

## Cloacal Gland and Testes Development in Male Japanese Quail Selected for Divergent Adrenocortical Responsiveness<sup>1</sup>

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**ABSTRACT** The time course of sexual development in male quail from lines selected for either a reduced (low stress, LS) or an exaggerated (high stress, HS) plasma corticosterone response to brief restraint was determined. Sexual development was assessed by examination of cloacal gland area (CAREA) and volume (CVOL), proportion of individuals that produced cloacal gland foam, and the intensity of cloacal gland foam production (CFP) at 4, 5, 6, 8, 10, 14, and 16 wk of age. These intervals encompass ages during which growing, photostimulated quail would be expected to evolve from being totally prepubescent to well into adulthood. Testes weight (TW) and the proportion of individuals that had achieved a combined TW of 500 mg (PI500) were also measured at 6 and 16 wk of age. Mean CAREA and CVOL were similar in LS and HS quail at 4 wk of age. Beginning at 5 wk of age and thereafter, CAREA was greater ( $P < 0.05$ ) in LS than

in HS quail. Similarly, beginning at 6 wk of age and thereafter, CVOL was greater ( $P < 0.05$ ) in LS than in HS quail. More LS than HS birds also expressed foam at 4 ( $P < 0.05$ ), 5 ( $P = 0.15$ ), and 6 wk ( $P < 0.05$ ) of age. From 8 wk on, all birds were in foam production. CFP results mimicked those found for CAREA and CVOL in that LS quail tended toward higher CFP values than HS quail at all intervals of measurement. TW were higher ( $P < 0.02$ ) in LS than HS quail when data from the 2 ages at which testes were harvested were combined. At 6 wk of age, the LS and HS birds showed a PI500 line difference ( $P < 0.08$ ) of 1.0 and 0.91, respectively; by 16 wk, all birds exhibited a maximum PI500. The results suggest that 1) selection for reduced adrenocortical responsiveness in *Coturnix* is accompanied by an accelerated onset of puberty in males, and 2) enhanced reproductive development in LS males remains extant throughout early to middle-age adulthood.

(*Key words:* cloacal gland, corticosterone, Japanese quail, puberty, stress)

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### INTRODUCTION

In mammals (Collu et al., 1984; Gala, 1990; Knol, 1991; Rivier and Rivest, 1991; Almeida et al., 2000) and birds, activation of the hypothalamic-pituitary-adrenal (HPA) axis by a diversity of stressors has, for the most part, been associated with depression in the hypothalamic-pituitary-testicular (HPT) axis which, in turn, presents a plausible mechanism for observation of stress-induced inhibition of male reproductive functions. Deviche (1983) cited evidence that plasma luteinizing hormone (LH) and testosterone levels are reduced during both acute and chronic

stress states in male avians. Moreover, dexamethasone-induced chronic hypocorticalism in Leghorn chicks was associated with increased testis weight and better organization of the seminiferous cords and interstitium, whereas hypercorticalism induced by exogenous corticosterone led to a reduction in testis weight and poor histological organization (Joseph and Ramachandran, 1993). Deviche et al. (1982) have also shown that exogenous corticosterone partially blocked photoinduced development of the cloacal gland in male Japanese quail; administration of adrenocorticotrophin (ACTH) as well as social stress treatment in this species induces decreases in body and relative testes weights (Edens, 1987).

In prepubertal and pubertal Japanese quail, cloacal gland hypertrophy and foam production are androgen-

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**Abbreviation Key:** ACTH = adrenocorticotrophin; CAREA = cloacal gland area; CFP = cloacal gland foam production; CVOL = cloacal gland volume; FSH = follicle-stimulating hormone; G = generation; HPA = hypothalamic-pituitary-adrenal; HPT = hypothalamic-pituitary-testicular; HS = high stress; LH = plasma luteinizing hormone; LS = low stress; LSD = least significant difference; PICF = proportion of individuals that produced cloacal gland foam; PI500 = combined testes weight of 500 mg; TW = testes weight.

