Selection of Japanese Quail for Reduced Adrenocortical Responsiveness Accelerates Puberty in Males[1]

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ABSTRACT Differences in the onset of puberty were assessed in male Japanese quail from a random-bred (RB, control) line and two lines that had been genetically selected for reduced (low stress, LS) or exaggerated (high stress, HS) plasma corticosterone response to brief mechanical restraint. At 42 d of age, cloacal gland area (CAREA) and volume (CVOL), proportion of individuals that produced cloacal gland foam (PICF), and intensity of cloacal gland foam production (CFP) were examined in 60 representatives from each of these quail lines. 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 expression). Mean CAREA and CVOL were similar in quail of the RB and HS lines, but these measures were greater ($P < 0.01$) in the LS quail. In addition, more ($P < 0.05$) LS than HS birds expressed foam at 42 d, whereas RB quail exhibited an intermediate PICF response that was not different from either selected line. CFP results mimicked those found for PICF (i.e., LS quail produced a greater ($P < 0.05$) amount of foam than HS birds, whereas RB quail showed intermediate production that was not different from LS or HS levels). In prepubertal and pubertal Japanese quail, cloacal gland hypertrophy is androgen-dependent and highly positively correlated with testes size as well as sexual activity. Cloacal gland foam production is also considered a reliable indicator of testicular size and activity. Thus, we conclude that selection for reduced adrenocortical responsiveness in Coturnix is associated with acceleration in the onset of puberty in males. The potential interaction between adrenocortical and testicular activity as it relates to male reproductive performance is discussed.

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

INTRODUCTION

In mammals (Collu et al., 1984; Gala, 1990; Knol, 1991; Rivier and Rivest, 1991; Almeida et al., 2000) and birds (see below), 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 (Collu et al., 1984; Gala, 1990; Knol, 1991; Rivier and Rivest, 1991; Almeida et al., 2000). However, sporadic reports that stimulation of the HPA axis is associated with increases in plasma testosterone levels or enhanced male reproductive function have been published for both species. To explain literature discrepancies in mammals, Collu et al. (1984) proposed that, depending on an individual's coping abilities and its perception of stressful stimuli, different behavioral and hormonal patterns evolve that center more or less on activation of sympathetic adrenomedullary or adrenocortical pathways. When the former pathway is more activated than the latter, elevations in testosterone and aggressive behavior result. When the latter pathway predominates, reductions in testosterone and libido are evinced. Moreover, the interplay of various neurotransmitters, hypothalamic, pituitary and gonadal hormones, as well as the potency, duration and additivity of stressful stimuli and ontogenic events that occur during fetal, pubertal, and adult life provide the bases for an extremely complex regulatory system for the mammalian HPA-HPT axes (Collu et al., 1984; Almeida et al., 1998, 2000).

Abbreviation Key: CAREA = cloacal gland area; CFP = cloacal gland foam production; CVOL = cloacal gland volume; G_x = number of generations; HPA = hypothalamic-pituitary-adrenal; HPT = hypothalamic-pituitary-testicular; HS = line selected for high stress; LS = line selected for low stress; PICF = proportion of individuals producing cloacal gland foam; RB = random-bred control line.

Similar complex, interactive factors as those discussed above for mammals (sensory, neuroendocrine, and external stimuli) would logically be expected in the control of the HPA-HPT axes in birds as well. To wit, Deviche (1983) reviewed early evidence that plasma leuteinizing hormone and testosterone levels are reduced during acute and chronic stress states in male avians. Deviche et al. (1982) also showed that exogenous corticosterone partially blocked photoinduced development of the cloacal gland in male Japanese quail. Development of the cloacal gland in Coturnix, an androgen-dependent phenomenon, is a reliable indicator of testicular development and sexual activity (Coil and Wetherbee, 1959; MacFarland et al., 1968; Sachs, 1969; Siopes and Wilson, 1975; Oishi and Konishi, 1983; Delville et al., 1984). More recently, dexamethasone-induced chronic hypocorticalism in Leghorn chicks was associated with increased testes weight and better organization of the seminiferous cords and interstitium, whereas hypercorticalism induced by exogenous corticosterone led to a reduction in testes weight and poor histological organization (Joseph and Ramachandran , 1993). On the other hand, Heiblum et al. (2000) found that elevation of testosterone accompanied corticosterone secretion following short-term restraint stress in juvenile, pubertal, and adult cockerels.

