Research Note

Cloacal Gland Growth Differences in High and Low Plasma Corticosterone Stress Response Line Male Quail Reared Under Short Daylengths[1]

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ABSTRACT Mail quail selected (generation 32) for reduced [low stress (LS)] or exaggerated [high stress (HS)] plasma corticosterone stress response to brief mechanical restraint (5 min of immobilization) were studied for differences in the growth of their cloacal glands when reared essentially lifelong on short day lengths of 8L:16D. Postbrooding, at 4 wk of age, 96 quail (48 LS + 48 HS) were housed in cages (1 LS and 1 HS male/cage), and the short day light treatment was instigated. Using a digital caliper, cloacal gland (CG) size measurements (length and width, mm) were made biweekly beginning at 42 d of age and ending at 196 d of age (28 wk old). The CG volume (CVOL) was calculated from these measurements using a literature-proposed formula. The CVOL in both lines increased similarly with increasing age from 6 to 12 wk of age. However, beginning at 14 wk of age and thereafter, LS males showed greater ($P < 0.05$) CVOL than HS ones. No further increases in CVOL were observed in either line at 24 wk of age beyond that seen at 22 wk. This study demonstrated that although both lines show CG development under short days, eventually CG growth becomes comparatively stymied in the HS males. Furthermore, the maintenance of similarly lower CVOL in HS than LS males, CVOL that showed no further increase from 22 to 24 wk of age, suggests that holding these quail lifelong on short days results in, comparatively, yet another permanent negative reproductive consequence in quail selected for exaggerated plasma corticosterone stress responsiveness.

Key words: light, short day, cloacal gland, corticosterone, Japanese quail

INTRODUCTION

In Japanese quail, cloacal gland (**CG**) hypertrophy is controlled by day length, androgen-dependent, and moderately to highly positively correlated with testes size, CG foam production, fertility, and sexual activity (Coil and Wetherbee, 1959; McFarland et al., 1968; Sachs, 1969; Siopes and Wilson, 1975; Massa et al., 1980; Oishi and Konishi, 1983; Balthazart et al., 1979, 1984; Delville et al., 1984; Amet et al., 1986; Domjan, 1987; Mohan et al., 2002; Biswas et al., 2007). Thus, measurement of CG volume (**CVOL**) is an excellent nondestructive indicator of male gonadal development and function.

During rapid sexual development (at 42 d of age), Japanese quail selected for reduced [low stress (**LS**)] rather than exaggerated [high stress (**HS**)] plasma corticosterone (**B**) response to brief restraint possess greater CVOL (Sat-

terlee et al., 2002). In this snapshot pilot study, in which quail were held on essentially lifelong long days (14 h of light daily), more LS quail also produced CG foam of a greater amount. We have since shown 4 things. First, CG development and foam production occurs sooner in LS than in HS quail (i.e., puberty was accelerated in LS males; Marin and Satterlee, 2004). Second, line differences (LS > HS) in CVOL and testes weight persist well into adulthood in quail held on a stimulatory photoperiod of 14L:10D (Marin and Satterlee, 2004). Third, the adult quail stress line differences in CVOL and testes size found by Marin and Satterlee (2004) transiently persisted (LS > HS) during a period of very short day- (6L:18D) induced gonadal involution and permanently reemerged (LS > HS) during subsequent regrowth on long days of 14L:10D (Satterlee and Marin, 2004). Fourth, adult photostimulated (16 h of light) LS males are more resistant to CVOL reduction during a short mild light (13 h of light) crash, with LS > HS CVOL line differences again reemerging upon rephotostimulation with 16 h of light (Satterlee et al., 2006). In this most recent study, LS males also were shown to have greater absolute and BW-adjusted testes weights than did HS ones after rephotostimulation.