dependent and highly positively correlated with testes size as well as sexual activity (Coil and Wetherbee, 1959; MacFarland et al., 1968; Sachs, 1969; Siopes and Wilson, 1975; Oishi and Konishi, 1983; Delville et al., 1984a). We recently showed that, at a critical age of rapid sexual development, 42 d of age, Japanese quail selected for reduced (low stress, LS) rather than exaggerated (high stress, HS) plasma corticosterone response to brief restraint have cloacal glands of larger size, and more LS quail produced cloacal gland foam of a greater amount at this time (Satterlee et al., 2002). Thus, it appears that the onset of puberty may be advanced in the LS genotype. In addition, we have since shown that LS quail adults (age range: 22 to 23 wk) have a higher copulatory efficiency as estimated by the number of times that copulation sequences are completed once they have been initiated (Marin and Satterlee, 2003).

The present study was conducted to determine whether sexual development during an expanded time course that encompassed the age studied by Satterlee et al. (2002) differed between LS and HS males. At periodic intervals from 4 to 16 wk of age, sexual development was assessed by examination of cloacal gland area (CAREA) and volume (CVOL), the proportion of individuals that produced cloacal gland foam (PICF), the intensity of cloacal gland foam production (CFP), testes weight (TW), and the proportion of individuals that achieved the threshold TW of 500 mg (PI500). A TW greater than or equal to 500 mg is believed to be needed for full spermatogenesis in *Coturnix* (Mather and Wilson, 1964; Purcell and Wilson, 1975). The age range was chosen to include ages during which growing, photostimulated quail would be expected to have: 1) no cloacal gland development and foam production (i.e., all birds being prepubescent), 2) some cloacal gland development and foam production, and 3) full development of the cloacal gland with all birds in foam production (i.e., 100% of birds having reached puberty).

## MATERIALS AND METHODS

### Birds

We studied male Japanese quail (*Coturnix japonica*) from 2 lines selected for either an LS or an HS plasma corticosterone response to brief mechanical immobilization (Satterlee and Johnson, 1988). The more recent genetic history [from generation ( $G_{13}$ ) to  $G_{29}$ ] that verifies maintenance of divergent adrenocortical responsiveness to the genetic selection stressor in these lines is discussed in detail elsewhere (Satterlee et al., 2000; 2002). The lines were reproduced without selection for 2 additional generations before their use in the present study ( $G_{31}$ ).

The quail were taken from a larger population of approximately 200 hatchlings per line. Egg incubation, chick

brooding, feeding, 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, mixed-line groups of approximately 100 within each of 4 compartments of a Model 2SD-12 Petersime<sup>4</sup> brooder battery modified for quail. In order 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, quail were sexed by plumage coloration, and 48 LS and 48 HS males were randomly (and individually) housed within 2 Alternative Cage Designs<sup>5</sup> 4-tier cage batteries (each battery comprising 48 laying cages). Individual cage dimensions were 50.8 × 15.2 × 26.7 cm (length × width × height). At this time, birds were also switched to a breeder ration (21% CP; 2,750 kcal of ME/kg) with feed and water continuing ad libitum. The daily photostimulatory cycle was 14L:10D with a light intensity of approximately 280 luxes during the lighted portion of the day and lights-on occurring at 0600 h daily. Daily maintenance and feeding chores were carried out at the same time each day (0800 h).

### Traits Measured

Cloacal gland size measurements, length (mm) and width (mm) were made using a digital caliper. Cloacal gland area and CVOL were calculated from these measurements according to the formulas proposed by Siopes and Wilson (1975) for CAREA (i.e., gland length × width) and Chaturvedi et al. (1993) for CVOL ( $\frac{4}{3} \times 3.5414 \times a \times b^2$ , where  $a = 0.5 \times$  long axis and  $b = 0.5 \times$  short axis). In addition, 2 measures of cloacal gland foam production were made: PICF and CFP. CFP was quantified by subjective scaling of the amount of foam ejected upon manual expression (squeezing) of the foam gland, using a scale of 1 (no foam expressed) to 5 (maximum amount of foam expressed). Testes weight measurements were made using a digital scale that weighed to the nearest 0.001 g.