Fear and distress can exert many deleterious effects on the welfare and productivity of fowl, including energy wastage; decreased growth, feed conversion, and egg production and product quality; delayed maturation; compromised hatchability; decreased immunocompetence; development of feather pecking; and increased likelihood of injury, pain, and even death (Mills and Faure, 1990; Jones, 1996, 1997; Jones and Hocking, 1999). To reduce fear and distress and thereby improve welfare and productivity in commercial poultry species, genetic selection for less pronounced fear responses and decreased adrenocortical responsiveness (often associated with reduced fearfulness) has been suggested (Jones, 1996; Jones and Hocking, 1999; Jones et al., 2000; Faure et al., in press). This hypothesis has gained considerable support from studies conducted with the divergent lines of Japanese quail selected for low (LS, low stress) or high (HS, high stress) plasma corticosterone response to brief mechanical restraint (Satterlee and Johnson, 1988). In comparison to HS quail, the LS counterparts not only show a non-specific reduction in adrenal stress responsiveness to a wide variety of stressors (e.g., cold, crating, feed and water deprivation, social tension, and manual restraint) (Satterlee and Johnson, 1988; Jones et al., 1994; Jones, 1996), but they also show lower fearfulness (i.e., they are less easily frightened by diverse events such as exposure to human beings, exposed areas, unfamiliar objects and places, or mechanical restraint) (Jones et al., 1992a,b, 1994, 1999; Satterlee and Jones, 1995; Jones and Satterlee, 1996). It is important to note here that not only are Japanese quail an important agricultural species in many countries (Baumgartner, 1994), but they are also considered to be a most useful model for the extrapolation of data to other,

more commercially important species such as the domestic fowl (Mills and Faure, 1992; Aggrey and Cheng, 1994).

Apart from reports that body and liver weights were lower in HS than LS quail (Satterlee and Johnson, 1985) and that bone strength was less severely compromised in LS than HS birds after sequential exposure to stressors (Satterlee and Roberts, 1990), these quail lines have not been extensively characterized for differences in production performance traits. Because genetic selection for a given trait can often be associated with co-selection of other (unselected) traits that may or may not be desirable (Siegel, 1979; Jones, 1996), and because alteration of adrenocortical responsiveness by genetic selection might conceivably impact male gonadal function (see above), it is important to examine male reproductive performance characteristics in the LS and HS quail lines before making recommendations concerning the overall benefits of selection for reduced adrenocortical responsiveness. Herein, we determined whether divergent selection altered sexual development in males of these lines by examination of their cloacal gland area (CAREA) and volume (CVOL), the proportion of individuals that produced cloacal gland foam, and the intensity of cloacal gland foam production at 42 d of age. Study of foam production was included because, like cloacal gland size, foam production is considered to be a reliable indicator of testicular size and sexual activity in Coturnix (Siopes and Wilson, 1975).

MATERIALS AND METHODS

Genetic Stocks and Husbandry

Male Japanese quail (*Coturnix japonica*) from a randombred (RB, control) line and two lines selected over 29 generations for LS or HS plasma corticosterone response to brief mechanical immobilization (Satterlee and Johnson, 1988) were studied. The more recent history [from Generations 13 to 24 (G_{13} to G_{24})] that verifies maintenance of divergent adrenocortical responsiveness to the genetic selection stressor in these lines is discussed in detail elsewhere (Satterlee et al., 2000). Genetic history beyond G_{24} is as follows. The lines remained closed to outside blood and were maintained without selection pressure in producing generations G_{25} and G_{26}. Nonselection in all three lines during these two generations was accomplished by colony breeding of 12 family crosses within a line, avoiding only full-sib matings. Examination of the lines at G_{26} showed that divergence ($P < 0.001$) had been maintained; means ± SEM of the circulating corticosterone concentrations in HS and LS quail exposed to the immobilization stressor were 13.1 ± 0.1 and 6.8 ± 0.1 ng/mL, respectively. Selection pressure was reimposed in the LS and HS lines to produce G_{27} wherein immobilization resulted in plasma corticosterone concentrations of 14.7 ± 0.3 and 6.3 ± 0.2 ng/mL in the HS and LS quail, respectively. An intermediate plasma corticosterone level (7.7 ± 0.2 ng/mL) that was different ($P < 0.05$) from either of the two selected lines was observed in RB quail at G_{27}. The lines reproduced for an additional two generations

