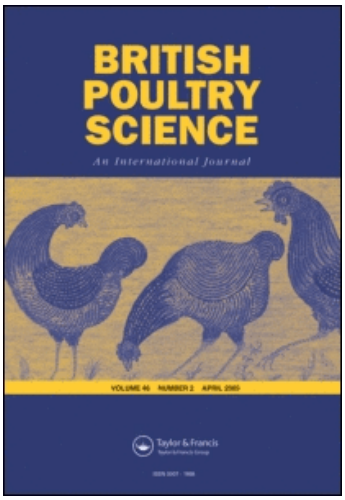

British Poultry Science
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713408216

Ontogeny of copulatory behaviour in male Japanese quail classified by their T-maze performance as hatchlings

M. C. Lábaque [a]; J. M. Kembro [a]; D. A. Guzmán [a]; F. N. Nazar [a]; R. H. Marin [b]
[a] Instituto de Ciencia y Tecnología de los Alimentos, Cátedra de Química Biológica, [b] Consejo Nacional de Investigaciones Científicas y Técnicas, Edificio de Investigaciones Biológicas y Tecnológicas, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina

Online Publication Date: 01 July 2008

To cite this Article Lábaque, M. C., Kembro, J. M., Guzmán, D. A., Nazar, F. N. and Marin, R. H.(2008)'Ontogeny of copulatory behaviour in male Japanese quail classified by their T-maze performance as hatchlings',British Poultry Science,49:4,409 — 417
To link to this Article: DOI: 10.1080/00071660802262050
URL: http://dx.doi.org/10.1080/00071660802262050

British Poultry Science Volume 49, Number 4 (July 2008), pp. 409–417

Taylor & Francis
Taylor & Francis Group

Ontogeny of copulatory behaviour in male Japanese quail classified by their T-maze performance as hatchlings

M.C. LÁBAQUE, J.M. KEMBRO, D.A. GUZMÁN, F.N. NAZAR AND R.H. MARIN[1]

Instituto de Ciencia y Tecnología de los Alimentos, Cátedra de Química Biológica and [1]Consejo Nacional de Investigaciones Científicas y Técnicas, Edificio de Investigaciones Biológicas y Tecnológicas, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina

Abstract 1. This study examines the time courses of male mating behaviours using quail that were categorised at 2 d of age as high performance (HP) or low performance (LP) individuals in a T-maze.
2. Individually caged males from each T-maze category were observed for 5 min after a female of the same category (HP or LP) was introduced into their home cages as a sexual partner at 4, 5, 6, 8, 10 and 12 weeks of age. The number of grabs, mounts and cloacal contacts performed by each male and his copulatory efficiency (number of cloacal contacts/number of grabs; CE) were determined at each time interval.
3. No differences were observed in the proportion of HP and LP males performing grabs at any of the ages evaluated. However, a greater proportion of HP males showed mounting and cloacal contact behaviour, coupled with a higher CE than did their LP counterparts at 5 and 6, 6 and 8, and 8 weeks of age, respectively. At those ages, a higher mean number of mounts and cloacal contacts were also observed. No significant sexual behaviour differences between HP and LP quail were observed at 10 and 12 weeks of age.
4. The results suggest that rapid negotiation of the T-maze in hatchlings is associated with accelerated puberty in male quail. The differential reproductive behaviour of HP males during the development of puberty does not remain extant in fully developed quail.
5. The finding of accelerated male developmental sexual activity responses in HP quail indicates that selection for T-maze HP behaviour may allow males to be successfully bred at an earlier age.

INTRODUCTION

Many behavioural characteristics (such as aggression, mating behaviour, fearfulness, feather pecking and sociality) vary substantially between and within genetic strains of modern commercial egg- and meat-type chicken stocks (Siegel, 1993; Jones, 1996; Craig and Muir, 1998; Faure and Mills, 1998). Some traits influence the bird's ability to adapt to their social and physical environment and exert profound effects on the productivity and welfare of farmed poultry (Jones, 1996; Faure and Mills, 1998; Jones and Hocking, 1999). Because these traits are sensitive to genetic manipulation, the establishment of selection programmes for both performance- and welfare-friendly characteristics has been suggested (Mench, 1992; Jones, 1996; Jones and Hocking, 1999). Indeed, such genetic selection may be the quickest and most reliable method of eliminating harmful characteristics and promoting desirable ones.

The T-maze test combines elements of fear and social stress, both of which can damage animal productivity and welfare (Jones, 1996; Jones and Hocking, 1999). The test involves measuring the time taken by the chick to leave an isolation chamber, and reinstate visual contact with its companions in a nearby enclosure. Chicks are then assigned to one of two categories: those that perform the task in a short time are classified as high performance (HP) birds, and

Correspondence to: Dr R.H. Marin, Instituto de Ciencia y Tecnología de los Alimentos, Edificio de Investigaciones Biológicas y Tecnológicas, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina. Tel: +54 351 4334141 ext. 429. E-mail: rmarin@efn.uncor.edu
Accepted for publication 18th March 2008.

ISSN 0007–1668(print)/ISSN 1466–1799 (online)/08/040409–9
DOI: 10.1080/00071660802262050

those that take a long time as low performance (LP) birds. Broiler chicks classified as HP are known to grow faster in the laboratory (Marin *et al.*, 1997) and under different commercial conditions (Marin *et al.*, 1999, 2003). High performance chicks also show greater sociality in their home cages as well as in runway tests (Jones *et al.*, 1999; Marin *et al.*, 2003) and, in response to an acute stressor, HP chicks had more benzodiazepine/GABA receptors (Marin and Arce, 1996) and a lower adrenocortical response (Marin and Jones, 1999) than their slower LP counterparts. Thus, selection of commercially important poultry stocks for HP in a T-maze may provide avian geneticists with a selection criterion for enhancing production performance and well-being. Although a selection programme based on T-maze response has yet to be established, the substantial variation in the T-maze responses of individually tested, 2- to 3-d-old broiler chicks and Japanese quail (Marin and Arce, 1996; Jones *et al.*, 1999; Marin *et al.*, 2002) suggests that selective breeding for HP would be possible (assuming sufficient heritability for this trait exists).

