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Sociality in Japanese quail (*Coturnix japonica*) genetically selected for contrasting adrenocortical responsiveness

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Abstract

The growing realisation that selective breeding may offer rapid solutions to certain animal welfare problems and the associated production losses lends urgency to the search for suitable selection criteria. We have already shown that genetic selection of Japanese quail for a reduced (low stress, LS) rather than an exaggerated (high stress, HS) adrenocortical response to brief mechanical restraint was associated with marked reductions in underlying fearfulness, non-specific stress responsiveness and developmental instability. However, since genetic selection for one trait can also modify others, monitoring of other important characteristics is imperative before we can make any recommendations. Inappropriate levels of sociality (motivation to be near conspecifics) could cause pronounced social stress. The present study compared underlying sociality in LS and HS quail in two ways. In experiment 1, when undisturbed, same-line groups of six chicks were observed at 4 days of age we found that LS quail stayed closer together than HS ones. When naive, individually tested chicks were tested in a runway at 11–12 days of age in experiment 2, LS quail spent longer near a goal box containing cagemates than did the HS birds. Social proximity in the home cage and reinstatement responses in runway tests of social affiliation are positively related to underlying sociality. Therefore, these findings strongly suggest that underlying sociality is greater in quail of the LS than the HS line. Enhanced sociality could be regarded as an additional advantage of this type of selection programme, particularly if the phenomenon generalised to include commercially important species that are often housed at high stocking densities, like chickens or turkeys.

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1. Introduction

Genetic selection is increasingly thought to offer the most rapid, reliable method of eliminating harmful traits and promoting desirable ones in farm animals; thereby improving their welfare (Mench, 1992; Craig and Swanson, 1994; Jones, 1996; Faure and Mills, 1998; Jones and Hocking, 1999). Many behavioural, physiological and performance-related traits can exert powerful influences on the ability of animals to adapt to their environment and, consequently, on their health, productivity and welfare (Siegel, 1979; Faure and Mills, 1998; Jones, 1996; Jones and Hocking, 1999). Some of the deleterious effects of fear and stress on performance and profitability are described in Section 5. The appreciable phenotypic differences that are apparent in many of the influential characteristics illustrate the potential for beneficial selective breeding programmes if these can be shown to translate to genetic variation. For example, lines of Japanese quail have been genetically selected at Louisiana State University (LSU) for a reduced (low stress, LS) or exaggerated (high stress, HS) plasma corticosterone response to brief mechanical restraint (Satterlee and Johnson, 1988). In this case, selection for low stress has been accompanied by a number of intuitively desirable changes. Firstly, LS quail showed lower adrenocortical responses than HS ones to a wide range of stressors, including cold, cooping, social tension, human contact, and food and water deprivation (Satterlee and Johnson, 1988; Jones et al., 1994). Secondly, the reduction in body weight following exposure to multiple sequential stressors was less pronounced in quail of the LS than the HS line (Satterlee and Johnson, 1985). Thirdly, quail of the LS line showed less fear of restraint as well as of novel places, objects and human beings than did their HS counterparts (Jones et al., 1992a,b, 1994, 2000; Jones and Satterlee, 1996). Fourthly, developmental instability, which reflects small random deviations from symmetry in otherwise bilaterally symmetrical characteristics was less pronounced in LS than in HS quail (Satterlee et al., 2000). Developmental instability (fluctuating asymmetry) is regarded as a sign of genetic and/or environmental stress (Moller and Swaddle, 1997; Thomson, 1999). Collectively therefore, these findings indicate that selection for a dampened adrenocortical response to mechanical restraint also reduced underlying fearfulness, non-specific stress responsiveness, and developmental instability. This conclusion could have important implications for the identification of appropriate selection criteria for future breeding programmes.

