Selection for contrasting adrenocortical responsiveness in Japanese quail (*Coturnix japonica*) influences sexual behaviour in males[☆]

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Abstract

Selection of Japanese quail for a reduced (low stress, LS) rather than exaggerated (high stress, HS) adrenocortical response to brief restraint is associated with a non-specific reduction in stress responsiveness, decreased fearfulness, greater sociality, and enhanced male reproductive function, e.g. greater cloacal gland size, foam production, and testes weight. Because sexual behaviour has components that may be affected by all of these traits, the copulatory behaviour of male LS and HS adults was compared herein. In experiment 1, males from each line were individually tested in a runway (novel environment) in two consecutive steps. First, the approach (social proximity) of a test male (LS or HS) to a compartment containing two females (one LS + one HS) that he could see but not reach was examined. Second, after allowing the test male and both females to mingle, the male's latency to first grab and the numbers of grabs, mounts and cloacal contacts were recorded. A tendency for LS males to spend a longer ($P = 0.08$) amount of time near the females before the sexes were mingled was observed. When the birds were allowed contact, LS males showed a significantly higher ($P < 0.04$) number of cloacal contacts and greater ($P < 0.04$) copulatory efficiency (number of cloacal contacts/number of grabs) than HS males. No line differences were observed in the latency to the first grab, grabs, and mounts. In experiment 2, individually-caged males from each line were observed when one female (LS or HS) was introduced into their home cages as a sexual partner. The LS males showed a lower latency to the first grab and greater cloacal contacts and copulatory efficiency than HS quail (all $P < 0.03$). The present findings suggest that quail selection for reduced adrenocortical stress responsiveness prior to the attainment of puberty has a positive impact on adult sexual behaviour of males.

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1. Introduction

Sexual behaviour of Japanese quail has both approach and avoidance components (Burns et al., 1998; Jones and Mills, 1999). For reproductive success, potential sexual partners have to be attracted to, and approach, one another. The tendency to approach must be stronger than the tendency to withdraw. Therefore, higher levels of sociality and success in previous copulatory encounters may predict an enhanced tendency to approach the partner while withdrawal may occur because of an enhanced fearfulness elicited by the other animal (which may be a rival or a predator rather than a safe sexual partner) or other cues and/or previous situations perceived as stressful.

Sexual behaviour in males is also under the control of androgen hormones (for review, see Mills et al., 1997). Androgen involvement in sexual behaviour has been demonstrated by experiments showing that: copulatory behaviour is eliminated by bilateral removal of the testes or photic castration by restricted photostimulation, and restored under these conditions by treatment with exogenous testosterone (Beach and Inman, 1965; Sachs, 1969; Adkins and Adler, 1972; Adkins and Nock, 1976).

It is widely accepted that distress and fear can exert many deleterious effects on the welfare and productivity of fowl, including energy wastage, decreased growth, feed conversion, egg production and product quality, delayed maturation, compromised hatchability, decreased immunocompetence, the development of feather pecking, and the increased likelihood of injury, pain, and even death (Mills and Faure, 1990; Jones, 1996, 1997; Jones and Hocking, 1999). Jones (1996) has suggested that one way of reducing fear and distress and thereby improving welfare and productivity in commercial poultry species may be to select birds not only for less pronounced fear responses but also for decreased adrenocortical responsiveness that, in turn, has been associated with reduced fearfulness (Jones, 1996; Jones and Hocking, 1999; Jones et al., 2000; Faure et al., 2003). This proposal has gained considerable support from studies conducted with the divergent lines of Japanese quail selected for low (low stress, LS) or high (high stress, HS) plasma corticosterone response to brief mechanical restraint (Satterlee and Johnson, 1988). For example, when LS quail were compared to their HS counterparts, they showed a non-specific reduction in stress responsiveness, lower fearfulness, greater sociality, and less developmental instability (Jones and Satterlee, 1996; Jones et al., 1992a,b, 1994, 1999, 2000, 2002; Satterlee and Johnson, 1985; Satterlee et al., 2000). Moreover, LS quail presented higher body and liver weights, and less severely compromised bone strength after sequential exposure to stressors than did their LS counterparts (Satterlee and Johnson, 1985; Satterlee and Roberts, 1990). Finally, and of particular importance for the present study, an accelerated puberty in LS males (evidenced by an increase in cloacal gland area and foam production at 42 day of age), was recently documented (Satterlee et al., 2002). Development of the cloacal gland and foam production in *Coturnix* are androgen dependent and these two variables are considered to be reliable indicators of testicular development and sexual activity (Coil and Wetherbee, 1959; McFarland et al., 1968; Sachs, 1969; Siopes and Wilson, 1975; Oishi and Konishi, 1983; Delville et al., 1984). In general, activation of the hypothalamic–pituitary–adrenal axis by a diversity of stressors has been associated with depression in the hypothalamic–pituitary–testicular axis which presents a plausible mechanism for observation of stress-induced inhibition of male reproductive functions. For example, Deviche (1983) cited evidence that plasma LH and testosterone levels are reduced during