without selection before their use in the present study (G_{29}).

The quail studied (n = 60 males/line, see below) were taken from a larger population of a hatch of 1,884 birds (607 LS, 666 RB, and 611 HS). 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 Day 1 in mixed-sex, mixed-line groups of approximately 100 within each of 19 compartments of two Model 2SD-12 Petersime brooder batteries[3] 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 32 d of age, quail were sexed by plumage coloration and same-line groups of 10 females and five males (birds chosen as G_{29} breeders) were placed into 36 colony cages (12 cages of LS + 12 cages of RB + 12 cages of HS quail). Quail were beak-trimmed by hot-blade debeaker and switched to a breeder ration (21% CP; 2,750 kcal ME/kg) at this time with feed and water continuing ad libitum. Upon housing in breeder cages, birds were subjected to a daily photostimulatory cycle of 14L:10D. Light intensity was approximately 280 lx during the lighted portion of the day with lights-on occurring at 0600 h daily. Daily maintenance and feeding chores occurred at the same time each day (0800 h).

Traits Measured

At 42 d of age, an age slightly beyond the average age at which growing, photostimulated quail would be expected to have experienced the onset of foam production, data were collected on all breeder males as follows. Cloacal gland size measurements, length (mm) and width (mm), were made with a digital calipers. CAREA 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 [$4/3 \times 3.5414 \times a\, b^2$, where $a = 0.5 \times$ (long axis) and $b = 0.5 \times$ (short axis)]. In addition, two measures of cloacal gland foam production were made: proportion of individuals that produced cloacal gland foam (PICF) and intensity of cloacal gland foam production (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 expression).

Statistical Analyses

The potential existence of line differences in CAREA and CVOL means was examined using a one-way ANOVA (PROC ANOVA; SAS Institute, 1985). Duncan's new

multiple-range test was used as a posthoc test to partition line means. The Kruskal-Wallis one-way nonparametric ANOVA was used to analyze line differences in CFP with posthoc testing by comparison of mean ranks. The proportion test (Analytical Software, 2000) that compared the number of birds that were producing foam (successes) as a proportion of sample size was used to evaluate line differences in PICF.

RESULTS

The ANOVA F-values (and their respective P-values) associated with line effects for CAREA, CVOL, and CFP were 10.81 ($P < 0.0001$), 10.76 ($P < 0.001$), and 4.34 ($P < 0.0145$), respectively. After considering the results of the parametric ANOVA, post-ANOVA testing by Duncan's new multiple-range test was conducted at $P < 0.01$ for CAREA and CVOL. For CFP, post-Kruskal Wallis ANOVA separation of line means was conducted with tests of the comparison of mean ranks at $P < 0.05$.

Figure 1 depicts quail line differences in CAREA and CVOL at 42 d of age. Mean (±SE) CAREA and CVOL of LS quail (126.1 ± 6.6 mm^2 and 800.5 ± 61.7 mm^3, respectively) were greater ($P < 0.01$) than those found in quail of the RB (104.4 ± 3.8 mm^2 and 590.5 ± 33.8 mm^3, respectively) and HS (93.4 ± 4.3 mm^2 and 509.8 ± 36.5 mm^3, respectively) lines. There were no detectable differences in CAREA or CVOL between RB and HS quail. More (Figure 2, $P < 0.05$) males expressed foam at 42 d in the LS line (30 of 60) than in the HS line (18 of 60), whereas RB quail exhibited an intermediate PICF response (26 of 60 males) that was not different from either selected line. Finally, as was the case for PICF data, LS quail produced a greater ($P < 0.05$) amount of foam (2.13 ± 0.17) than HS birds (1.48 ± 0.11), whereas RB quail exhibited an intermediate amount of CFP (1.60 ± 0.12) that was not different from either selected line (Figure 2).