Studying divergent lines like the LS and HS quail can help us to determine how practical and desirable it might be to select against certain fear and stress responses. However, since genetic selection for one trait can also be accompanied by modification of one or more other traits (Siegel, 1979; Jones, 1996; Jones and Hocking, 1999) our studies must be extended to include other potentially important characteristics before we can make any firm recommendations. For instance, because quail and other poultry species are highly social animals, underlying sociality (motivation to be near conspecifics) is likely to be important, particularly since this trait has been linked to fearfulness in certain circumstances in domestic chicks (Jones, 1996; Marin et al., 2001). Similarly, shyness and social withdrawal have been positively linked with circulating cortisol levels and general fearfulness in children (Kagan et al., 1988; Schmidt and Fox, 1998). Inappropriate levels of sociality could also 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). Thus, for example, low-sociality birds might be poorly suited for housing in very large or in very confined groups.

Therefore, in the present study we compared underlying sociality in quail of the LS and HS lines in two ways. Firstly, we measured social proximity in the home cage in undisturbed same-line groups of chicks (experiment 1). Secondly, we compared the social affiliation responses of individually tested LS and HS chicks in a runway when the goal box situated at the opposite end contained two cagemates (experiment 2). Social proximity (which was calculated by measuring the distance between the two furthest birds in the home cage at regular intervals) has been successfully used as a measure of underlying sociality in domestic chicks; the premise is that the more sociable the birds are the closer they stay together (Vallortigara, 1992; Jones et al., 1999). Runway tests have also been widely used to measure social reinstatement responses; these behaviours are considered to be indicative of underlying sociality in birds as well as of their ability to make social discriminations (Suarez and Gallup, 1983; Vallortigara et al., 1990; Mills et al., 1995; Jones and Mills, 1999; Jones et al., 1999; Marin et al., 2001). For example, both domestic chicks and Japanese quail approached a goal box containing conspecifics more readily than an empty one or a box containing members of different avian or mammalian species (Suarez and Gallup, 1983; Mills et al., 1995; Jones and Mills, 1999). Sex differences in social reinstatement behaviour have been reported in domestic chicks (Vallortigara, 1992). However, we were unable to control for this variable in the present study because the quail cannot be feather-sexed at the early ages used here.

2. General methods

2.1. Animals

Japanese quail chicks (*Coturnix japonica*) from two genetic lines that have been selected over several generations at LSU for low (LS) or high (HS) plasma corticosterone responses to brief mechanical immobilisation (Satterlee and Johnson, 1988) were used throughout the present study. Following pedigree selection for 12 generations, average plasma corticosterone levels post-immobilisation were 156 and 54% of the values measured in non-selected controls in the HS and LS lines, respectively (Satterlee and Johnson, 1988). Selection pressure was continued for two additional generations, after which the lines were maintained for six generations without selection. During the latter phase, colony breeding of family crosses within a line was used, avoiding only full-sib matings. Despite relaxation of the selection pressure during the fifteenth to nineteenth generations (G_{15} to G_{19}), examination of the lines at G_{20} showed that divergence had been maintained; mean \pm S.E.M. of the circulating corticosterone concentrations in HS and LS quail

exposed to the immobilisation stressor were 19.4 ± 0.7 and 10.0 ± 0.5 ng/ml, respectively. Selection pressure was re-imposed to produce G₂₁ wherein immobilisation resulted in plasma corticosterone concentrations of 29.0 ± 5.4 and 13.7 ± 4.1 ng/ml in the HS and LS quail, respectively (Jones and Satterlee, 1996). The lines reproduced for an additional six generations without selection before their use in the present study (G₂₇). The quail studied in the present work were taken from a larger population of approximately 1900-bird hatch. Egg incubation procedures were similar to those described elsewhere (Jones and Satterlee, 1996).

3. Experiment 1

3.1. Animals, housings and husbandry

Immediately upon hatching, a total of 144 quail (72 LS and 72 HS) were housed in 24 same-line groups of six in sturdy cardboard boxes (30 cm × 30 cm × 30 cm, length × width × height). The birds housed in each of these home boxes were derived from different families and they were allocated to the different boxes at random. All families were equally represented in the study. The quail were not sexed because plumage differences are not apparent at the early ages used here. The floor of each home box was covered with wood shavings. Water and feed (LSU quail starter, 28% CP; 2800 kcal ME/kg) were provided ad libitum in jars and dishes, respectively. Constant lighting (280–300 lx) was provided using fluorescent lamps. Two dead birds (1 LS, 1 HS) were replaced on day 1 of the experiment. One other chick died on day 3; the home box that contained this bird was then omitted from the study to avoid any potentially confounding effects of differences in group size.