All *Coturnix* strains apparently show full CG development on long days, but in certain stocks, the CG may develop fully, partially, or not at all on chronic short days (see "Discussion"). In the present study, we assessed differences in CVOL development between males of the LS and HS quail lines reared under essentially lifelong short day lengths (8L:16D) to see if we have quail stocks that develop their cloacal glands under such habitually photo-deprived conditions and, if so, if line differences exist in their developmental profiles. Examination of the latter (possibility of line differences in CG development) was deemed justifiable considering the numerous forerunner photoperiod treatment studies we have conducted that have detected stress line differences in CG physiology and the growing literature that supports a negative relationship between B and reproductive function.

MATERIALS AND METHODS

Genetic Stocks and Animal Husbandry

Male Japanese quail from generation (**G**) 32 of 2 lines selected for either a low (LS) or high (HS) plasma B response to brief mechanical restraint (Satterlee and Johnson, 1988) were studied. The genetic history of the lines, up to G_{31}, is discussed elsewhere (Satterlee et al., 2000; Marin and Satterlee, 2004). Although line differences in levels of plasma B were not measured herein, recent findings in the stress lines attest to the maintenance of divergent adrenocortical responsiveness to a variety of nonspecific systemic stressors. For example, J. Cockrem (Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Palmerston North, New Zealand) and D. G. Satterlee (unpublished data) studied the same generation of quail as that used here (G_{32}) and found significant line differences, HS > LS, in levels of plasma B that were approximately 4-fold and 2-fold different at 15 and 30 min, respectively, after 5 min of handling (i.e., repetitive capture from and release back into a cardboard box). Furthermore, Hayward et al. (2005), studying this same generation, reported egg yolk B concentrations to be greater in yolks collected from eggs of HS hens than in yolks from LS hens by 62 and 96%, respectively, when hens were undisturbed or socially stressed during egg formation.

The quail used were taken from a larger population of approximately 600 hatchlings per line. Egg incubation, chick brooding, feeding, and lighting procedures were similar to those described by Jones and Satterlee (1996), with the exception that chicks were brooded from d 1 in mixed-sex, mixed-line groups of approximately 50 chicks within each of 24 compartments of 2 Petersime brooder batteries (model 2S-D, Petersime Incubator Co., Gettysburgh, OH) modified for quail. During brooding, birds were fed a quail starter ration (28% CP; 2,800 kcal of ME/kg) and water ad libitum. To maintain the line identity of each bird, leg bands (placed on chicks at hatching) were replaced with permanent wing bands at 21 d of age.

At 28 d of age, brooding in the Petersime brooder batteries (see above) was discontinued, quail were sexed by plumage coloration, and 48 LS and 48 HS males were housed in a separate light-tight room within 48 cages (1 LS + 1 HS/cage) of a Alternative Cage Designs 4-tier cage battery (the battery contained 48 pedigree-style breeder cages; Alternative Cage Designs, Alternative Design Manufacturing and Supply Inc., Siloam Springs, AR). Individual cage dimensions were $50.8 \times 15.2 \times 26.7$ cm (length $\times$ width $\times$ height). Care was taken to insure that the sum of the occupants of all cages, although randomly selected within a line, constituted equal representation of the 12 different families that make up each line (i.e., 4 males/family per line were used).

Commensurate with cage housing at 28 d of age, birds were also switched to a breeder ration (21% CP; 2,750 kcal of ME/kg) with feed and water continued ad libitum. A daily cycle of short days (8L:16D; approximately 280 lx during the lighted portion of the day) was instigated at this time. Lights-on was at 0600 h, and lights-off was at 1400 h daily. Daily maintenance and feeding chores were done at the same time each day (0800 h).

CVOL Measurement

Cloacal gland volume was determined in all males (LS and HS) beginning at 42 d of age (14 d after brooding was discontinued and the quail were placed on the short photoperiod regimen). The CVOL determinations were also made every 14 d thereafter until the quail reached 196 d of age (which constituted a full 24 wk or 168 d on short days). To calculate CVOL, CG size measurements (length and width, mm) were made using a digital caliper. The 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 $a = 0.5 \times$ long axis and $b = 0.5 \times$ short axis). To avoid potential effects of different operators and biases of knowing test quail line identities, the same experimenter who was blinded to the study treatments made all CG length and width measurements.