DISCUSSION

Neither quail of the divergent lines nor the controls were intentionally stressed in the present study. Nevertheless, we would expect differential adrenocortical responses consistent with each line's genetic background to have occurred throughout the study. For example, nonspecific systemic stress responses were anticipated 1) at times of routine maintenance chores (e.g., during daily manual feed replenishment, removal and scraping of droppings pans, etc.), 2) whenever birds were captured, crated, transported, and handled (e.g., immediately after hatching, and during leg- and wing-banding, beak-trimming, and housing), and 3) as a result of placement into novel environments and groups with the attendant modification of social structures (e.g., movement of birds from hatching baskets to battery brooder decks and from brooder decks to laying cages).

Cloacal gland size and foam production as well as testicular volume and weight vary as a function of age and photoperiod (Sachs, 1967; Siopes and Wilson, 1975; Cha-

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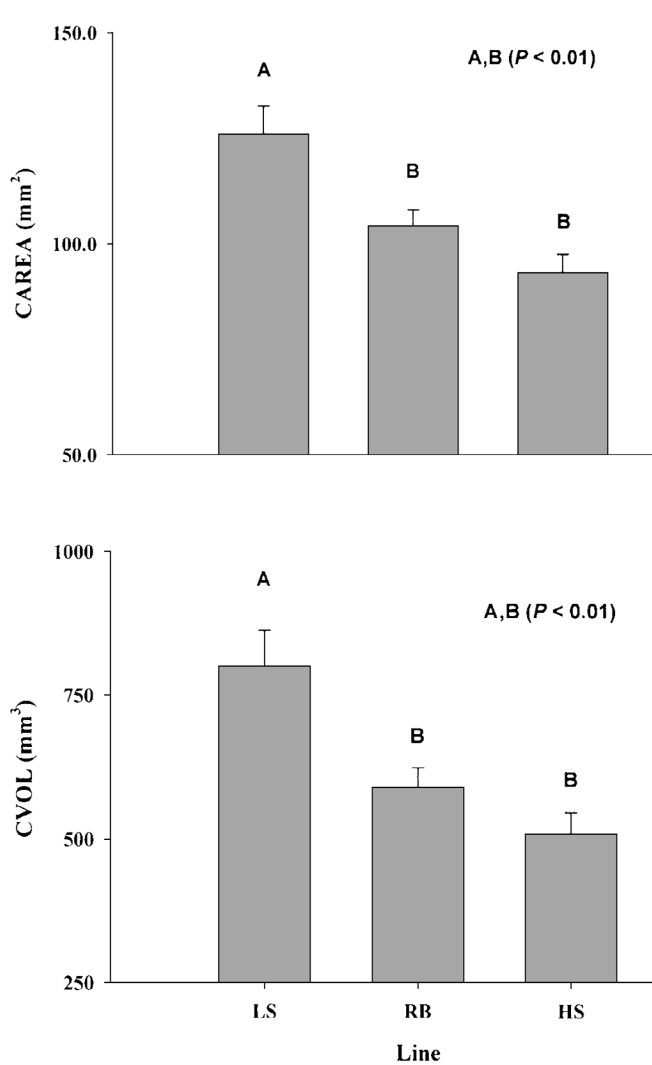[3]Petersime Incubator Co., Gettysburg, OH.

FIGURE 1. Mean (± SE, vertical bars) cloacal gland area (CAREA) and volume (CVOL) in low stress (LS), random-bred (RB; controls), and high stress (HS) Japanese quail at 42 d of age.