Female HP Japanese quail from a line selected for reduced (low stress; LS) rather than exaggerated (high stress; HS) adrenocortical responsiveness (HP–LS quail) matured sooner and had a higher early hen-d egg production rate than LP–HS quail (Marin *et al.*, 2002), with both HP–HS and LP–LS quail showing intermediate female reproductive performance. Furthermore, rapid negotiation of the T-maze has been associated with accelerated somatic growth and puberty in male quail (Lábaque *et al.*, 2007). In this study, reproductive development was assessed measuring cloacal gland size and the expression of cloacal gland foam which are considered to be excellent indicators of male gonadal and general reproductive development as well as sexual activity (McFarland *et al.*, 1968; Sachs, 1969; Siopes and Wilson, 1975; Oishi and Konishi, 1983; Delville *et al.*, 1984). The above findings suggest additional advantages that a selection programme based on T-maze performance may have beyond general improvements in growth, sociality and stress hormone responsiveness: the potential to improve both male and female reproduction.

Sexual behaviour in males is under the control of androgen hormones (Mills *et al.*, 1997) and is also affected by bird fearfulness, stress susceptibility and prior experience (Burns *et al.*, 1998; Marin and Satterlee, 2003). 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, increased sociality and success in previous copulatory encounters may predict an enhanced tendency to approach a partner while withdrawal may occur because of fearfulness elicited by the other animal or other cues and/or previous situations perceived as stressful. Because of the links between T-maze performance and social behaviour, the physiological responses, somatic growth, and female and male reproductive development cited above, it is conceivable that T-maze classified quail may differ during development in their male reproductive behaviour as well.

In our study, the ontogeny of male reproductive behaviour in HP and LP T-maze classified Japanese quail chicks was evaluated by studying temporal differences in the consummatory components of sexual behaviour (neck grabs, mounts and cloacal contacts). The study was conducted at ages during which growing photostimulated quail normally exhibit (1) no sexual activity (all birds prepubescent), (2) rapid increases in the numbers of copulatory-related behaviours and mating attempts, and (3) full sexual maturation (all birds being able to consummate sexual encounters).

MATERIALS AND METHODS

Subjects and husbandry

Male Japanese quail (*Coturnix coturnix japonica*) were used, taken from a larger population of a 456-bird hatch. Egg incubation, chick brooding and lighting procedures were similar to those described by Jones and Satterlee (1996) with the exception that chicks were brooded from d 1 in mixed-sex groups of 38 within each of 12 brooder cages measuring 85 cm × 45 cm × 50 cm (length × width × height). Upon hatching, birds were leg-banded in order to identify each bird. At 2 d of age, all birds were categorised as HP or LP birds according to the time they took to traverse a T-maze to reinstate contact with their companions (see below). At 21 d of age, leg bands were replaced with wing bands of the same colour and number. Quail were sexed by plumage colouration at 28 d of age, at which time 40 HP and 40 LP males were randomly and individually housed into the cages of two 5-tier cage batteries. Forty HP and 40 LP females were also randomly housed in same category pairs into the cages of one 5-tier breeder cage battery. Each cage measured 45 cm × 20 cm × 25 cm (length × width × height).

From hatch to 4 weeks of age, birds were fed a starter ration (280 g CP, 11·71 kJ ME/kg) and water *ad libitum*. From 4 weeks on, birds

were switched to a breeder ration (210 g CP, 11·51 kJ ME/kg) with feed and water continuing *ad libitum*. The light regimen was 14 h light:10 h dark provided by fluorescent lamps and light intensity was approximately 350 lux during the lighted portion of the day. During the trial, birds that died or escaped were not replaced. Thus, 37 HP and 38 LP males were included in the statistical analyses at the end of the study.

Hatchling T-maze testing

The T-maze used was a smaller version of the one described by Marin *et al*. (1997) for domestic chicks. It consisted of an isolation chamber (12·5 cm × 12·5 cm, length × width) leading to a 15 cm × 5 cm (length × width) corridor that ended in two 5 cm × 5 cm perpendicular arms (top of the T). A 10 cm × 10 cm (length × width) mirror was situated at the junction of the corridor with the perpendicular arms to facilitate movement of the chick toward this point.

The T-maze apparatus was made of wood and painted white. It was placed in a 25 cm × 40 cm (length × width) section of a larger (60 cm × 40 cm) wooden brooder box, also painted white. A wire-mesh was used to separate the area within the box that contained the T-maze apparatus from a separate 35 cm × 40 cm (length × width) brooder box area that contained 18 test quail on wood shavings litter (see below). Food and water were freely available in the brood area and an overhead lamp provided light for the entire apparatus. Four identical T-maze apparatuses were used in the present study and they were situated in a separate room from the one containing the brooder cages. Ambient temperature and light intensity were similar between the two rooms.