both acute and chronic stress states in avian males. Moreover, dexamethasone-induced chronic hypoadrenocortical responses in Leghorn chicks was associated with increased testis weight and better organisation of the seminiferous cords and interstitium, whereas challenge with 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 photo-induced development of the cloacal gland in male Japanese quail. Not surprisingly then, greater testes weights have also been observed in LS birds when compared to HS ones (Satterlee and Marin, unpublished data).

The behavioural, physiological and morphological findings cited above support the contention that selection for decreased adrenocortical responsiveness would likely enhance productivity and animal well-being in commercially important poultry species (Jones, 1996; Jones and Hocking, 1999; Jones et al., 2000; Satterlee et al., 2000). It is important to note 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 (Padgett and Ivey, 1959; Wilson et al., 1961; Kovach, 1974; Mills and Faure, 1992; Aggrey and Cheng, 1994; Jones, 1996).

It is well-known that selection for one trait can also be accompanied by modification of one or more other traits (Siegel, 1979; Jones, 1996; Jones and Hocking, 1999). Indeed, that is why it is important to continue to study correlated traits that may be affected by selection for the LS trait before making a final recommendation that selection for reduced adrenocortical responsiveness in avians is justified. Because selection for divergent adrenocortical responsiveness has affected many characteristics that may play an important role in mating behaviour (see above), the sexual behaviour of male LS and HS adults was compared in two different situations herein. Tests were conducted both in a runway (novel environment) and in the home cages (familiar environment) of the males. The effects of stress and fearfulness on sexual behaviour were expected to be enhanced in the runway because of the novelty of the situation and the handling necessary to transport the birds to the testing room. The use of the runway also permitted us to measure adult social proximity behaviour that is considered an appetitive component of the sexual behaviour sequence (Domjan and Hall, 1986a). When first placed, a LS or HS test male was allowed to approach a compartment containing the females that he could see but not reach. Previous studies with unselected Japanese quail have shown that, under similar conditions, males approach the female compartment and spend more than half of the testing time close to the female compartment (Domjan and Hall, 1986a; Domjan and Nash, 1988). After measuring the male's approach to the female compartment, the test male was then allowed to mingle with its females by removing the barrier between them. Subsequently, the consummation components of sexual copulatory behaviour (neck-grabs, mounts and cloacal contacts) were observed. Because the behaviour of females from the divergent lines may influence the sexual performance of the males differently, in the present studies, males from each of the selected lines where tested in the runway with female representatives of both lines (LS female + HS female) or, in their home cages, wherein the same number of males from each selected line were exposed to either a LS or HS female.

The present study enabled us to address two main questions: (1) did selection for divergent adrenocortical stress responsiveness have an influence on male sexual behaviour? and if so,

(2) was selection for reduced adrenocortical responsiveness accompanied by any undesirable characteristic(s) relative to male sexual behaviour?

2. Materials and methods

2.1. Genetic stocks and husbandry

Male Japanese quail (*Coturnix japonica*) from lines selected for either a low stress or high stress plasma corticosterone response to brief mechanical immobilization (Satterlee and Johnson, 1988) were used. The more recent genetic history (from generation G_{13} to G_{29}) that verifies maintenance of divergent adrenocortical responsiveness to the selection stressor in these lines is discussed in detail elsewhere (Satterlee et al., 2000, 2002). The lines were reproduced without selection for one additional generation before their use in the present study (G_{30}).

The quail studied were taken from a larger population of an 1190-bird hatch (625 LS and 565 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 12 compartments of two Model 2SD-12 Petersime brooder batteries 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 days of age.