Cloacal gland measurements (CAREA, CVOL, PICF, and CFP) were made in all 48 LS and 48 HS quail at 4, 5, and 6 wk of age. At 6 wk of age, half of the birds from each line were sacrificed by cervical dislocation and their testes removed by blunt dissection for determination of TW. The other half of the birds (24 LS and 24 HS) were kept in the study for the continuation of the cloacal gland measurements made at 8, 10, 12, 14, and 16 wk of age. At 16 wk of age, all remaining birds were sacrificed for TW determination. In addition, because it was proposed that full spermatogenesis occurs when a combined TW of 500 mg is achieved in *Coturnix* (Mather and Wilson, 1964; Purcell and Wilson, 1975), the proportion of individuals within each line that had achieved PI500 was determined at 6 and 16 wk of age.

### Statistical analyses

Cloacal gland volume, CAREA, and CFP were subjected to a repeated measures ANOVA that examined the

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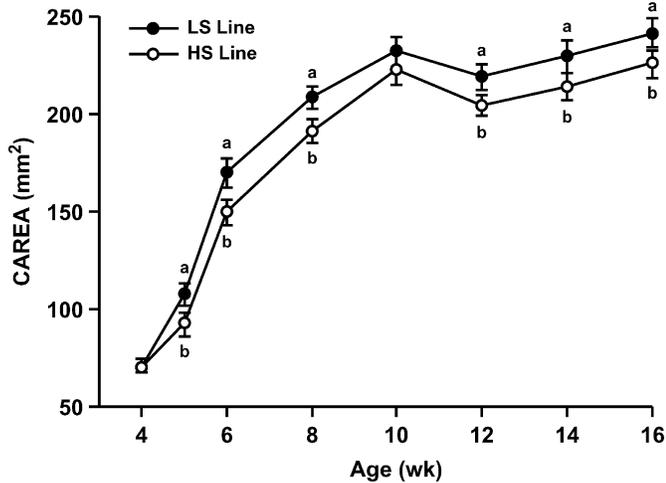


FIGURE 1. Mean ( $\pm$ SE; vertical bar) cloacal gland area (CAREA) in low stress (LS) and high stress (HS) Japanese quail from 4 to 16 wk of age.

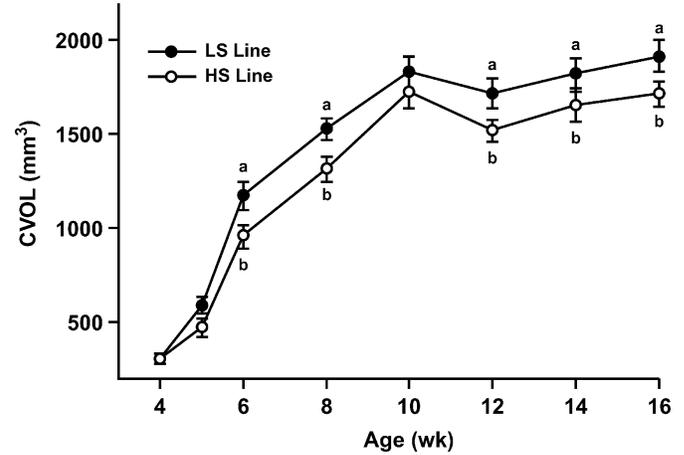


FIGURE 2. Mean ( $\pm$ SE; vertical bar) cloacal gland volume (CVOL) in low stress (LS) and high stress (HS) Japanese quail from 4 to 16 wk of age.

main effects of line (LS and HS), time of sampling (4, 5, 6, 8, 10, 12, 14, and 16 wk of age; the repeated measure), and their interaction. In order to better fit the assumptions of the ANOVA, CFP values were transformed to ranks (Shirley, 1987). Testes weight data were subjected to a 2-way ANOVA that examined the main effects of line (LS and HS), time of sampling (6 and 16 wk of age), and their interaction. Where appropriate, least significant difference (LSD) tests were used for post hoc comparisons of means. To evaluate line differences in PICF and PI500, the proportion test (Analytical Software, 2000) was used to compare the number of birds that were producing foam (successes) and the number of birds having a combined testes weight greater than 500 mg (successes) as a proportion of sample size.