The T-maze responses of 432 quail were measured at 2 d of age. Prior to testing, groups of quail ($n = 18$) were placed in the brood areas of each of 4 T-mazes. Birds were allowed a 10-min acclimation period before testing began (at 08:30 h). This arrangement allowed 4 experimenters to test birds simultaneously and it was continued until all 18 chicks from each T-maze had been tested. At test, a quail was removed from the brood area and placed in the centre of the isolation chamber facing away from the entrance to the T corridor. The time it took to emerge from the arm of the T-maze facing the brood area was then recorded. Exit from the T-maze arm nearest the brood area allowed a test chick visual contact with its companions. The floor of the T-maze apparatus was wiped clean after each test. To prevent them from being retested, birds were lightly marked on the head with a fast-drying non-toxic colour marker before being returned to the brood area. The procedures were repeated by each experimenter until all quail within a given experimenter's T-maze brood area were tested. When this occurred, the entire group of tested quail were returned to their home cages. The procedures were repeated with new groups until all 432 quail had been tested. Quail that successfully negotiated the maze in less than 20 s were categorised as HP chicks; those that took longer than 100 s were classified as LP birds. These time intervals were chosen to include only those individuals that occupied approximately the top and bottom quartile of the T-maze performance distribution. Birds with intermediate time scores (medium performers) were not included in the study.

Home cage tests

Males were repeatedly tested in their home cages at 4, 5, 6, 8, 10 and 12 weeks of age. Because of cage space limitations (that is, in order to clearly determine the different sexual behaviours upon post-test reviewing of the tape recordings, see below), testing of HP and LP quail were performed in the presence of one female of either the HP or LP category. Females from each T-maze category (HP or LP) were paired with test males such that there were two test groups: HP males treated with a HP female and LP males treated with a LP female. The same pair combination was evaluated at each of the 6 testing time intervals. At each time interval, tests were conducted between 09:00 and 15:00 h on two consecutive days (approximately half of the birds were tested each day). Within each time interval, test order was randomised and each male tested once only. Testing started when a given female (HP or LP) was removed from her home cage, wing band identified, transported approximately 2 m, and placed inside her test male's home cage. Subsequently, behavioural events were recorded during a 5-min period using a closed circuit television system with a video camera placed 1 m directly in front of the cage unit. This arrangement made certain that the experimenter was completely hidden from the chick's view during testing. At the end of a test period, the female was removed from the male's cage and returned to her home cage. The males could not see their intended potential mates from their home cages.

A male quail initiates sexual activity by using its beak to grab and hold the head or neck feathers of the female (termed a 'grab'). Once the male has both feet on the female's back (a 'mount'), it arches its back and moves its cloaca in contact with that of the female, making several cloacal thrusts ('cloacal contacts'). The number of grabs, mounts and cloacal contacts were determined by replay of the test recordings.

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 estimated the efficiency of copulatory behaviour (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. The numbers of HP and LP males that performed grabs, mounts and cloacal contacts during each of the time intervals were also assessed as a proportion of the total HP or LP group size. Copulatory behaviour typically improves with practice (repetitive attempts) (Domjan *et al*., 1986). Indeed, cloacal contacts are often observed only after several copulatory sequences are initiated. Thus, the proportion of male individuals (HP or LP) having a copulatory efficiency higher than 0·3 (at least one cloacal contact made after three copulatory attempts; CE > 0·3) was also determined. This milestone was chosen by identification of those birds within the entire population (considering all HP and LP quail) that at the end of the study possessed a copulatory efficiency that excluded them from being members of the bottom 30% of the combined HP and LP population.

Data analysis

Differences in the proportion of HP and LP birds that performed grabs, mounts and cloacal contacts and who had a CE > 0·3 at each of the 6 testing time intervals (at 4, 5, 6, 8, 10 and 12 weeks of age) were evaluated using a two-sample proportion test (Analytical Software, 2000). Separate analyses were calculated for each response variable measured, where a male was considered successful and scored a '1', if it performed a mating behaviour at a given age, and unsuccessful and scored a '0', if it did not perform a mating behaviour at a given age.

Copulatory behaviour data were evaluated with repeated measures analyses of variance (ANOVAs), with quail age (4, 5, 6, 8, 10 and 12 weeks of age) as the within-subject variable (repeated measure) and T-maze category (HP and LP) as the between-subject variable. To better fit the assumptions of the ANOVA, values were transformed to ranks (Shirley, 1987). Separate ANOVAs were conducted for each response variable measured. Fisher's least significant difference tests were used for *post hoc* comparisons of treatment means. A probability level of $\leq 0{\cdot}05$ was considered to represent significant differences.

RESULTS

The Table shows the proportion of birds who performed at least one or more grabs and mounts and at least one or more cloacal contacts and a CE > 0·3 at the ages evaluated (4, 5, 6, 8, 10 and 12 weeks of age). At 4 weeks of age, no HP or LP males exhibited sexual behaviour. However, at 5, 6 and 8 weeks of age, an increasingly higher number of males showed sexual activity. At 5 weeks of age, a trend ($P < 0{\cdot}07$) for a greater proportion of males grabbing females was found in the HP compared to the LP group. At 6 weeks of age, almost all males (95 *vs* 97%, respectively, for LP and HP) grabbed their test females at least once and, at 8 weeks of age, all males (100%) were showing female grabbing behaviour. At 5 and 6 weeks of age, a greater ($P < 0{\cdot}05$) proportion of HP males mounted their similarly categorised target females when compared to their LP male counterparts. Beginning at 8 weeks of age, 87 *vs* 95% (respectively for LP and HP) of the males performed mounts and no differences were found between the HP and LP male quail. A small incidence of cloacal contacts were first observed at 6 weeks of age, wherein a higher ($P < 0{\cdot}05$) proportion of males performed cloacal contacts in the HP (33%) than in the LP (18%) group. The higher proportion of HP males performing cloacal contacts than LP males was maintained at 8 weeks of age. Thereafter, cloacal contact behaviour seemed to peak and no further T-maze category influences were evident. Similar to the cloacal contact results, the number of males performing a CE > 0·3 was numerically higher in HP than in LP male quail at 6 weeks of age ($P < 0{\cdot}09$; 18 *vs* 33%, respectively, for LP and HP) and greater at 8 weeks of age ($P < 0{\cdot}05$; 71 *vs* 84%, respectively, for LP and HP).