FIGURE 2. Mean proportion of individuals producing cloacal gland foam (PICF) and mean (± SE, vertical bars) cloacal gland foam production (CFP) in low stress (LS), random-bred (RB; controls), and high stress (HS) Japanese quail at 42 d of age.

turvedi et al., 1992, 1993). Accordingly, we chose a study age of 42 d, an age at which we predicted nearly half of the growing, photostimulated control quail would be producing foam. This age was selected for study because we wanted to ensure that sufficient numbers of our controls (RB) would have experienced puberty by the time of study, thus allowing meaningful line comparisons.

Genetic selection for exaggerated adrenocortical responsiveness (HS quail) did not alter CAREA and CVOL when compared to the controls (RB quail), but selection in the opposite direction (i.e., for reduced adrenocortical responsiveness, LS quail) was associated with a marked increase in both of these variables at 42 d of age. The latter findings support the contention that hypocorticalism may augment avian male gonadal development and function (Joseph and Ramachandran, 1993). We tentatively suggest that our LS quail would likely have larger testes because of their reduced adrenocortical responsiveness. Larger testes may, in turn, result in enhanced testosterone secretion and thereby provide greater stimulation for cloacal
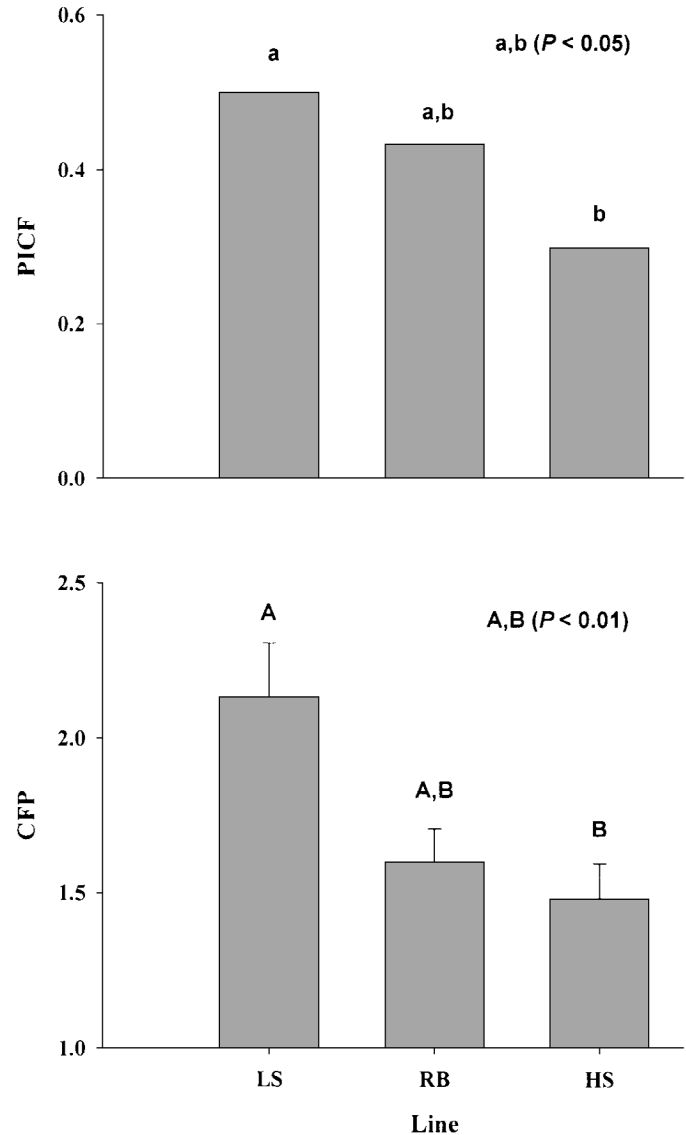
gland growth. Indeed, it is widely accepted that development of the cloacal gland in Coturnix is an androgen-driven mechanism and that cloacal gland growth is a reliable indicator of testicular development and sexual activity (Coil and Wetherbee, 1959; MacFarland et al., 1968; Sachs, 1969; Siopes and Wilson, 1975; Oishi and Konishi, 1983; Delville et al., 1984). Line comparisons of testicular development are underway (see below).