At 28 days of age, quail were sexed by plumage coloration and re-housed in same-line groups of three females and two males in each of 24 cages (12 cages of LS + 12 cages of HS quail). Individual cage dimensions were 50.8 cm × 15.2 cm × 26.7 cm (length × width × height). At this time, birds were also switched to a breeder ration (21% CP; 2750 kcal ME/kg) with feed and water continuing ad libitum. The daily photostimulatory cycle was 14 h L:10 h D with a light intensity of approximately 280 lx during the lighted portion of the day and lights-on occurring at 06:00 h daily. Daily maintenance and feeding chores were done at the same time each day (08:00 h).

At 20 weeks of age, all males ($n = 48$; 24 LS + 24 HS) were re-housed individually into separate cages (same cage type and dimensions as described above) and kept in isolation until the end of the experiments (see below). Cages were arranged in a single caging unit that had four tiers of 12 cages per tier. Within each tier both lines were equally represented (i.e. six LS males and six HS males per tier). Females remained in their home cages during the entire study. The daily light intensities and cycle beginning at 20 weeks of age and thereafter were the same as that described above.

2.2. Runway test (novel environment)

At 22 weeks of age, 46 male quail (23 LS and 23 HS) were tested individually and once only in a runway apparatus (novel environment; see below) in the presence of two age-matched, unfamiliar females (one LS and one HS present in the goal box). The tests were conducted between 09:00 and 15:00 h during two consecutive days (approximately half of the birds were tested each day). The apparatus consisted of an unpainted, closed

wooden runway measuring $140 \, \text{cm} \times 30 \, \text{cm} \times 30 \, \text{cm}$ (length × width × height). This was divided into three compartments by removable wire-mesh (hardware cloth) partitions. The start box and goal box compartments (each 20 cm long) were situated at opposite ends of the runway. Thus, the actual runway (middle section situated between the start and goal boxes) was 100 cm long. To allow the passage of excreta during testing, the runway apparatus was fitted with a wire-mesh floor (1 cm grid) that was raised 2 cm above the surface upon which the apparatus was placed. A transparent lid was used to cover the runway and a video camera was suspended 1.5 m above the chamber to record behavioural activity during the experiment. Lighting and temperature in the test room was similar to that within the room in which the birds were housed.

At test, a male from a given line and two females (one from each line) were removed from their home cages, transported to the test room, and placed, respectively, into the start and goal boxes of the runway. Before placement, in order to facilitate the identification of each female with her line, one of the two females (randomly chosen) in each test was faintly marked on top of the head with an inert dye. During each test day, males from the LS and HS lines were tested in random order and each male was tested with a different pair of females. When a test male was placed into the start box, he could see the females through the wire-mesh partitions of both the start and goal boxes. After a 1 min acclimation period in the start box, the partition that kept the male in the box was removed. Thereafter, the latencies for the chick to leave the start box (latency to emerge) and to enter a 20 cm "close" zone nearest to the goal box (latency to enter close zone) were measured, as well as the total time that the male spent within the close zone (time in close zone) during a 5 min period. The amount of time spent in the close zone was also expressed as a percentage of the time available to remain in the close zone after first entry to that zone (PCZ) according to the following formula:

$$
\text{PCZ} = \left(\frac{\text{time in close zone}}{\text{total time of the trial, } 300 \, \text{s} - \text{latency to enter close zone}} \right) \times 100.
$$

Calculation of PCZ is regarded as one of the most sensitive measures of affiliation in runway tests because it minimizes the potentially confounding effects of individual differences in locomotor ability and in fear-induced immobility in the start box (Jones et al., 2002).

After the 5 min period of social proximity testing, the wire partition dividing the goal box and the runway was removed which allowed the test male to mingle with the two females. During the next 5 min, the number of times that the male grabbed the head or neck feathers of the female with his beak (grabs), mounted on the back of the female with both feet (mounts), and made cloacal contacts by arching his back and lowering his cloaca into contact with that of the female were recorded. Measurement of cloacal contacts is considered to be an excellent indicator of completed copulations and successful sexual performance (Beach and Inman, 1965; Adkins and Adler, 1972). We also made an estimate of the efficiency of copulatory behaviour (i.e. the number of times that the copulatory sequence is completed once it has been initiated) by dividing the number of cloacal contacts by the number of grabs for each test subject (Burns et al., 1998). This variable was termed copulatory efficiency. Finally, the latency to first grab was also recorded.