Figure 1 depicts the mean (±SEM) number of grabs of HP and LP quail at 4, 5, 6, 8, 10 and 12 weeks of age. The number of grabs was affected by quail age (number of grabs increasing in time; $F_{5,365} = 31{\cdot}19$, $P < 0{\cdot}001$), but was not affected by T-maze category (HP = LP; $F_{1,73} = 0{\cdot}58$, $P < 0{\cdot}44$). No interaction ($F_{5,365} = 0{\cdot}49$, $P = 0{\cdot}78$) between these treatments on the number of grabs was found.

The number of mounts was affected by T-maze category (HP>LP; $F_{1,73} = 4{\cdot}98$, $P < 0{\cdot}03$) and quail age (number of mounts increasing in time; $F_{5,365} = 32{\cdot}86$, $P < 0{\cdot}001$) and these treatments failed to show a significant interaction ($F_{5,365} = 1{\cdot}85$, $P = 0{\cdot}10$). *Post hoc* least significant difference tests showed that the number of mounts were similar in HP and LP quail initially (at 4 weeks of age) and from 8 to 12 weeks of age (by the end of the study). However, HP males showed more ($P < 0{\cdot}05$) mounts than LP males from 5 to 6 weeks of age (Figure 2).

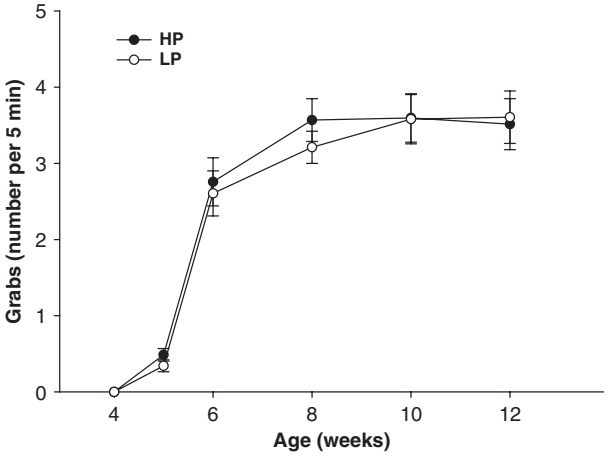

Figure 1. *Age influences on male grabs (mean number per 5 min observation period ±SEM) made on females in breeder pairs that were categorised as high (HP) or low performers (LP) in a T-maze at 2 d of age.*

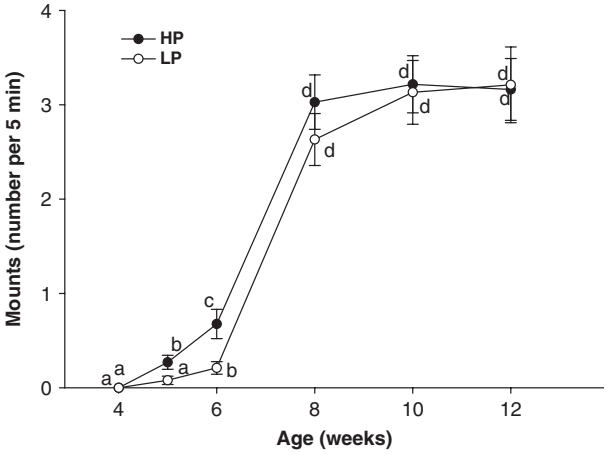

Figure 2. *Age influences on male mounts (mean number per 5 min observation period ±SEM) made on females in breeder pairs that were categorised as high (HP) or low performers (LP) in a T-maze at 2 d of age. [a–d]Means having no common superscripts differ significantly (P ≤ 0·05).*

The number of cloacal contacts made by males was affected by quail age (number of cloacal contacts increasing in time; $F_{5,365} = 38{\cdot}26$, $P < 0{\cdot}001$) and there was an interaction ($F_{5,365} = 2{\cdot}23$, $P < 0{\cdot}05$) between T-maze category and quail age on the number of cloacal contacts performed as well (Figure 3). *Post hoc* tests showed that the mean number of cloacal contacts were similar in HP and LP quail at 4 and 5 weeks of age, and from 10 to 12 weeks of age (by the end of the study). However, as with the mounting behaviour results, at the intermediate ages tested (from 6 to 8 weeks of age), HP males showed more ($P < 0{\cdot}05$) cloacal contacts than did the LP males. Copulatory efficiency results generally mimicked the number of cloacal contacts—higher copulatory efficiency was observed in HP than LP quail from 6 to 8 weeks of age (Figure 4).

