol. 95:165–173.

Edens, F. W. 1987. Manifestations of social stress in grouped Japanese quail. Comp. Biochem. Physiol. A 86:469–472.

Faure, J. M., and A. D. Mills. 1998. Improving the adaptability of animals by selection. Pages 235–264 in Genetics and the Behavior of Domestic Animals. T. Grandin, ed. Acad. Press, San Diego, CA.

Jones, R. B. 1996. Fear and adaptability in poultry: Insights, implications and imperatives. World's Poult. Sci. J. 52:131–174.

Jones, R. B. 1997. Fear and distress. Pages 75–87 in Animal Welfare. M. C. Appleby and B. O. Hughes, ed. CAB Int., Wallingford, UK.

Jones, R. B., and P. M. Hocking. 1999. Genetic selection for poultry behaviour: Big bad wolf or friend in need? Anim. Welf. 8:343–359.

Jones, R. B., R. H. Marin, D. G. Satterlee, and G. G. Cadd. 2002. Sociality in Japanese quail (*Coturnix japonica*) genetically se-

lected for contrasting adrenocortical responsiveness. Appl. Anim. Behav. Sci. 75:337–346.
Jones, R. B., A. D. Mills, and J. M. Faure. 1991. Genetic and experiential manipulation of fear-related behavior in Japanese quail chicks (*Coturnix coturnix japonica*). J. Comp. Psychol. 105:15–24.
Jones, R. B., and D. G. Satterlee. 1996. Threat-induced behavioural inhibition in Japanese quail genetically selected for contrasting adrenocortical response to mechanical restraint. Br. Poult. Sci. 37:465–470.
Jones, R. B., D. G. Satterlee, and G. G. Cadd. 1999. Timidity in Japanese quail: Effects of vitamin C and divergent selection for adrenocortical response. Physiol. Behav. 67:117–120.
Jones, R. B., D. G. Satterlee, and F. H. Ryder. 1992a. Fear and distress in Japanese quail chicks of two lines genetically selected for low or high adrenocortical response to immobilization stress. Horm. Behav. 26:385–393.
Jones, R. B., D. G. Satterlee, and F. H. Ryder. 1992b. Open-field behavior of Japanese quail genetically selected for low or high plasma corticosterone response to immobilization stress. Poult. Sci. 71:1403–1407.
Jones, R. B., D. G. Satterlee, and F. H. Ryder. 1994. Fear of humans in Japanese quail selected for low or high adrenocortical response. Physiol. Behav. 56:379–383.
Jones, R. B., D. G. Satterlee, D. Waddington, and G. G. Cadd. 2000. Effects of repeated restraint in Japanese quail genetically selected for contrasting adrenocortical responses. Physiol. Behav. 69:317–324.
Joseph, J., and A. V. Ramachandran. 1993. Effect of exogenous dexamethasone and corticosterone on weight gain and organ growth in post-hatched White Leghorn chicks. Ind. J. Exp. Biol. 31:858–860.
Kirby, J. D., M. V. Mankar, D. Hardesty, and D. L. Kreider. 1996. Effects of transient prepubertal 6-*N*-propyl-2-thiouracil treatment on testis development and function in the domestic fowl. Biol. Reprod. 55:910–916.
Kovach, J. K. 1974. The behaviour of Japanese quail: Review of literature from a bioethological perspective. Appl. Anim. Ethol. 1:77–102.
Marin, R. H., and A. Arce. 1996. Benzodiazepine receptors increase induced by stress and maze learning performance, in chick forebrain. Pharmacol. Biochem. Behav. 3:581–584.
Marin, R. H., A. Arce, and I. D. Martijena. 1997a. T-maze performance and body weight relationship in broiler chicks. Appl. Anim. Behav. Sci. 54:197–205.
Marin, R. H., and R. B. Jones. 1999. Latency to traverse a T-maze at 2 days of age and later adrenocortical responses to an acute stressor in domestic chicks. Physiol. Behav. 66:809–813.
Marin, R. H., R. B. Jones, D. A. Garcia, and A. Arce. 1999. Early T-maze performance and subsequent growth in commercial broiler flocks. Br. Poult. Sci. 40:434–438.