3.2. Social proximity test

When the chicks were 4 days old, a video camera was suspended above one of the home cages at 10:00 h (morning observation). This camera remained in place for a 3 min acclimatisation period before the chicks were videotaped for a further 5 min period. Each of the remaining 23 groups was then tested similarly and in random order over the next 3 h. This procedure was repeated at 15:00 h (afternoon observation), thus affording two values for each group. Upon analysis of the videotapes, we recorded the distance between the mid-points of the two chicks that were deemed to be furthest apart (social proximity) as well as the number of birds that were not in physical contact with any of their companions (ungrouped birds) at regular intervals of 15 s throughout the 5 min observation period (starting at 0 s). Overall values for each of these measures were calculated for each group of six chicks in both phases (morning, afternoon) by summing and then averaging the results of the 21 scanning observations. This procedure was then repeated to provide overall scores for each line. Daily maintenance was carried out at the usual time, this coincided with completion of the morning observations. The experimenter was blind to the identity of the birds during recording and analysis of the videotapes.

Table 1

Distances between furthest chicks (social proximity) and the numbers of ungrouped birds (not in physical contact with their cagemates) in undisturbed groups of 4 days old quail chicks of the LS and HS lines in the morning (a.m.) and afternoon (p.m.) (mean \pm S.E.)

Measures	LS		HS		Effects		
	a.m.	p.m.	a.m.	p.m.	Line	Time	Line \times time
Distances between furthest chicks (cm)	18.40 \pm 1.03	21.31 \pm 0.69	21.33 \pm 1.19	23.18 \pm 0.57	<0.03	<0.006	0.51
Ungrouped birds (number)	2.37 \pm 0.25	3.33 \pm 0.23	3.03 \pm 0.31	3.55 \pm 0.18	0.09	<0.005	0.38

3.3. Statistical analysis

The untransformed social proximity scores and the numbers of ungrouped birds were subjected to a repeated measures analysis of variance. The effects of line (LS versus HS) and the time of observation (morning versus afternoon) as well as their interaction were evaluated. A P -value of <0.05 was considered to represent significant differences.

3.4. Results

Quail chicks of both the LS and HS lines stayed closer together ($F_{1,21} = 9.10$; $P < 0.01$) and fewer birds moved away from the group ($F_{1,21} = 9.51$; $P < 0.01$) in the morning than in the afternoon (Table 1). There were no detectable effects of interactions between line and time of observation on either the social proximity ($F_{1,21} = 0.45$; $P < 0.51$) or the “ungrouped birds” ($F_{1,21} = 0.82$; $P < 0.38$) scores.

The distances measured between the two furthest birds were significantly lower ($F_{1,21} = 5.58$; $P < 0.03$) in groups of LS than HS quail (Table 1). Although a numerical tendency for there to be fewer birds that were not in physical contact with their cagemates in groups of LS than HS quail failed to reach significance ($F_{1,21} = 3.05$; $P < 0.09$), these findings collectively suggest that LS quail housed in groups maintained greater social proximity in the home cage than did their HS counterparts.

4. Experiment 2

4.1. Animals, housing and husbandry

Immediately upon hatching, a total of 144 quail (72 LS and 72 HS) were leg-banded and housed in two mixed-line groups of 72 (36 LS plus 36 HS) in each of two compartments in a model 2S-D, six-deck Petersime brooder battery modified for quail. Each compartment measured 102 cm \times 64 cm \times 20 cm, length \times width \times height. The initial brooding temperature was 37.8 °C; this was reduced by 2.8 °C in the second week. A quail starter diet (28% CP; 2800 kcal ME/kg) and water were provided ad libitum and they were exposed to

continuous dim light (22 lx) with a 14 h light (280–300 lx): 10 h dark override. The chicks then remained undisturbed, apart from routine maintenance, until testing began.