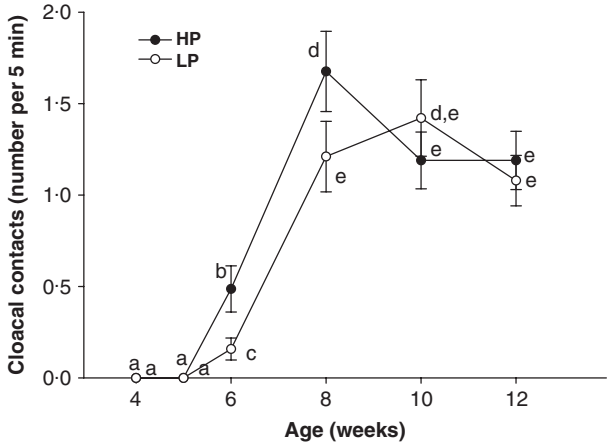

Figure 3. *Age influences on cloacal contacts (mean number per 5 min observation period ±SEM) in male and female breeding pairs that were categorised as high (HP) or low performers (LP) in a T-maze at 2 d of age. [a–e]Means having no common superscripts differ significantly (P ≤ 0·05).*

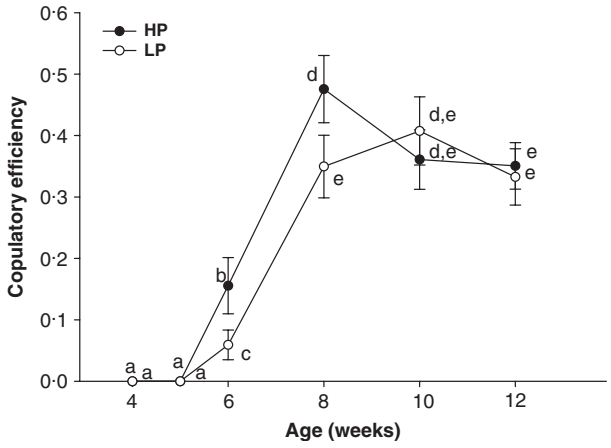

Figure 4. *Age influences on copulatory efficiency (measured as number of cloacal contacts/number of grabs per 5 min observation period ±SEM) of males in breeder pairs that were categorised as high (HP) or low performers (LP) in a T-maze at 2 d of age. [a–e]Means having no common superscripts differ significantly (P ≤ 0·05).*

DISCUSSION

Our findings demonstrate that T-maze classification at the very early age of 2 d post-hatching is predictive of the onset of sexual behaviour. Significant differences in several copulatory behaviours during the early ages of sexual development were observed between the two classification groups (HP *vs* LP). Evidently, T-maze performance is related to a greater range of behaviours than those directly associated with the T-maze classification procedure, and these relationships continue to be evident in birds that are older than those used in previous experiments (Jones *et al*., 1999; Marin and Martijena, 1999). Behaviour early in life is not

always predictive of later performance. For example, Nol *et al.* (1996) found that dominance ranking of quail is not stable during ontogenetic development.

The differences in sexual behaviour observed in the present study extend the effects of the T-maze classification to new measures of behaviour. Previous studies have shown that T-maze classified HP males are more social and have a reduced stress responsiveness (Jones *et al.*, 1999; Marin and Martijena, 1999). The present findings indicate that T-maze classification also correlates with differences in various measures of male sexual behaviour. The effects on sexual behaviour are of particular interest because they show that T-maze classification based on non-sexual behavioural responses at only 2 d of age is related to sexual responses that occur much later on and that are not in the behavioural repertoire of the birds at the time of classification. Both LP and HP test males were tested only with like (same T-maze classified) females because of the potential proposed usefulness of the T-maze test in future selection programmes. A selection programme would be applied in very young birds where, in most cases, the sex is unknown. In that case, the breeder should only keep HP birds (males and females) and discard the LP ones. Moreover, it should also be easier to develop an HP line considering that both males and females should be selected for the same trait (HP in a T-maze). However, because HP and LP quail differ in their social responses and stress susceptibility, experiments evaluating different T-maze pair combinations would be needed to help elucidate the influence of sex differences in social and stress responsiveness characteristics on mating behaviour.

As previously stated, the number of grabs of a female by a male is indicative of the number of times that a copulatory encounter is initiated and the number of cloacal contacts have been considered to be an excellent indicator of a completed copulation (successful sexual performance) (Beach and Inman, 1965; Adkins and Adler, 1972). There were no significant differences in the number of grabs (a forerunner act to actual copulation) performed by HP and LP males at any of the ages evaluated in home cage tests. This suggests that the libido in T-maze classified birds does not differ. However, the number of cloacal contacts and the copulatory efficiency showed significant differences between HP and LP quail (HP > LP) when those behaviours began to appear in the sexual activity repertoire of the quail (from 6 to 8 weeks of age). Because the differences between HP and LP birds in the number of cloacal contacts and CE are lost later in life (at 10 and 12 weeks of age), our data further suggest that males from the HP category are more effective than their LP counterparts in completing a copulatory event once it has been initiated only during the early stages of sexual development.

The measurement of the proportion of quail performing mounts and the use of absolute numbers of mounts may be even more sensitive than measurement of cloacal contacts in first detecting HP *vs* LP developmental reproductive differences in copulatory behaviour. Beginning at 5 weeks of age, a full week earlier than was found for the significant T-maze group differences in cloacal contacts and copulatory efficiency, a higher number of HP than LP males had mounted their females. At 5 weeks of age, a trend for a greater proportion ($P < 0{\cdot}07$) of males grabbing females was also found in HP than in LP males. Perhaps use of a larger number of observations would have allowed a higher degree of confidence in detecting T-maze group differences in the proportion of males grabbing females at this very early age. Nevertheless, the greater number of male HP quail that performed mounts at 5 weeks, a difference that continued at 6 weeks of age, supports our thesis that the onset of puberty (precociousness) was advanced in birds that more quickly traversed the T-maze as hatchlings. Even though the number of cloacal contacts were still rising differently by T-maze group (HP > LP) at 8 weeks of age, all males, regardless of their T-maze category, were at least attempting to initiate a sexual encounter (grab females by 8 weeks of age). This is not surprising, because unless birds began to show sexual activity by this time, they would be considered sexually dysfunctional adults. Collectively, our previous findings of the interactive effects of T-maze classified low stress and high stress quail chicks on female quail sexual maturation as evidenced by early egg laying (Introduction and Marin *et al.*, 2002), our study showing earlier cloacal gland development in HP compared to LP male quail (Lábaque *et al.*, 2007) and the present findings on male copulatory behaviour suggest that ability to rapidly negotiate a T-maze as a chick is associated with accelerated puberty in both quail sexes.