Statistical Analyses

The CVOL data were subjected to a repeated measures ANOVA that examined the main effects of the 2 lines (LS vs. HS), the 12 times of CVOL measurement (i.e., the biweekly CVOL measurements made from 42 to 196 d of age), and their interaction. To better fit the assumptions of the ANOVA, data were transformed to ranks (Shirley, 1987). Duncan's tests were used for posthoc testing for differences between the line $\times$ sampling time means. Best-fit regression equations for the relationship between age and CVOL were determined within each line. A *P*-value of 0.05 or less was considered to be significant.

RESULTS

Profound differences in mean CVOL by line (LS > HS; $F_{1,89} = 20.17$; *P* < 0.000002) and time of sampling (nearly
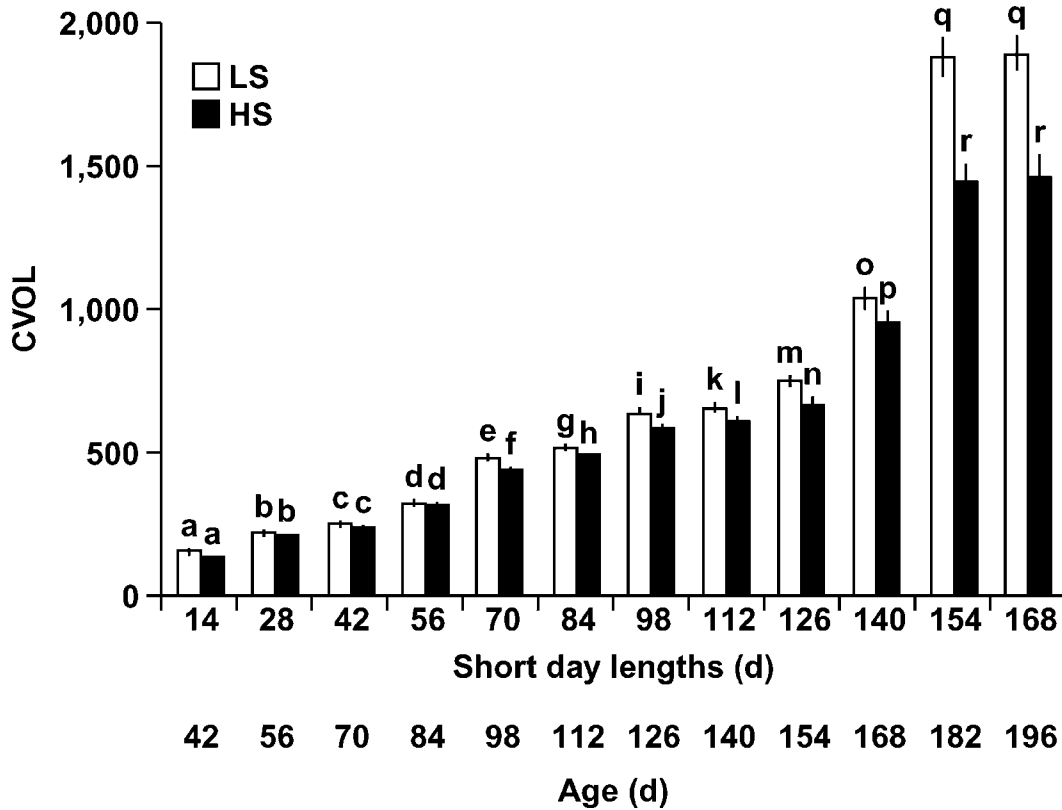
Figure 1. Mean (±SE; vertical bars) cloacal gland volume (CVOL) in quail lines selected for reduced [low stress (LS)] or exaggerated [high stress (HS)] plasma corticosterone response to brief mechanical restraint and held essentially lifelong on short day lengths. [a–r]$P < 0.01$.

continual temporal increases; $F_{11,979} = 1,546.24$; $P < 0.0000001$) were evident. A significant interaction between these factors ($F_{11,979} = 2.74$; $P < 0.00172$) was detected as well.