## RESULTS

Figure 1 depicts the mean ( $\pm$ SE) CAREA of LS and HS quail at 4, 5, 6, 8, 10, 12, 14, and 16 wk of age. CAREA was significantly affected by line [ $F(1,44) = 4.34$ ;  $P < 0.04$ ] and quail age [ $F(7,308) = 318.02$ ;  $P < 0.001$ ], but these treatments did not interact to affect CAREA. Post hoc LSD tests showed that mean CAREA values were similar in LS and HS quail at 4 wk of age. Thereafter, LS quail showed a consistently greater ( $P < 0.05$ ) CAREA than HS quail except at 10 wk of age.

In support of CAREA findings, CVOL was similarly affected by line ( $F(1,44) = 5.01$ ;  $P < 0.03$ ) and quail age ( $F(7,308) = 245.40$ ;  $P < 0.001$ ), but not by the interaction of these treatments. LSD tests showed that mean ( $\pm$ SE) CVOL was similar in LS and HS quail at 4 and 5 wk of age (Figure 2). Thereafter, LS quail showed enhanced ( $P < 0.05$ ) CVOL compared with their HS counterparts except at 10 wk of age.

A greater PICF was evident in LS birds than in HS birds at 4 ( $P < 0.05$ ), 5 ( $P = 0.15$ ), and 6 ( $P < 0.05$ ) wk of age (Figure 3). Beginning at 8 wk and thereafter, all birds (100%) were in foam production.

CFP results generally mimicked those found for the 2 cloacal gland size measurements (i.e., LS quail tended toward higher CFP than HS quail beginning at 6 wk of age), but these line differences were not statistically relevant (Figure 4). Comparison of Figures 3 and 4 shows that both PICF and CFP peaked at 8 wk of age.

Mean ( $\pm$  SE) TW for LS and HS quail at 6 and 16 wk of age are given in Table 1. Again, an ANOVA detected significant line ( $F(1,89) = 6.10$ ;  $P = 0.01$ ; LS > HS) and time ( $F(1,89) = 58.64$ ;  $P < 0.001$ ; 16 wk > 6 wk) effects, but no significant interaction between these treatments was found. Post hoc analyses showed that within each age of measurement (i.e., at both 6 and 16 wk of age), TW was greater ( $P < 0.10$ ) in LS than HS quail.

At 6 wk of age, the LS and HS birds showed a PI500 of 1.0 and 0.91, respectively. This line difference approached significance at  $P < 0.08$ . By 16 wk of age, all LS and HS birds exhibited a maximum PI500.

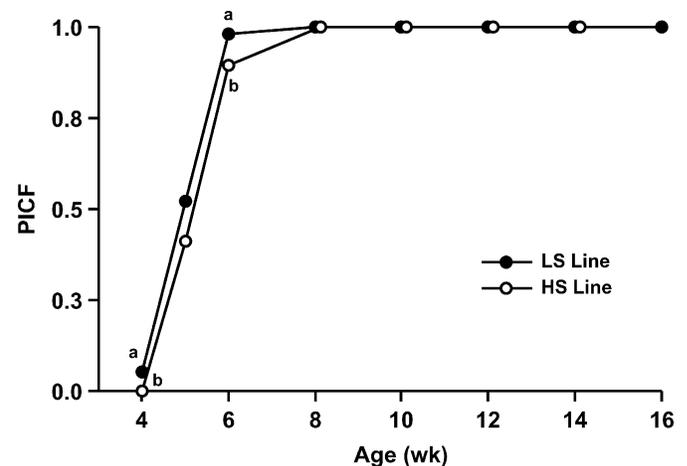


FIGURE 3. Proportion of individuals producing cloacal gland foam (PICF) in low stress (LS) and high stress (HS) Japanese quail from 4 to 16 wk of age.

