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Too hungry to learn? Hungry broiler breeders fail to learn a Y-maze food quantity discrimination task

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Abstract

*Choice tests may aid determining whether qualitative dietary restriction improves the welfare of feed-restricted broiler breeder chickens (*Gallus gallus domesticus*). However, hunger-stress may reduce competency to choose by impairing learning. The effect of chronic feed restriction on the ability of broiler breeders to learn a hunger-relevant discrimination task was investigated using a Y-maze paradigm. The task was to associate black and white arms with large and small quantities of feed. Birds were reared to three growth curves by means of severe (n = 12), moderate (n = 12) or very mild feed restriction (n = 12). Learning the task and selecting the larger food option allowed birds to increase their feed intake. Time taken to traverse the Y-maze was also measured. Birds from all treatment groups traversed the Y-maze more quickly over time, indicating that they had learnt that running down the Y-maze arms was associated with a rewarding outcome (food). However, feed restriction significantly reduced their ability to associate the black and white cues with differences in food quantity. Consequently, average pay-offs in terms of daily feed increments disproportionately accrued to the less feed-restricted treatment groups. It is concluded that feed restriction affected the performance of broiler breeders in this task, perhaps by narrowing their attention such that they ignore potentially hunger-relevant contextual cues. However, low overall group success rates demonstrate that this task was difficult to learn even for less severely feed-restricted birds. Therefore, Y-maze choice tests may not be the most appropriate method for determining hungry broiler breeder dietary preferences.*

Keywords: *animal welfare, broiler breeders, choice test, feed restriction, learning, stress*

Introduction

Hunger is the most pressing welfare issue facing the modern-day broiler breeder. Selective breeding for large appetites facilitates rapid growth in birds destined for consumption but also results in parent stock that must be feed restricted to ensure optimal growth rates. *Ad libitum* feeding regimes are associated with obesity and co-morbid conditions, such as ascites syndrome (Baghbanzadeh & Ducuypere 2008), increased lameness (Kestin *et al* 2001) and reproductive failure (Robinson & Wilson 1996). Thus, it is necessary to feed restrict broiler breeders to 25–50% of *ad libitum* intake (Savory & Maros 1993). However, this results in a bird that experiences chronic hunger for most of its life. By six weeks of age, broiler breeders consume their daily ration within 5–7 min (Savory & Maros 1993), show various behavioural and physiological indicators of stress (Hocking *et al* 1993, 1996; de Jong *et al* 2002, 2003) and are prepared to work for additional feed even when reared on double the recommended ration of feed (Savory *et al* 1993).

A popular scientific approach has been to try to improve satiety by modifying the quality of the feed ration. Low- or non-nutritive fillers, such as ground oat hulls and/or appetite suppressants (eg Zuidhof *et al* 1995; Savory *et al* 1996; Rozenboim *et al* 1999; Vermaut *et al* 1999; Savory & Lariviere 2000; Nielsen *et al* 2003; Hocking *et al* 2004; Hocking 2006; Sandilands *et al* 2006) are added to the ration to try and increase satiety without increasing energy intake. However, the evidence that this improves welfare in broiler breeders is unclear and variable (see: Savory *et al* 1996; Savory & Lariviere 2000; Nielsen *et al* 2003; de Jong *et al* 2005; Sandilands *et al* 2005; Hocking 2006; Sandilands *et al* 2006). Therefore, there is a need for additional methods. D'Eath *et al* (2009) suggested that choice tests could be a valuable additional tool to enable us to identify whether broiler breeders prefer traditional, quantitative or qualitative dietary restriction. Buckley *et al* (2010) used a T-maze closed economy choice test task to determine hungry broiler breeder preferences for quantitative or qualitative dietary restriction. They found that whilst birds easily learnt a food versus no food discrimination task, irrespective of the food type offered, the birds failed to show a preference for either diet in a similar food quality discrimination task. However, the same birds largely failed to learn a food quantity discrimination task. Thus, the authors concluded that the failure to show a preference was indicative of a failure to learn the discrimination task and not a lack of dietary preference *per se*.