Figure 1 depicts the biweekly changes in mean CVOL responses of LS and HS male quail held for the entire 24 wk (from 28 to 196 d of age) on short day lengths of 8L:16D. Duncan's testing of these interactive means showed that, although CVOL steadily increased from 2 to 8 wk on short days, the increases observed were similar in both lines. However, beginning at 10 wk on short days (at 98 d of age) and biweekly thereafter, LS male quail grew their CG at a significantly greater ($P < 0.01$) rate than did HS ones. By the last 2 time intervals of measurement (22 and 24 wk on short days, or 182 and 196 d of age, respectively), CVOL was approximately 23% less in the HS compared with LS males. Because no further increases in CVOL were observed in either line from 22 to 24 wk on short days, it was assumed that maximal gland growth had been achieved in the 2 lines by the former of these 2 times, and so the study was ended. Within each line, the best-fit regression relationship between age (d) and CVOL was a fourth-order polynomial (CVOL $= -655.674 + 42.047 \times \text{age} - 0.666 \times \text{age}^2 + 4.359\text{e-}3 \times \text{age}^3 - 8.814\text{e-}6 \times \text{age}^4$, r $= 0.95$, $P < 0.01$ and CVOL $= -425.981 + 28.645 \times \text{age} - 0.442 \times \text{age}^2 + 2.967\text{e-}3 \times \text{age}^3 - 6.179\text{e-}6 \times \text{age}^4$, r $= 0.96$, $P < 0.01$ for LS and HS quail, respectively).

DISCUSSION

We have discussed elsewhere (Satterlee et al., 2000, 2002; Marin and Satterlee, 2004; Satterlee and Marin, 2004; Satterlee et al., 2006) the evidence that 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 in birds. This has led us to hypothesize that these relationships, in turn, present a plausible explanation for the observation of stress-induced inhibition of male reproductive functions (Deviche et al., 1982; Deviche, 1983; Edens, 1987; Joseph and Ramachandran, 1993). We have attempted to explain the typically observed reductions in avian male reproductive function that have been associated with activation of the hypothalamic-pituitary-adrenal axis by the following possible mechanisms. First, B release has been linked to declines in the release of or effects on the gonadotrophin release factors, the gonadotrophic hormones themselves, the gonadal steroids, or both gonadotrophic hormones and gonadal steroids. Corticosterone may inhibit gonadotroin-releasing hormone and therefore secretion of follicle-stimulating hormone, luteinizing hormone (**LH**), or both, and the positive effects of these gonadotrophins on the testes and LH-induced secretion of testosterone (Satterlee et al., 2000, 2002; Marin and Satterlee, 2004; Satterlee and Marin, 2004, 2006). Folli-

cle-stimulating hormone, of course, through its action on the Sertoli cells of the testes, is becoming increasingly known to be needed to maintain optimum testicular mass to support a high level of daily sperm production. On the other hand, LH targets the testicular Leydig cells to bring about maturation of spermatagonia and the release of testosterone. Thus, because CG development and foam production are androgen-dependent (see above), the proposed B-induced reductions in blood testosterone levels from healthy Leydig cells could result in a reduced testosterone signal to support CG maintenance. Second, B may also be active in promoting Leydig cell apoptosis, which thereby also supports a case of insufficient testosterone to support maximum CVOL (Satterlee et al., 2007).

The LS and HS male quail have shown numerous differences in their photic responsiveness in terms of changes in CVOL, CG foam production, and testicular mass. For example, compared with HS individuals, LS ones show an acceleration of puberty and maintenance of enhanced reproductive function when maintained on long days (as evidenced by earlier CG development and foam production coupled with persistently greater CVOL and testes weight in adults) and a greater resistance to reproductive declines coupled with quicker recovery to permanently higher reproductive function during both mild (13 h of light) and more extreme (6 h of light) light crashes and relighting experiences (as evidenced by various changes in CVOL and testes weight; see "Introduction"). Until now, line differences in CG development in male quail held under short days had not been investigated.