2.3. Home cage test

After testing in the runway apparatus, all male quail (23 LS and 23 HS) were returned to their home cages for 1 week before being tested again at 23 weeks of age for differences in copulatory behaviour. However, this time, males were tested in their home cages which represented familiar environments.

Because of cage space limitations (i.e. in order to clearly determine the different sexual behaviours upon post-test reviewing of the tape recordings, see below), tests were performed in the presence of one non-familiar female of either the LS or HS lines. Once tested, females were not reused. Female identity was balanced with test males such that there were four test groups: LS male + LS female, LS male + HS female, HS male + LS female, and HS male + HS female. The tests were conducted between 09:00 and 15:00 h during two consecutive days (approximately half of the birds were tested each day). Each consecutive block of four tests comprised representatives from each of the four test groups, and test order was random within these testing blocks. Each male, tested individually and once only, was paired with a different female for testing. Testing started when a given female (LS or HS) was removed from her home cage and placed inside the test male's home cage. Subsequently, behavioural observations were made during a 5 min period and recorded using a video camera that was placed 1 m directly in front of the cage unit. At the end of a test period, the female was removed from the male's cage and returned to her home cage. Review of the video recordings allowed calculation of the latency to the first grab and number of grabs, mounts, and cloacal contacts that a given male performed with his female. The copulatory efficiency was also calculated as described in the runway test procedures.

Analyses of videos also allowed evaluation of the extent to which the female held still and refrained from locomotor activity while the male mounted. This is considered a behavioural indicator of female receptivity (Adkins and Nock, 1976) and highly correlated with blood levels of oestrogen and with successful sperm transfer in quail (Adkins, 1975). The still behaviour was scored on a 4-point scale as described by Adkins and Nock (1976), 0: female never held still, moved constantly; 1: held still less than half the time; 2: held still more than half the time, and 3: held still always, never moved.

2.4. Statistical analyses

Runway social proximity data (latencies to emerge and to enter the close zone, the time spent in the close zone, and PCZ) were subjected to a one-way analysis of variance (ANOVA) that evaluated the effect of male line (LS or HS). Runway copulatory behaviour data (latency to first grab, grabs, mounts, cloacal contacts, and copulatory efficiency) were analyzed by a split-plot ANOVA with female line identity as a within-subject variable and male genetic line as the between-subject variable.

Home cage data were subjected to a two-way ANOVA with male and female genetic lines as variables. Because the home cage latency to first grab data exhibited a significant heterogeneity of variance and/or non-normal distribution (even after $\log_{10}(x + 1)$, $\log(x + 1)$, and square root transformations of the data), values were transformed to ranks (Shirley, 1987) prior to conducting the ANOVA. Female held still behaviour was analyzed

by Mann–Whitney non-parametric test. A *P*-value of <0.05 was considered to represent significant differences.

3. Results

Social proximity results during runway testing are shown in Table 1. There were no differences between males of the divergent adrenocortical stress response lines in the latencies to emerge and to enter the close zone, and in the time spent in the close zone. However, a tendency for LS males to spend a higher PCZ near females than HS ones to do the same barely failed to reach significance ($P = 0.08$).

After birds were allowed to mingle in the runway test, while significant main effects of male line were not evident in the latency to first grab and the number of grabs and mounts, a significant male line effect was observed for cloacal contacts and copulatory efficiency (Table 2). Specifically, LS males showed a higher ($P < 0.04$) number of cloacal contacts and a greater ($P < 0.04$) copulatory efficiency than HS males. No effect of female line was observed in the number of grabs, mounts, cloacal contacts, and copulatory efficiency (data not shown).

Table 3 shows the copulatory behaviour results of the home cage test. The ANOVA revealed a significant main effect of male line on the latency to first grab, cloacal contacts and copulatory efficiency ($P < 0.01$, 0.03 and 0.02, respectively), such that, irrespective of female line identity, LS males started grabbing the females sooner, exhibited a higher number of cloacal contacts, and had a higher copulatory efficiency than HS males. The

Table 1

Social proximity responses of adult male quail of the low stress (LS) and high stress (HS) lines tested in a runway (means ± S.E.)