In prepubertal and pubertal Japanese quail, cloacal gland hypertrophy and foam production are androgen-dependent and highly positively correlated with testes size as well as sexual activity (Coil and Wetherbee, 1959; McFarland *et al.*, 1968; Sachs, 1969; Siopes and Wilson, 1975; Oishi and Konishi, 1983; Delville *et al.*, 1984). Androgen involvement in sexual behaviour has been demonstrated by experiments that have shown copulatory behaviour is eliminated by bilateral removal of the testes or by photic castration during restricted photostimulation, while such behaviours are restored under these same conditions by treatment with exogenous

testosterone (Beach and Inman, 1965; Sachs, 1969; Adkins and Nock, 1976). Recently, temporal developmental differences were found in cloacal gland size (HP > LP) and also in body weight (Lábaque *et al.*, 2007). Thus, the accelerated somatic growth may also be considered as a factor influencing the accelerated puberty found in HP male quail of the present study. However, HP males also showed higher-body-weight-adjusted cloacal gland size compared to LP males (Lábaque *et al.*, 2007) during a very similar (6 to 10 weeks of age) timeframe as that used herein. These glandular findings suggest that the present enhanced copulatory efficiency of HP quail during weeks 6 and 8 is probably a direct result of altered endocrinology (increased testosterone) independent of somatic growth. Because the present differences in copulatory behaviour detected at 6 and 8 weeks of age (HP > LP) were lost at 10 and 12 weeks of age, it appears that any changes in testosterone are transient because the increased sexual behaviour in HP males is not maintained at older ages. However, it would be interesting to determine whether T-maze category differences in copulatory behaviour re-emerge in very aged quail when circulating testosterone falls and sexual senescence occurs (Ottinger *et al.*, 1997).

Of relevance to the present study is the fact that male quail selected for reduced (low stress, LS) rather than exaggerated (high stress, HS) plasma corticosterone response to brief restraint, like the present HP males, also show an accelerated onset of puberty (Satterlee *et al.*, 2002; Marin and Satterlee, 2004; Satterlee and Marin, 2004; Satterlee *et al.*, 2007*a*, *b*). In addition, quail from the LS line show lower fearfulness, a non-specific reduction in stress responsiveness and greater sociality than HS quail (Jones *et al.*, 1992*a*, *b*, 1994, 2002; Jones and Satterlee, 1996). In avians, the administration of corticosterone or adrenocorticotrophin, as well as activation of the hypothalamic–pituitary–adrenal axis by various non-specific systemic stressors, is associated with depression in the hypothalamic–pituitary–testicular axis (Deviche *et al.*, 1982; Deviche, 1983; Edens, 1987; Joseph and Ramachandran, 1993). Thus, it has been proposed that the reported negative relationships between corticosterone and male reproductive function may reflect corticosterone-induced alterations of pituitary gonadotrophin hormone release and/or Leydig cell apoptosis, phenomena that may simply underlie the compromised reproductive functioning found in HS quail when compared to LS ones (Satterlee *et al.*, 2000, 2002, 2006, 2007*b*; Marin and Satterlee, 2004; Satterlee and Marin, 2004). Plasma corticosterone responses to a partial water immersion stressor were lower in HP than LP chicks (Marin and Jones, 1999) indicating a differential susceptibility to stressful stimulation in T-maze categorised birds. Therefore, because adrenocortical stress responses are considered to be non-specific in terms of the stressors that induce such responsiveness, HP quail may also be less sensitive to other stressors as well. In the present study, while the quail were not intentionally exposed to stressors, it may well be that periodic differential adrenocortical responses in the direction of HP < LP may have occurred during daily routine maintenance chores, and during the unavoidable stress associated with bird capture, transport and handling for the purposes of hatching, leg and wing banding, housing and copulatory behaviour measurements. Thus, the aetiology of the accelerated ability to consummate a sexual encounter found in HP quail in the present study may be linked to a decreased adrenocortical responsiveness.

It has been proposed (Jones, 1996; Jones and Hocking, 1999; Jones *et al.*, 2000; Satterlee *et al.*, 2000) that selection for reduced adrenocortical responsiveness and/or reduced fearfulness and/or heightened sociality may be worthwhile in ameliorating the incidence of stress-induced behavioural, physiological and morphological responses that are associated with decreased animal welfare and productivity in commercially important poultry species. Two of these traits (reduced adrenocortical responsiveness and increased sociality) are apparent in HP birds. Thus, assuming that HP behaviour is sufficiently heritable, early age T-maze testing may provide yet another useful alternative for poultry breeders to identify genotypes that possess significant potential for improved productivity and animal welfare.

In conclusion, the present findings of accelerated male developmental sexual activity responses in HP quail represent another favourable outcome that selection for T-maze HP behaviour may provide—may allow males to be successfully bred at an earlier age, thus reducing the associated costs of male maintenance. Our original proposal that selection for rapid negotiation of the T-maze will probably reduce the incidence of stress-induced behavioural, physiological and morphological responses that are associated with decreased welfare and productivity in commercially important poultry species is consistent with other research (Jones, 1996; Jones and Hocking, 1999; Jones *et al.*, 2000; Satterlee *et al.*, 2000; Lábaque *et al.*, 2007).