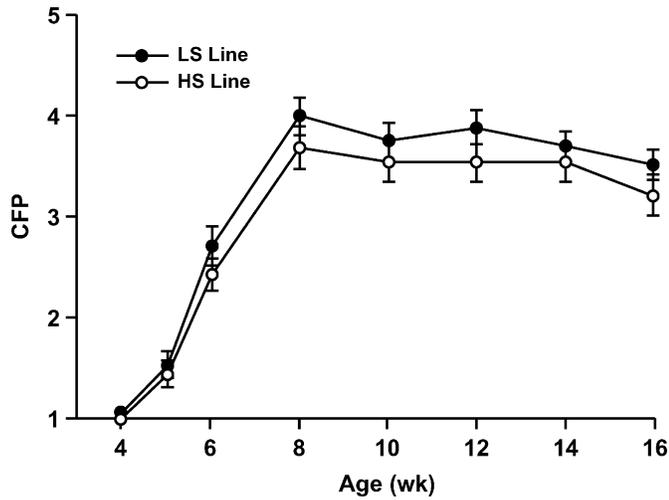


FIGURE 4. Mean ( $\pm$ SE; vertical bar) cloacal gland foam production (CFP) in low stress (LS) and high stress (HS) Japanese quail from 4 to 16 wk of age.

## DISCUSSION

Cloacal gland size and foam production, as well as testicular volume and weight, increase with age in photostimulated male Japanese quail (Wilson et al., 1962; Tanaka et al., 1965; Sachs, 1967; Siopes and Wilson, 1975; Chaturvedi et al., 1992, 1993). Thus, the enhancements seen in all of the reproductive variables, CAREA, CVOL, PICF, CFP, PI500, and TW, with increasing age in both quail lines of the present study were expected outcomes for the photoperiod regimen used (i.e., our age-related cloacal gland and testes weight findings reflect natural endocrine-influenced processes).

In comparison with HS quail, LS quail show a nonspecific reduction in adrenal stress responsiveness to a wide variety of stressors (e.g., cold, crating, feed and water deprivation, manual restraint, and social tension) (Satterlee and Johnson, 1988; Jones et al., 1994; Jones, 1996). In the present study, the quail were not intentionally stressed. Nevertheless, because of the apparent nonspecific nature of stress responsiveness in the lines, we would expect differential adrenocortical responses consistent with each line's genetic background to have occurred often during the course of the study. For example, stress was likely: 1) at times of routine maintenance chores (e.g., during 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., hatching baskets, battery brooders, and laying cages) with the attendant modification of social structures.

Activation of the HPA axis by a diversity of stressors has been generally associated with depression in the HPT axis. Thus, because the lines differ in their adrenocortical responsiveness to nonspecific stressors, because corticosterone responses to ACTH challenge are attenuated in LS compared with HS quail (D. G. Satterlee, unpublished data), and because a line (LS > HS) difference in cloacal gland physiology existed at a key time point during sexual development under husbandry conditions similar to those used herein (Satterlee et al., 2002), it was anticipated that, once lighted, males of the 2 quail lines would differ in their temporal sexual development.

At 4 wk of age, no differences were observed between LS and HS quail in CAREA or CVOL, suggesting that genetic selection did not alter cloacal gland size at this early prepubescent age. This is not surprising because the birds were not lighted until this age and, thus, significant interactions between the HPA and HPT axes would not be expected prior to this time. However, CAREA at 5 and 6 wk of age, 1 and 2 wk postphotostimulation, respectively, and CVOL at 6 wk of age were found to be greater in LS than in HS quail. These results suggest that sexual development is accelerated in birds of the LS line and point out the need to examine the stress lines for differences in brain and blood levels of the gonadotropic hormones that may underlie the observed line differences.