Variables	LS	HS	Male line *P*-value
Latency to emerge (s)	82.9 ± 22.4	78.1 ± 23.6	0.88
Latency to enter close zone (s)	134.5 ± 26.4	175.3 ± 27.5	0.29
Time in close zone (s)	161.0 ± 26.0	110.1 ± 26.2	0.18
PCZ (%)[a]	71.6 ± 10.3	45.8 ± 10.1	0.08

[a] PCZ = percentage of the time available to remain in the close zone after first entry to the close zone or (time in close zone/(total time of the trial, $300 \, \text{s} - $ latency to enter close zone)) × 100.

Table 2

Sexual behaviour responses of adult male quail of the low stress (LS) and high stress (HS) lines tested in a runway (means ± S.E.)

Variables	LS	HS	Male line *P*-value
Latency to first grab (s)	134.0 ± 25.9	158.4 ± 29.5	0.54
Grabs (no.)	3.0 ± 0.7	2.1 ± 0.6	0.31
Mounts (no.)	2.6 ± 0.5	1.4 ± 0.5	0.11
Cloacal contacts (no.)	1.4 ± 0.3	0.7 ± 0.2	0.04
Copulatory efficiency[a]	0.5 ± 0.1	0.2 ± 0.1	0.04

[a] Copulatory efficiency = number of cloacal contacts/number of grabs.

Table 3
Sexual behaviour responses (means ± S.E.) of adult male (M) quail of the low stress (LS) and high stress (HS) lines tested in their home cages with either a LS or a HS female (F)

Variable	LS-M/LS-F	LS-M/HS-F	HS-M/LS-F	HS-M/HS-F	*P*-value	
					Male line	Female line
Latency to first grab (s)	2.0 ± 0.4	1.5 ± 0.2	6.2 ± 2.4	88.6 ± 39.3	0.001	0.71
Grabs (no.)	6.3 ± 1.4	2.6 ± 0.6	3.9 ± 0.7	2.7 ± 0.7	0.24	0.01
Mounts (no.)	7.5 ± 1.4	3.3 ± 0.9	5.2 ± 1.1	2.9 ± 0.7	0.22	0.004
Cloacal contacts (no.)	4.2 ± 0.9	1.7 ± 0.3	2.0 ± 0.4	1.4 ± 0.3	0.03	0.009
Copulatory efficiency[a]	0.8 ± 0.1	0.9 ± 0.1	0.7 ± 0.1	0.4 ± 0.1	0.02	0.67

[a] Copulatory efficiency = number of cloacal contacts/number of grabs.

ANOVA also revealed a significant main effect of female line identity on the number of grabs, mounts, and cloacal contacts ($P < 0.02$ in all cases), such that both LS and HS males grabbed, mounted, and exhibited more cloacal contacts when a LS female was presented as a sexual partner than when the partner was a HS female. However, for both LS and HS males, there was no significant difference between the copulatory efficiency achieved in the presence of a LS or HS female partner. With regards to female behaviour during the sexual encounter, no differences were detected between LS ($2.2 ± 0.2$ s) and HS ($2.3 ± 0.2$ s) female lines in the female held still behaviour.

Although measurements of damage to the female during mating, such as pecking or pulling feathers were not systematically made, our subjective impression was the incidences of such behaviours were rare and did not differ between the selected lines.

4. Discussion

While the social proximity behaviour measurements of the latencies to emerge and to enter the close zone, and time spent in the close zone of LS and HS quail in the runway did not differ, there was a trend ($P = 0.08$) for LS males to spend longer periods of time near the females once they reached close proximity to them (PCZ variable). Social proximity behaviour of adult male Japanese quail has been suggested to be sexually motivated (Domjan, 1987). For example, this behaviour appears to be stimulated specifically by the presence of a female conspecific and males are much less likely to remain near a window to a compartment housing a male conspecific or a bird of another species (Domjan and Hall, 1986a). Moreover, Domjan and Hall (1986b) have suggested that quail social proximity behaviour is dimorphic as males tend to remain near females while females show little interest in remaining near males. Therefore, it is conceivable that adult male quail selected for reduced rather than higher stress responsiveness desire greater social contact with females because they (LS males) have a greater sexual appetite. On the other hand, the higher PCZ in adult LS males may also reflect a higher sociality (motivation to be near conspecifics) regardless of the sexual appetite. Indeed, pre-pubescent LS quail have been shown to possess greater sociality than HS ones in that LS juveniles spend more time near live conspecifics and they show shorter inter-individual distances than do their HS counterparts

(Jones et al., 2002). Further studies on line differences in sociality of adults are needed to help clarify why adult LS quail appear to be more motivated to spend time near live conspecifics.