4.2. Runway test of social affiliation

At 11 and 12 days of age, 36 LS and 36 HS chicks were tested individually and once only in a straight runway when the goal box at the opposite end contained age-matched conspecifics. Thus, we tested 18 chicks from each line from each of the two brooder compartments. The unpainted wooden runway measured 200 cm × 30 cm × 30 cm (length × width × height) and it was divided into three compartments with removable wire mesh partitions. The compartments situated at opposite ends of the runway were 20 and 30 cm long and they comprised the start box and the goal box, respectively. Thus, the actual runway was 150 cm long. The floor of the runway consisted of wire mesh.

Two age-matched cagemates (1 LS and 1 HS taken from the same brooder compartment) were used as stimulus birds; these were placed in the goal box and allowed 30 s to acclimatise before testing began. We thought it likely that the test chicks would be more attracted to these conspecifics if they were active rather than immobile. Therefore, we changed the stimulus birds after each block of four tests to decrease the likelihood that they would sit, lie down or sleep. At test, a chick was gently removed from the brooder and placed in the start box where it was allowed 30 s to acclimatise; it could see the stimulus birds through the wire mesh partition at this time. The partition was then raised and we measured the latencies for the chick to leave the start box, to reach a point 50 cm along the runway, and to enter the 20 cm “close” zone nearest the goal box, as well as the number of entries made into the close zone and the accumulated time spent there during the 10 min test period. We also expressed the amount of time spent in the close zone as a percentage of the time available after first entry using the following formula:

$$\begin{aligned} & \text{percentage of time spent near goal box} \\ &= \left(\frac{\text{time spent in close zone}}{\text{total time of the trial} - \text{latency to reach the close zone}} \right) \times 100 \end{aligned}$$

We regard this as one of the most sensitive measures in runway tests of affiliation, because it minimises the potentially confounding effects of individual differences in locomotor ability and in fear-induced immobility in the start box. Each bird was returned to a separate compartment in the brooder after test to ensure that it would not be inadvertently retested. None of the tested chicks were used as stimulus birds or vice versa.

4.3. Statistical analysis

The runway responses of LS and HS quail were compared using non-parametric Mann–Whitney *U*-tests. A *P*-value of <0.05 was considered to represent significant differences.

4.4. Results

The LS birds showed numerical, albeit non-significant, tendencies to leave the start box, to reach the 50 cm mark, to enter the close zone of the runway sooner, and to make more

Table 2

Social affiliation responses of individually tested 11–12 days old quail chicks of the LS and HS lines in a runway when the goal box contained cagemates (mean \pm S.E.)

Behavioural measure	Line		<i>P</i> -value
	LS	HS	
Latencies to leave start box (s)	81.55 \pm 18.93	109.86 \pm 29.48	0.85
Latencies to reach 50 cm (s)	100.41 \pm 19.51	129.11 \pm 29.44	0.86
Latencies to reach close zone (s)	162.50 \pm 25.18	226.50 \pm 35.67	0.26
Number of entries	4.41 \pm 0.68	4.00 \pm 0.71	0.50
Time in close zone (s)	319.58 \pm 29.89	226.63 \pm 35.68	0.06
Percent time spent in close zone	71.22 \pm 4.71	53.91 \pm 6.41	0.04

entries into it than did HS ones (Table 2). Similarly, a tendency for LS birds to spend longer in the close zone nearest the goal box than HS ones only narrowly failed to reach significance ($U = 485.5$; $P = 0.06$). Furthermore, the time spent in the close zone expressed as a percentage of the time available after first entry was significantly greater in LS than in HS birds ($U = 387.5$; $P = 0.04$). It is pertinent to note that all the line differences were in the same direction.