The proposal that selection for reduced adrenocortical responsiveness is associated with precociousness is strengthened by the additional present findings of: 1) a higher number of LS quail in foam production between 4 to 6 wk of age, and 2) a trend toward a greater mean TW in LS quail at 6 wk of age. The hypothesis that puberty is accelerated in the LS genotype is yet further supported by our earlier finding of an increased CAREA and foam production in birds of the LS line at 42 d of age (Satterlee et al., 2002). It should be noted here that, in prepubertal and pubertal Japanese quail, cloacal gland hypertrophy and foam production are known to be androgen-dependent and highly positively correlated with testes size as well as sexual activity (Coil and Wetherbee, 1959; Nagra et al., 1959; McFarland et al., 1968; Sachs, 1969; Siopes and Wilson, 1975; Oishi and Konishi, 1983; Delville et al., 1984a; Seiwert and Adkins-Regan, 1998). Thus, we hypothesize that LS quail likely also possess higher blood levels of testosterone postphotostimulation than the HS genotype. Moreover, the presence of higher TW in LS quail (as demonstrated herein by the significant line effect) when coupled with this hypothesis helps explain our recent finding of enhanced copulation efficiency in this line (Marin and Satterlee, 2003). However, this conclusion should be guarded because, whereas testosterone was found to activate male copulatory behavior through its action in the peptic area of the quail brain (Balthazart, 2000), other investigators (Beani et al., 2000) were unable

TABLE 1. Mean ( $\pm$ SE) testes weight (g) at 6 and 16 wk of age in low stress (LS) and high stress (HS) Japanese quail

Age (wk)	Line		LS + HS
	LS	HS	
6	3.05 $\pm$ 0.18	2.64 $\pm$ 0.20	2.84 $\pm$ 0.14 <sup>c</sup>
16	4.42 $\pm$ 0.15	3.96 $\pm$ 0.16	4.19 $\pm$ 0.11 <sup>d</sup>
6 + 16	3.74 $\pm$ 0.16 <sup>a</sup>	3.32 $\pm$ 0.16 <sup>b</sup>	

<sup>a-d</sup>Means without a common letter differ significantly ( $P < 0.02$ ).

to alter attempted mating in quail using testosterone hormone manipulations. Interestingly, testosterone is well known for its ability to restore sexual behavior in aged, reproductively senescent males (Ottinger et al., 1997).

It has been proposed that full spermatogenesis occurs when a left and right TW of 500 mg is achieved in *Coturnix* (Mather and Wilson, 1964; Purcell and Wilson, 1975). Although daily sperm production was not measured in the present study, all LS birds were in foam production and had greatly exceeded this 500-mg TW threshold by 6 wk of age. In contrast, at this same age, approximately 10% of the HS quail had not yet reached this milestone. Again, these results support our contention that sexual maturity is accelerated in male quail of the LS line. Because all LS and HS birds exhibited a maximum PI500 by 16 wk of age, it is likely that full spermatogenesis was extant in both lines at this late age, notwithstanding the finding of a marginally ( $P < 0.10$ ) greater TW in LS than in HS quail at 16 wk of age. The finding of identical PI500 in both quail lines at 16 wk of age is not too surprising as male *Coturnix* at that age are about 5 to 7 wk beyond their sexual peak. However, it would be interesting to determine whether line differences re-emerge in very aged quail when blood levels of testosterone decrease and sexual senescence is known to occur (Ottinger et al., 1997).

Beginning at 8 wk of age and thereafter, all birds, regardless of their genetic background, were in foam production. However, unlike LS quail, a small number of HS quail had yet to achieve a TW in excess of 500 mg 2 wk earlier by 6 wk of age. Because TW data were collected initially at 6 wk and not again until the end of the study at 16 wk, we cannot ascertain exactly when between 6 and 16 wk the entire HS quail population achieved a PI500 of 1.0. Thus, while a reasonable expectation would be that all HS quail reached a combined TW of 500 mg well before the late age of 16 wk, due to data collection restraints, we can state only that all HS birds had reached the PI500 milestone by this time. Thus, when the PICF and PI500 data are considered together, it can be concluded that all quail, regardless of their genetic background, were clearly pubescent by 16 wk of age. However, during the last 8 wk of the trial, from 8 to 16 wk of age, with the exception of PICF, the remaining cloacal gland reproductive variables that were measured bi-weekly, CAREA, CVOL, CFP, were found consistently to be statistically or numerically augmented in LS birds. These findings suggest that the enhanced LS male reproductive development seen early on in these variables remains extant well into middle-age adulthood.