In the present study, the fact that LS and HS male quail were both able to grow their CG when held essentially on lifelong short day lengths of 8 h of light daily suggests that these lines were derived from a progenitor stock that possessed such ability. Quail stocks that apparently do (Sharp and Sterling, 1985), do not fully (Sharp and Sterling, 1985; Chaturvedi et al., 1993; Phillips et al., 1997), or do not at all (T. Siopes, Department of Poultry Science, North Carolina State University, Raleigh, and C. M. Chaturvedi, Department of Zoology, Banaras Hindu University, Varanasi, India, personal communication) develop their gonads when held under short days apparently exist. Indeed, Chaturvedi et al. (1993) found that quail held under short day lengths since hatch showed cyclicity in their CG size responses. In their study, CG remained undeveloped for the first 7 wk of life (scotosensitivity), spontaneous and progressive development occurred from 8 to 11 wk of age (a scotorefractory response), then CG size regressed again up to 17 wk (a second demonstration of scotosensitivity), followed by redevelopment of the CG and maintenance of a plateau out to 32 wk of age (a second scotorefractory response). What is most noteworthy herein were the findings that selection for either reduced or exaggerated adrenocortical stress responsiveness caused the 2 lines to develop their CG at significantly different rates (HS < LS) under a habitual light deprivation regimen. Moreover, the comparatively stymied growth rate eventually observed in the HS males

persisted well into adulthood, and the latter likely represented a permanent comparative outcome (see below).

At 16 wk of age, mean CVOL in LS and HS males of approximately 1,950 and 1,700 mm^3, respectively, were found when quail were held on lifelong long day lengths (14L:10D; Marin and Satterlee, 2004). Yet, higher mean CVOL in LS and HS males of approximately 2,500 and 2,200 mm^3, respectively, have been reported when these quail stocks were held on the same lifelong long day photostimulatory conditions but measured at the later age of 29 wk (Satterlee and Marin, 2004), an indication that CVOL is still increasing in both lines from 16 to 29 wk of age. The quail of these 2 studies were reared under identical husbandry conditions as those used presently except that the quail of the earlier studies were photostimulated on long days and were derived from forerunner generations to the generation used herein. Thus, the eventually highest and no longer increasing mean CVOL observed presently in the LS males (slightly more than 1,900 mm^3 at 26 wk of age) suggests that very high, although not maximal, CG growth can be achieved in LS males even when they are grown under habitual short day lengths, provided that the LS quail are grown an additional 10 wk beyond the younger age (16 wk) used by Marin and Satterlee (2004) in growing quail on long days. On the other hand, the present HS male quail grown under short days only achieved a maximal and no longer increasing (26 wk of age) CVOL of about 1,450 mm^3, a nearly 15% lesser size than the maximum CVOL (1,700 mm^3) found for this line when grown under lifelong long days for 16 wk when comparisons are made to the Marin and Satterlee (2004) study. Because CVOL showed no further increase in either line at 28 wk of age from that seen at 26 wk of age, it was concluded that the above cited line differences most likely represent permanent changes, outcomes that would have persisted even had the study been conducted for a longer duration. If so, then the results suggest that lifelong short day length treatment prevents additional increases in CVOL of 24 and 34% in the LS and HS quail, respectively, when comparisons are made to what is known to be possible when these stocks are grown lifelong on long days, or until 29 wk of age as was done by Satterlee and Marin (2004).

The present results add to the growing list of intuitively desirable traits that have accompanied selection of the LS quail line for reduced adrenocortical stress responsiveness [see reviews of Jones (1996) and Jones and Hocking (1999); Satterlee et al., 2000; Jones et al., 2000, 2002, 2004; Marin et al., 2002; Satterlee et al., 2002; Marin and Satterlee, 2003, 2004; Satterlee and Marin, 2004, 2006]. It is now further known that LS quail much more readily grow their CG to a bigger final size even when held on habitual short day lengths. Why do LS male quail generally possess larger CG than do HS ones under multiple photoperiodic regimes? We continue to suggest that the proposed negative relationships between B and reproductive function (via B-induced alterations of pituitary gonadotrophic hormone release, Leydig cell apoptosis, or both) underlie our previous and present light findings.