Inappropriate levels of sociality could exert undesirable effects on all aspects of social interaction in birds, including affiliation, aggression, dispersal, and mating, as well as on their ability to cope with social disruption, such as isolation, exposure to strangers, or crowding (Vallortigara, 1992; Jones, 1996; Jones and Mills, 1999). Furthermore, a perceived mismatch between a bird's underlying sociality and its social environment could elicit either a series of acute stress responses or chronic social distress with associated negative effects on performance (Mills et al., 1993; Jones and Hocking, 1999; Jones and Mills, 1999). Therefore, regardless of the underlying motivation for the enhanced adult sociality by the LS quail, this characteristic deserves further study in order to ascertain whether increased sociality is or is not associated with deleterious effects such as uneven use of resources from clustering and piling and suffocation during outbreaks of hysteria.

The second part of the runway experiment and the home cage test were focused on consummation components of sexual behaviour, i.e. the number of grabs, mounts, and cloacal contacts performed during mating. Logically, the development of a copulatory encounter may be facilitated by higher levels of sociality and/or sexual appetite, and delayed because of an increased fearfulness. Indeed, fear tends to suppress most other forms of behaviour including mating (Jones, 1987). The effects of stress and fearfulness on sexual behaviour were expected to be enhanced in the runway test because of bird capture by the experimenter and transport to the testing room, as well as the novel properties of the testing situation per se that included all the stressors associated with placement of the test bird in a strange environment (runway apparatus). Thus, mating behaviour may have been somewhat compromised in the runway experiment due to the potential for there to have been heightened levels of stress and fear. Furthermore, in the runway, each male was allowed to mingle with two females in a novel space. In contrast, in the home cage test, each male was exposed to the presence of only one female in familiar surroundings. Thus, the greater number of females used in the novel environment runway test may represent an even more stressful situation, one in which a male placed in a new environment with two females (placed at the opposite end of the apparatus) would perceive the female strangers as more of a frightening stimulus rather than as safe sexual partners. Consistent with a hypothesis of enhanced fear responses being evident during runway testing, the latency to first grab (i.e. the latency to initiate a copulatory encounter) was considerably higher and the numbers of grabs, mounts, and cloacal contacts were considerably lower in the runway test than in the home cage test (Tables 2 and 3, respectively).

Although non-significant, in the runway test (Table 2), LS males showed a numerically shorter (approximately 8.5%) latency to first grab when compared to HS birds. In the home cage experiment, LS males showed a much more dramatic and significantly shorter ($P < 0.001$) latency to first grab than did their HS counterparts (Table 3). The existing differences between the quail lines in corticosterone stress responsiveness, sociality, fearfulness, cloacal gland size, and testes weight (see Section 1), and perhaps sexual appetite (proposed above), may independently or collectively account for the faster initiation of a sexual encounter in LS males than in HS ones, particularly when males are allowed to mate under familiar (less stressful, fearful) circumstances.

The males' number of grabs is indicative of the number of times that a copulatory encounter is initiated and cloacal contacts have been considered (Beach and Inman, 1965; Adkins and Adler, 1972) to be an excellent criterion of a completed copulation and successful sexual performance. Interestingly, in both experiments, there were no significant differences in the number of grabs or mounts (forerunner acts to actual copulation) performed by LS and HS males in both the runway and home cage tests. This suggests that no difference in libido exists between the selected lines. However, the number of cloacal contacts and the copulatory efficiency were significantly higher in LS than in HS males in both studies ($P < 0.04$ for cloacal contacts and copulatory efficiency in the runway experiment, and $P < 0.03$ for cloacal contacts and $P < 0.02$ for copulatory efficiency in the home cage experiment) (Tables 2 and 3). These results indicate that males from the LS line are more effective than their HS counterparts in completing a copulatory event once it has been initiated irrespective of the differences between testing situations employed in these studies.