ACKNOWLEDGEMENTS

This research was supported by grants from FONCYT, SECyT UNC and CONICET, Argentina. M.C.L. and R.H.M. are career members of

CONICET, Argentina. J.M.K. holds research fellowships from CONICET and D.A.G. from SECyT UNC and are graduate students of the Doctorado en Ciencias Biológicas, FCEFyN, UNC, Argentina. We thank the anonymous reviewers for the comments and suggestions made to improve this manuscript.

REFERENCES

Adkins, E.K. & Adler, N.T. (1972) Hormonal control of behavior in Japanese quail. *Journal of Comparative Physiology and Psychology*, **81**: 27–36.

Adkins, E.K. & Nock, B.L. (1976) The effects of the antiestrogen CI-628 on sexual behavior activated by androgen or estrogen in male quail. *Hormones and Behaviour*, **7**: 417–429.

Analytical Software (2000) *Statistix7*: *A User's Manual*, Version 7 (Tallahassee, FL, Analytical Software).

Beach, F.A. & Inman, N.G. (1965) Effects of castration and androgen replacement on mating in male quail. *Proceedings of the National Academy of Sciences of the USA*, **54**: 1426–1431.

Burns, M., Domjan, M. & Mills, A.D. (1998) Effects of genetic selection for fearfulness or social reinstatement behavior on adult social and sexual behavior in domestic quail (*Coturnix japonica*). *Psychobiology*, **26**: 249–257.

Coil, W.H. & Wetherbee, D.K. (1959) Observations on the cloacal gland of the Eurasian quail *Coturnix coturnix*. *Ohio Journal of Science*, **59**: 268–270.

Craig, J. & Muir, W. (1998) Genetics and the behavior of chickens: welfare and productivity, in: Grandin, T. (Ed.) *Genetics and the Behavior of Domestic Animals*, pp. 265–297 (San Diego, Academic Press).

Delville, Y., Hendrick, J., Sulon, J. & Balthazart, J. (1984) Testosterone metabolism and testosterone-dependent characteristics in Japanese quail. *Physiology and Behaviour*, **33**: 817–823.

Deviche, P. (1983) Interaction between adrenal function and reproduction in male birds, in: Mikami, S. (Ed.) *Avian Endocrinology: Environmental and Ecological Perspectives*, pp. 243–254 (Berlin, Springer-Verlag).

Deviche, P., Massa, R., Bottoni, L. & Hendrick, J. (1982) Effect of corticosterone on the hypothalamic–pituitary–gonadal system of male Japanese quail exposed to either short or long photoperiods. *Journal of Endocrinology*, **95**: 165–173.

Domjan, M., Lyons, R., North, N.C. & Bruell, J. (1986) Sexual Pavlovian conditioned approach behaviour in male Japanese quail (*Coturnix coturnix japonica*). *Journal of Comparative Psychology*, **100**: 413–421.

Edens, F.W. (1987) Manifestations of social stress in grouped Japanese quail. *Comparative Biochemistry and Physiology, A*, **86**: 469–472.

Faure, J.M. & Mills, A.D. (1998) Improving the adaptability of animals by selection, in: Grandin, T. (Ed.) *Genetics and the Behavior of Domestic Animals*, pp. 235–264 (San Diego, Academic Press).

Jones, R.B. (1996) Fear and adaptability in poultry: insights, implications and imperatives. *World's Poultry Science Journal*, **52**: 131–174.

Jones, R.B. & Hocking, P.M. (1999) Genetic selection for poultry behaviour: big bad wolf or friend in need? *Animal Welfare*, **8**: 343–359.

Jones, R.B. & Mills, A.D. (1999) Divergent selection for social reinstatement behaviour in Japanese quail: effects on sociality and social discrimination. *Poultry Avian Biology Review*, **10**: 213–223.

Jones, R.B. & Satterlee, D.G. (1996) Threat-induced behavioural inhibition in Japanese quail genetically selected for contrasting adrenocortical response to mechanical restraint. *British Poultry Science*, **37**: 465–470.

Jones, R.B., Satterlee, D.G. & Ryder, F.H. (1992*a*) Fear and distress in Japanese quail chicks of two lines genetically selected for low or high adrenocortical response to immobilization stress. *Hormones and Behaviour*, **26**: 385–393.

Jones, R.B., Satterlee, D.G. & Ryder, F.H. (1992*b*) Open-field behavior of Japanese quail genetically selected for low or high plasma corticosterone response to immobilization stress. *Poultry Science*, **71**: 1403–1407.

Jones, R.B., Satterlee, D.G. & Ryder, F.H. (1994) Fear of humans in Japanese quail selected for low or high adrenocortical response. *Physiology and Behaviour*, **56**: 379–383.

Jones, R.B., Satterlee, D.G. & Cadd, G.G. (1999) Timidity in Japanese quail: effects of vitamin C and divergent selection for adrenocortical response. *Physiology and Behaviour*, **67**: 117–120.

Jones, R.B., Satterlee, D.G., Waddington, D. & Cadd, G.G. (2000) Effects of repeated restraint in Japanese quail genetically selected for contrasting adrenocortical responses. *Physiology and Behaviour*, **69**: 317–324.

Jones, R.B., Marin, R.H., Satterlee, D.G. & Cadd, G.G. (2002) Sociality in Japanese quail (*Coturnix japonica*) genetically selected for contrasting adrenocortical responsiveness. *Applied Animal Behaviour Science*, **75**: 337–346.