REFERENCES

Amet, Y., J. H. Abalain, J. Y. Daniel, S. Di Stefano, and H. H. Floch. 1986. Testosterone regulation of androgen receptor levels in the uropygial gland of quails (*Coturnix coturnix*): A further proof for the androgen dependency of the uropygial gland. Gen. Comp. Endocrinol. 62:210–216.

Balthazart, J., R. Massa, and P. Negri-Cesi. 1979. Photoperiodic control of testosterone metabolism, plasma gonadotrophins, cloacal gland growth, and reproductive behavior in the Japanese quail. Gen. Comp. Endocrinol. 39:222–235.

Balthazart, J., M. Schumacher, and G. Malacarne. 1984. Relative potencies of testosterone and 5 α-dihydrotestosterone on crowing and cloacal gland growth in the Japanese quail (*Coturnix coturnix japonica*). J. Endocrinol. 100:19–23.

Biswas, A., O. S. Ranganatha, J. Mohan, and K. V. Sastry. 2007. Relationship of cloacal gland with testes, testosterone and fertility in different lines of male Japanese quail. Anim. Reprod. Sci. 97:94–102.

Chaturvedi, C. M., R. Bhatt, and D. Phillips. 1993. Photoperiodism in Japanese quail (*Coturnix coturnix japonica*) with special reference to relative refractoriness. Indian 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.

Delville, Y., J. 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.

Domjan, M. 1987. Photoperiodic and endocrine control of social proximity behavior in male Japanese quail (*Coturnix coturnix japonica*). Behav. Neurosci. 101:385–392.

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

Hayward, L. S., D. G. Satterlee, and J. C. Wingfield. 2005. Japanese quail selected for high plasma corticosterone response deposit high levels of corticosterone in their eggs. Physiol. Biochem. Zool. 78:1026–1031.

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

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, and D. G. Satterlee. 2004. A 'pebble test of anxiety' did not differentiate between Japanese quail chicks from genetic lines differing in fearfulness and stress responsiveness. Appl. Anim. Behav. Sci. 87:287–291.

Jones, R. B., R. H. Marin, D. G. Satterlee, and G. G. Cadd. 2002. Sociality in Japanese quail (*Coturnix japonica*) genetically selected for contrasting adrenocortical responsiveness. Appl. Anim. Behav. Sci. 75:337–346.

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, 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. Indian J. Exp. Biol. 31:858–860.

Marin, R. H., and D. G. Satterlee. 2003. Selection for contrasting adrenocortical responsiveness in Japanese quail influences sexual behavior in males. Appl. Anim. Behav. Sci. 83:187–199.

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.

Massa, R., D. T. Davies, and L. Bottoni. 1980. Cloacal gland of the Japanese quail: Androgen dependence and metabolism of testosterone. J. Endocrinol. 84:223–230.

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.

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. Theriogenology 58:29–39.

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.

Phillips, D., A. B. Singh, U. S. Das, and C. M. Chaturvedi. 1997. Effect of gonadotrophin and sex steroid on the scoto-responses of day old chicks of Japanese quail, *Coturnix coturnix japonica.* Life Sci. 61:1487–1495.

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. 2007. 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. 1988. Selection of Japanese quail for contrasting blood corticosterone response to immobilization. Poult. Sci. 67:25–32.

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., and R. H. Marin. 2006. Stressor-induced changes in open-field behavior of Japanese quail selected for contrasting adrenocortical responsiveness to immobilization. Poult. Sci. 85:404–409.

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.

Sharp, P. J., and R. J. Sterling. 1985. Photoperiodic requirement for the dissipation of scotorefractoriness in Japanese quail. Gen. Comp. Endocrinol. 58:169–173.

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 indicator of testicular development in *Coturnix.* Poult. Sci. 54:1225–1229.