In order to explore possible female line effects on male sexual performance, the number of grabs, mounts, and cloacal contacts received by a given female, as well as the efficiency at which they copulated with a given male, were measured. In the runway or more novel environment, males (LS or HS) had the option to copulate with two females from different line identity (i.e. a LS and HS female were both presented to a test male). There were no differences between LS and HS males in the number of grabs, mounts, and cloacal contacts, or in the copulatory efficiency performed with a LS or HS female (Table 3). This suggests that under potentially frightening conditions, males of both lines were sexually interacting with the females regardless of their line identity. On the other hand, in the home cage experiment, LS females experienced a significantly higher number of grabs ($P < 0.01$), mounts ($P < 0.004$), and cloacal contacts ($P < 0.009$) than did HS females irrespective of the male line identity. These findings, when coupled with the home cage female line copulatory efficiency finding mentioned above, suggest that differences in the characteristics (e.g. behaviour) of the female line may play important roles in influencing the copulatory behaviour of the males when the latter are given the opportunity to mate under familiar conditions, but these same characteristics do not affect the ultimate outcome (successful copulation).

The extent to which a female holds still and refrains from locomotor activity while a male mounts may be an important variable influencing male behaviour. Female held still behaviour is also considered an indicator of female receptivity (Adkins and Nock, 1976) that is highly correlated with the level of oestrogen and successful sperm transfer in quail (Adkins, 1975). In the present study, the scores found for female held still behaviour in both lines were considered to be typical levels of female responsiveness since comparable female held still response ranging from 1.5 to 2.2 were reported (Adkins and Nock, 1976) for control quail females under light conditions similar to those used herein. No differences were evident between LS and HS females in the female held still behaviour suggesting that at least female receptivity was not influencing male sexual performance. In accordance with this observation, LS and HS males showed the same copulatory efficiency in the presence of a LS or HS female partner, i.e. males from both lines initiated and finished the copulatory sequence at the same rate in the presence of LS or HS females.

Because females were suddenly introduced into the home cages of males without previous acclimation, it is possible that the lower underlying fearfulness and/or greater sociality found in LS quail (Jones et al., 1992a,b, 1994, 1999, 2002; Satterlee and Jones, 1995; Jones and Satterlee, 1996) may play an important role in influencing the development of the male sexual response. However, this conclusion remains guarded as the referenced studies reflect work conducted with juveniles. Further studies are needed to determine whether fearfulness and sociality differences exist between adult LS and HS quail and studies are needed to clarify the participation of the females on male-mating choice and performance of these quail lines.

We already know that selection of the LS line for a low plasma corticosterone response to mechanical restraint is accompanied by intuitively desirable reductions in underlying fearfulness, in adrenocortical responsiveness to a wide range of stressful stimuli, in stress-induced developmental instability, in male puberty age as well as a higher sociality (Satterlee and Johnson, 1988; Jones et al., 1992a, 1994, 2002; Jones and Satterlee, 1996; Jones and Hocking, 1999; Satterlee et al., 2000, 2002). Enhanced male reproductive performance would likely be an additional benefit of this type of selection program, particularly if these effects generalize from quail to other more commercially important poultry species such as meat-type chickens. Broiler breeder males show a marked decline in testis weight with age that is highly correlated to daily sperm production and fertility (Vizcarra et al., 2000). Indeed, reductions in overall flock fertility related to problems with mating efficiency (which is ever decreasing by continued selection for higher body weight and comprised in general by the aging process) are occurring at a rate of approximately 0.5% per generation (Reddy and Sadjadi, 1990; Hammerstedt, 1999). Of specific importance to the present study, Duncan et al. (1990) found a lack of cloacal contact to be associated with reduced fertility in older broiler breeder males. 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/or the practice of increasing the male:female ratio to maintain fertility could perhaps be lessened or eliminated if selection for reduced adrenocortical responsiveness is confirmed as a lasting and positive effect on male broiler breeder reproductive performance. On the other hand, turkeys are primarily produced using artificial insemination and thus, increased copulatory efficiency would not impact breeding success per se in this specie. However, the earlier onset of puberty in LS quail (Satterlee et al., 2002) argues that selection for reduced adrenocortical response in turkeys may have some benefits in terms of being able to collect sperm at an earlier age. Collectively, the present findings suggest that selection for reduced adrenocortical stress responsiveness prior to the attainment of puberty has a positive impact on adult male sexual behaviour.

Acknowledgements

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