The absence of significant differences between HS and RB quail in CAREA and CVOL is inconsistent with reports that challenge with corticosterone or the induction of stress states can reduce male gonadal development and function in avians (Deviche et al., 1982; Deviche, 1983; Joseph and Ramachandran, 1993). Perhaps the findings of the corticosterone challenge studies (Deviche et al., 1982; Joseph and Ramachandran, 1993) represent pharmacological effects that would not be apparent in our HS

birds. However, this conclusion must remain guarded in lieu of the reports cited by Deviche (1983) that, in domestic cockerels and other avian species, both acute and chronic stress states are associated with reduced plasma leuteinizing hormone and testosterone levels. Furthermore, all the variables measured in the present study were numerically lower in HS than in RB quail, and evidence from an ongoing ontogeny experiment indicates that cloacal gland development is retarded in HS quail (Satterlee et al., unpublished observations). Thus, we simply cannot discount the hypothesis that, if reduced testosterone levels occur during stress in birds (Deviche, 1983), then a reduction in cloacal gland size may be a correlated stress event. On the other hand, there remains the lone report that short-term stress increases testosterone levels coincident with corticosterone increases in avian males throughout their lifetime (Heiblum et al., 2000). We cannot rectify this report with the current CAREA and CVOL findings in HS quail, our unpublished findings (see above), or the remaining avian literature.

The cloacal gland of male Japanese quail produces a large amount of meringue-like foam from the cloacal gland that is transferred to the female during copulation for the purpose of enhancing male fertilization success (Seiwert and Adkins-Regan, 1998). Administration of testosterone to castrates elicits foam secretion coincident with hypertrophy of the cloacal gland (Nagra et al., 1959; Sachs, 1969) and prevents cloacal gland regression induced by short-day photoperiods (Sachs, 1969). Moreover, foam secretion is positively related to testicular weight and sexual activity (Wilson et al., 1962; Sachs, 1967, 1969; Siopes and Wilson, 1975). In the present study, line differences in CFP at 42 d of age mimicked those found for CAREA and CVOL (i.e., a greater amount of CFP was evident in LS than in RB or HS quail). The PICF also generally supported this picture in that, although PICF in RB were not different from either selected line, PICF was greater in LS than HS quail. Collectively, the CFP and PICF findings further support our contention that puberty in male quail was accelerated by selection of the LS line for reduced adrenocortical responsiveness.

Regardless of the underlying endocrine mechanisms, our proposal remains viable that selection for decreased adrenocortical responsiveness is likely to reduce the incidence of stress-induced behavioral, physiological, and morphological responses that are associated with decreased welfare and productivity in commercially important poultry species (Jones, 1996; Jones and Hocking, 1999; Jones et al., 2000; Satterlee et al., 2000). In addition, the present findings of enhanced cloacal gland development and foam production in LS quail represent favorable reproductive outcomes of selection for reduced adrenocortical responsiveness. Because of the positive relationships between cloacal gland development, testicular size, and spermatozoa production (Siopes and Wilson, 1975; Kirby et al., 1996; Amann, 1999), such a selection program may allow males to successfully breed at an earlier age and thus reduce the associated costs of maintenance. We will soon determine whether enhanced male reproductive

ability remains evident in aged LS quail. Broiler breeder males show a marked decline in sexual potency with age, and the related reductions in flock fertility are occurring at a rate of approximately 0.5% per generation (Reddy and Sadjadi, 1990; Hammerstedt, 1999). This ever-increasing sexual senescence has resulted in the practice of "spiking" or replacing older males with younger ones over the life cycle of hens. Spiking and the practice of increasing the male:female ratio to maintain fertility could perhaps be lessened or eliminated if selection for reduced adrenocortical responsiveness has a lasting, positive effect on male reproductive performance.

In conclusion, genetic selection for hypocorticalism in Japanese quail was associated with an acceleration of puberty in males as evidenced by enhancement of cloacal gland size and foam secretion in LS quail. Longitudinal studies of line differences in testes weight, cloacal gland size and function, and daily sperm production in juvenile, pubertal, and adult quail are underway.

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