5. Discussion

Social proximity measures in the home cage and social reinstatement responses in runway tests of social affiliation are widely considered to be positively related to the underlying levels of sociality (motivation to be near conspecifics) (Suarez and Gallup, 1983; Vallortigara, 1992; Carmichael et al., 1998; Faure and Mills, 1998; Jones et al., 1999). Differences in this behavioural characteristic were apparent between LS and HS quails in the two tests carried out in the present study. Firstly, when undisturbed, same-line groups of six chicks were observed in their home cages at 4 days of age using a scanning technique, the distances measured between the two furthest birds were significantly lower in the LS than in the HS groups. A numerical tendency for there to be fewer birds not in physical contact with their companions in groups of LS rather than HS quail failed to reach significance ($P = 0.09$), but this finding is consistent with the social proximity score. Secondly, when tested in a runway at 11–12 days of age, LS quail spent significantly more of the time available after they had reached the close zone at that end of the runway where a goal box containing cagemates was positioned than did HS ones. Non-significant tendencies for the LS quail to leave the start box located at the opposite end of the runway and to reach the close zone near the goal box sooner than HS birds were also apparent. The findings of both experiments 1 and 2 are consistent. Collectively, they strongly suggest that underlying sociality is greater in quail of a line genetically selected for a low (LS) rather than a high (HS) adrenocortical response to brief restraint. This proposal is indirectly supported by reports that shyness and social withdrawal in children are associated with high levels of salivary cortisol and elevated fearfulness, measures that are indicative of low

thresholds for arousal in the limbic–hypothalamic–adrenocortical axis (Kagan et al., 1988; Schmidt and Fox, 1998).

Novelty is a potent fear-elicitor (Jones, 1996) and animals of many species move closer together and/or form groups when they are exposed to frightening stimuli (Pulliam and Caraco, 1984; Marin et al., 2001; Jones, personal observations). The chicks used in the present study had no previous experience of a video camera before one was used to record home-cage behaviour in experiment 1. Therefore, our finding that social dispersal was greater during the afternoon (second observation) than in the morning (first observation) probably reflected habituation to the frightening properties of the initially unfamiliar camera.

As a logical extension of this argument we might have expected HS quail to show more clumping than LS ones in the presence of the unfamiliar camera because they are more easily frightened (Jones et al., 1992a,b, 1994, 2000; Jones, 1996; Jones and Satterlee, 1996). That we found the reverse effect further strengthens our proposal that genetic selection for reduced adrenocortical responsiveness is associated with increased sociality.

The elicitation of inescapable or prolonged fear and distress can seriously damage poultry welfare and performance (Jones, 1996; Faure and Mills, 1998). Social stress can also contribute to the development of social withdrawal and depression, to impaired health and to poorer productivity (Duncan, 1981; Jones and Hocking, 1999; Jones and Mills, 1999). The deleterious effects of fear and distress on performance include marked reductions in egg production, egg and eggshell quality, and hatchability in laying hens (Bessei, 1984; Brake, 1987; Hughes et al., 1986; Jones, 1996) as well as decreased growth, food conversion efficiency (FCE) and meat quality in broiler type chickens and quail (Jones et al., 1993; Jones, 1997; Faure and Mills, 1998; Hemsworth and Coleman, 1998). Difficulties in obtaining accurate records of performance from poultry companies and an understandable reluctance to elicit fear in commercial flocks mean that few commercially meaningful cash values have been placed on fear-related losses. However, extrapolations from small-scale studies carried out on commercial farms yield strong economic arguments for the continued development of appropriate strategies to reduce fear and stress. First, for example, fear of humans accounted for at least 20% of the variation in egg production (a minimum of 54 eggs per year) and mortality in an Australian study (Barnett et al., 1992). If a similar situation prevailed in the UK it could cost the poultry industry several million pounds a year. Production losses caused by exposure to other frightening events could increase this estimate substantially. Second, fear of humans at commercial broiler farms in Australia was also negatively related to FCE; in fact, fear accounted for 28% of the variance (Jones et al., 1993; Hemsworth et al., 1994). An improvement of just 0.045 units in FCE would have translated to a saving of Australian \$8400 per farm 7 years ago. Furthermore, the UK Ministry of Defence paid poultry farmers approximately £700,000 in 1995 to compensate for fear-related losses caused by low-flying aircraft (Cooper, personal communication).

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, and in stress-induced developmental instability (Satterlee and Johnson, 1988; Jones et al., 1992a, 1994; Jones and Satterlee, 1996; Jones and Hocking, 1999; Satterlee et al., 2000).

Enhanced sociality would likely be an additional benefit of this type of selection programme, particularly if these effects generalise from quail to other more commercially important poultry species, like chickens or turkeys, that are frequently housed in large groups and at high stocking densities. Collectively, the above findings have potentially important implications for future breeding programmes intended to improve the welfare and productivity of poultry.

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