Marin, R. H., I. D. Martijena, and A. Arce. 1997b. Effect of diazepam and a β-carboline on open-field and T-maze behaviors in 2-day-old chicks. Pharm. Biochem. Behav. 58:915–921.
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.
Marin, R. H., D. G. Satterlee, G. G. Cadd, and R. B. Jones. 2002. T-maze behavior and early egg production in Japanese quail selected for contrasting adrenocortical responsiveness. Poult. Sci. 81:981–986.
Marin, R. H., D. G. Satterlee, S. A. Castille, and R. B. Jones. 2003. Early T-maze behavior and broiler growth. Poult. Sci. 82:742–748.
Mather, F. B., and W. O. Wilson. 1964. Post-natal testicular development in Japanese quail. Poult. Sci. 43:860–864.
McFarland, L. Z., R. L. Warner, W. O. Wilson, and F. B. Mather. 1968. The cloacal gland complex of the Japanese quail. Experientia 24:941–943.
Mills, A. D., and J. M. Faure. 1992. The behaviour of domestic quail. Pages 1–16 in Nutztierethologie. M. Nichelmann, ed. Gustav Fisher Verlag, Jena, Germany.
Oishi, T., and T. Konishi. 1983. Variations in the photoperiodic cloacal response of Japanese quail: Association with testes weight and feather color. Gen. Comp. Endocrinol. 50:1–10.
Ottinger, M. A., N. Thompson, C. Viglietti-Panzica, and G. C. Panzica. 1997. Neuroendocine regulation of GnRH and behaviour during aging in birds. Brain Res. Bull. 44:471–477.
Purcell, S. M., and W. O. Wilson. 1975. Growth and maturation of testes in young *Coturnix* and modification by exogenous FSH, LH, and testosterone-a stereologic evaluation. Poult. Sci. 54:1115–1122.
Puvadolpirod, S., and J. P. Thaxton. 2000. Model of physiological stress in chickens. 1. Response parameters. Poult. Sci. 79:363–369.
Sachs, B. D. 1969. Photoperiodic control of reproductive behavior and physiology of the Japanese quail. Horm. Behav. 1:7–24.
Satterlee, D. G., G. C. Cadd, and R. B. Jones. 2000. Developmental instability in Japanese quail genetically selected for contrasting adrenocortical responsiveness. Poult. Sci. 79:1710–1714.
Satterlee, D. G., C. A. Cole, and S. A. Castille. 2006. Cloacal gland and gonadal photoresponsiveness in male Japanese quail selected for divergent plasma corticosterone response to brief restraint. Poult. Sci. 85:1072–1080.
Satterlee, D. G., C. A. Cole, and S. A. Castille. 2007a. Maternal corticosterone further reduces the reproductive function of male offspring hatched from eggs laid by quail hens selected for exaggerated adrenocortical stress responsiveness. Poult. Sci. 86:572–581.
Satterlee, D. G., and W. A. Johnson. 1985. Metabolic traits in Japanese quail selected for low or high corticosterone response to stress. Poult. Sci. 64(Suppl. 1):176. (Abstr.)
Satterlee, D. G., and R. H. Marin. 2004. Photoperiod-induced changes in cloacal gland physiology and testes weight in male Japanese quail selected for divergent adrenocortical responsiveness. Poult. Sci. 83:1003–1010.
Satterlee, D. G., R. H. Marin, and R. B. Jones. 2002. Selection of Japanese quail for reduced adrenocortical responsiveness accelerates puberty in males. Poult. Sci. 81:1071–1076.
Satterlee, D. G., M. Tong, S. A. Castille, and R. H. Marin. 2007b. Cloacal gland growth differences in high and low plasma corticosterone stress response line male quail reared under short daylengths. Poult. Sci. 86:1213–1217.
Shirley, E. A. 1987. Application of ranking methods to multiple comparison procedures and factorial experiments. Appl. Stat. 36:205–213.
Siopes, T. D., and W. O. Wilson. 1975. The cloacal gland—An external indictor of testicular development in *Coturnix*. Poult. Sci. 54:1225–1229.