Joseph, J. & Ramachandran, A.V. (1993) Effect of exogenous dexamethasone and corticosterone on weight gain and organ growth in post-hatched White Leghorn chicks. *Indian Journal of Experimental Biology*, **31**: 858–860.

Lábaque, M.C., Satterlee, D.G., Guzman, D.A. & Marin, R.H. (2007) Ontogeny of the cloacal gland in male Japanese quail classified in a T-maze. *Poultry Science*, **86**: 2013–2019.

Marin, R.H. & Arce, A. (1996) Benzodiazepine receptors increase induced by stress and maze learning performance in chicks forebrain. *Pharmacology Biochemistry and Behavior*, **53**: 581–584.

Marin, R.H. & Jones, R.B. (1999) Latency to traverse a T-maze at 2 days of age and later adrenocortical responses to an acute stressor in domestic chicks. *Physiology and Behaviour*, **66**: 809–813.

Marin, R.H. & Martijena, I.D. (1999) Consecuencias de la exposición a un estresante sobre el comportamiento de pollos preseleccionados en un laberinto en T. *Archivos de Zootecnia*, **48**: 405–414.

Marin, R.H. & Satterlee, D.G. (2003) Selection for contrasting adrenocortical responsiveness in Japanese quail influences sexual behavior in males. *Applied Animal Behaviour Science*, **83**: 187–199.

Marin, R.H. & Satterlee, D.G. (2004) Cloacal gland and testes development in male Japanese quail selected for divergent adrenocortical responsiveness. *Poultry Science*, **83**: 1028–1034.

Marin, R.H., Arce, A. & Martijena, I.D. (1997) T-maze performance and body weight relationship in broiler chicks. *Applied Animal Behaviour Science*, **54**: 197–205.

Marin, R.H., Jones, R.B., Garcia, D.A. & Arce, A. (1999) Early T-maze performance and subsequent growth in commercial broiler flocks. *British Poultry Science*, **40**: 434–438.

Marin, R.H., Satterlee, D.G., Cadd, G.G. & Jones, R.B. (2002) T-maze behavior and early egg production in Japanese quail selected for contrasting adrenocortical responsiveness. *Poultry Science*, **81**: 981–986.

Marin, R.H., Satterlee, D.G., Castille, S.A. & Jones, R.B. (2003) Early T-maze behavior and broiler growth. *Poultry Science*, **82**: 742–748.

McFarland, L.Z., Warner, R.L., Wilson, W.O. & Mather, F.B. (1968) The cloacal gland complex of the Japanese quail. *Experientia*, **24**: 941–943.

Mench, J.A. (1992) The welfare of poultry in modern production systems. *Poultry Science Reviews*, **4**: 107–128.

Mills, A.D., Crawford, L.L., Domjan, M. & Faure, J.M. (1997) The behavior of the Japanese or domestic quail *Coturnix japonica*. *Neuroscience Biobehaviour Review*, **21**: 261–281.

Nol, E., Cheng, K. & Nichols, C. (1996) Heritability and phenotypic correlations of behaviour and dominance rank of Japanese quail. *Animal Behaviour*, **52**: 813–820.

Oishi, T. & Konishi, T. (1983) Variations in the photoperiodic cloacal response of Japanese quail: association with testes weight and feather color. *Genetic and Comparative Endocrinology*, **50**: 1–10.

Ottinger, M.A., Thompson, N., Viglietti-Panzica, C. & Panzica, G.C. (1997) Neuroendocrine regulation of GnRH and behavior during aging in birds. *Brain Research Bulletin*, **44**: 471–477.

Sachs, B.D. (1969) Photoperiodic control of reproductive behavior and physiology of the Japanese quail. *Hormones and Behaviour*, **1**: 7–24.

Satterlee, D.G. & Marin, R.H. (2004) Photoperiod-induced changes in cloacal gland physiology and testes weight in male Japanese quail selected for divergent adrenocortical responsiveness. *Poultry Science*, **83**: 1003–1010.

Satterlee, D.G., Cadd, G.C. & Jones, R.B. (2000) Developmental instability in Japanese quail genetically selected for contrasting adrenocortical responsiveness. *Poultry Science*, **79**: 1710–1714.

Satterlee, D.G., Marin, R.H. & Jones, R.B. (2002) Selection of Japanese quail for reduced adrenocortical responsiveness accelerates puberty in males. *Poultry Science*, **81**: 1071–1076.

Satterlee, D.G., Cole, C.A. & Castille, S.A. (2006) Cloacal gland and gonadal photoresponsiveness in male Japanese quail selected for divergent plasma corticosterone response to brief restraint. *Poultry Science*, **85**: 1072–1080.

Satterlee, D.G., Cole, C.A. & Castille, S.A. (2007*a*) Maternal corticosterone further reduces the reproductive function of male offspring hatched from eggs laid by quail hens selected for exaggerated adrenocortical stress responsiveness. *Poultry Science*, **86**: 572–581.

Satterlee, D.G., Tong, M., Castille, S.A. & Marin, R.H. (2007*b*) Cloacal gland growth differences in high and low plasma corticosterone stress response line male quail reared under short daylengths. *Poultry Science*, **86**: 1213–1217.

Shirley, E.A. (1987) Application of ranking methods to multiple comparison procedures and factorial experiments. *Applied Statistics*, **36**: 205–213.

Siegel, P.B. (1993) Behavior genetics in chickens: a review. *Poultry Science*, **72**: 1–6.

Siopes, T.D. & Wilson, W.O. (1975) The cloacal gland—an external indictor of testicular development in *Coturnix*. *Poultry Science*, **54**: 1225–1229.