The presence of males paired with females and reared on long days resulted in larger cloacal glands and testes and higher plasma levels of LH and testosterone than when male quail were reared in isolation (Delville et al., 1984b). In our previous study (Satterlee et al., 2002) that showed increases in cloacal gland size and enhanced foam production in LS males at 42 d of age, males were reared in mixed-sex groups of 1 male:2 females. Herein, enhanced cloacal gland development and foam production was observed in LS males reared in isolation. Thus, regardless

of whether females were present, the line differences in cloacal gland size and TW are still apparent.

Although explanation of the endocrine link between divergent adrenocortical function and gonadal and cloacal gland physiology is not the main focus of this paper, we submit that such a link likely involves the gonadotrophic hormones. In Japanese quail, follicle-stimulating hormone (FSH) level has been directly related to maximum testicular growth with daily photoperiods of 14 h light or more (Follett and Maung, 1978), and exogenous LH markedly increased testicular growth in birds held on short days (8 h of light) (Brown et al., 1975). Furthermore, circulating FSH is highly correlated to testes weight and development of the seminiferous tubules in male broiler breeder cockerels, and a strong link exists between testes weight and daily sperm production in these birds (Vizcarra et al., 2000).

Several researchers have demonstrated an association of the LH component of the HPT axis with adrenocortical activity in birds. For example, Deviche (1983) cited evidence that plasma LH and testosterone levels are reduced during both acute and chronic stress states in male avians, and Connolly and Callard (1987) showed that preincubation of quail adenohypophyseal cells with corticosterone inhibited gonadotropin-releasing hormone-induced LH secretion. While direct association of the FSH component of the HPT axis with adrenocortical activity in domestic birds could not be found, such an association is clearly evident in non-avian species (Xiao et al., 1989; Yajurvedi and Niagal, 2000; Ganesh and Yajurvedi, 2002).

In the present study, the birds were subjected to a stimulatory photoperiod (14L:10D) typically used to stimulate gonadal growth and achieve maximum reproductive ability in *Coturnix*. We submit that the inherent line differences in adrenocortical responsiveness resulted in circulating corticosterone states during growth and development that interacted divergently with the HPT axis to produce the accelerated puberty and enhanced reproductive fitness observed in the LS quail. It is possible that steady state or reproductive event-driven gonadotropin-releasing hormone-induced pituitary LH and FSH release is compromised in HS quail by day-to-day stress-induced exaggerated blood corticosterone responses that were expected to have occurred in the HS line. If so, a further expected consequence would be a reduction in gonadotropin-induced testicular growth and circulating levels of testosterone. Reduction in testosterone would, in turn, lessen the prime stimulus for cloacal gland growth and function (at least in terms of initial foam production).

Regardless of the endocrine mechanisms that underlie the differences observed in the male reproductive attributes of the prepubertal and pubertal stress line quail, the results presented may have strategic relevance to the poultry industry. *Coturnix* are well accepted as a pilot model for extrapolation of research findings to the more commercially viable species, such as chickens and turkeys (Aggrey and Cheng, 1994; Mills et al., 1997). Because sexual maturation is accelerated and the reproductive capacity appears to be enhanced in LS adults, selection

for decreased adrenocortical responsiveness in chickens and turkeys may be worthwhile. Such selection may allow producers to: 1) successfully breed males at an earlier age and thereby save on the costs to produce juveniles to the point of semen production, and 2) gain in flock fertility via a heightened sexual capacity in male adults. The latter may manifest itself economically by allowing for the production of more offspring while still using current industry-standard male:female breeder bird ratios or by reducing the number of males needed to maintain optimum fertility. In addition, assuming the line differences in reproductive attributes found in middle-aged adult males persist in very aged birds, then sexual problems (e.g., decreased copulation activity) associated with the marked decline in sexual potency at advanced ages may be avoided. Supporting this hypothesis, we found male LS quail adults (age range: 22 to 23 wk) to have a higher copulatory efficiency as estimated by the number of times that copulation sequences are completed once they have been initiated (Marin and Satterlee, 2003).

In conclusion, selection for reduced adrenocortical responsiveness in *Coturnix* has been accompanied by an accelerated onset of puberty in males. Furthermore, an enhanced reproductive development was evident in LS males well into adulthood.

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