One possible explanation for the findings of Buckley *et al* (2010) is that the birds were too stressed or aroused by hunger and that this negatively affected their ability to learn the more complex quantity and quality discrimination tasks. The interaction between stress (whether acute, chronic or both are present) and learning is complex. Experimentally induced chronic stress was found to negatively affect acquisition of food-rewarded cognitive spatial tasks in 75% of the studies examined by Conrad (2010). Nicol and Pope (1993) found that short-term feed restriction reduces social learning in hens which may have implications for any hen social preferences observed. If acute stress is experienced during testing this may also affect cognition by affecting the ability to learn or remember the key features necessary to make an informed choice (Mendl 1999). However, rats (*Rattus norvegicus*) in a Morris water maze performed better when tested in cold, rather than warm, water (Sandi *et al* 1997) suggesting that there is a positive relationship between performance and stressor severity when the task is relevant to removal or reduction of the stressor.

This has implications for feed restriction as a stressor in food-rewarded choice tests that have a strong discriminative and associative aspect to the study design. Hunger is considered to be both a negative stressor (Dawkins 1990; D'Eath *et al* 2009) and a positive motivator (Diano *et al* 2006). Feed-choice tests for hungry broilers are stressor-relevant. Using chronic feed restriction (to maintain 95, 85 and 75% of *ad libitum* bodyweight), Richman *et al* (1970) observed that rats learnt two different (but similar) food versus no-food T-maze tasks faster the greater the difference between their actual and *ad libitum* bodyweight (ie the more feed restricted the rats were the quicker they learnt the task). This suggests that hungry animals would learn a food-rewarded discrimination task more quickly than a sated one. In previous work (Buckley *et al* 2010), we found that chronically food-deprived broiler breeders easily learnt a food/no food T-maze task, but most failed to learn a task in which both options were rewarded but with different food quantities. However, discriminative tasks in which both options are rewarded are generally considered to be more difficult to learn than reward/no reward tasks (Capaldi & Molina 1979). Research by Yerkes and Dodson (1908) indicates that the more difficult the task, the lower the arousal level that is required for optimal learning. Thus, direct choice tests where the broiler breeder has to learn a feed-quality discrimination task may fail if the bird is trained and tested under the conditions of feed restriction in which such a preference could be welfare-relevant. Therefore, there is a need to identify the effects of feed restriction on broiler breeder ability to learn a feed discrimination task in which both options are differentially rewarded.

The present study investigated the ability of broiler breeder chickens (*Gallus gallus domesticus*), reared on three different levels of feed restriction, to learn a complex feed quantity discrimination task. It is assumed that birds prefer a larger over a smaller quantity of feed, which means that 'success' can be measured as number of choices for the larger feed reward. It was hypothesised that the degree of feed-restriction-induced arousal will alter task learning ability and the maintenance of the learnt response. It was predicted that there would be a negative relationship between the degree of feed restriction and bird performance in the discrimination task due to its complexity. The latency of birds to make a choice was also measured. It was predicted that birds would become faster at making a choice as they learnt to associate the ends of the Y-maze arms with the presence of feed.

Materials and methods

Subjects

Fifty-two Ross 308 broiler breeders were obtained as day-old chicks. At 14 days, the birds were ranked and blocked according to weight and randomly allocated to a treatment (level of feed restriction). The four treatment groups were: *Ad libitum* (n = 16); Eighty% (n = 12); Forty% (n = 12); and Control (n = 12). The *Ad libitum* birds were used only to establish *ad libitum* intake and did not take part in the choice test training/testing.

Housing and husbandry

Birds were spot-brooded in five groups (n = 16 each) until day 14 in 1 × 1 m (length × width) pens containing wood shavings, a perch and a drinker allowing *ad libitum* access to water. From day 14, birds were individually housed (two rooms, 26 pens in each room, with treatments equally distributed across both rooms) in pens 0.5 × 1.0 m with visual access to another bird (from the same treatment to reduce stress that could result from differential bird size or access to feed). Producer recommendations for lighting/heating were followed with a gradual reduction in light hours (from 23 h on day 1 to 8 h on day 10) and heating (from 31°C on day 1 to 21°C on day 21) (Aviagen 2006). However, shed temperatures frequently exceeded recommendations during the last few study weeks due to external ambient temperature: (mean [± SD])/maximum/minimum temperature, 23.4 (± 2.1)˚C/33˚C/19˚C and 22.1 (± 1.8˚C)/32˚C/19˚C for rooms 1 and 2, respectively.

Nutrition and feeding

Feed type

Birds were fed a standard broiler starter crumb (Laser SP Starter Crumb, BOCM Pauls Ltd, Ipswich, UK) containing 205 g crude protein (CP) kg^{-1} and 12.5 MJ ME kg^{-1} until day 28. They were then switched to a custom-made grower mash diet (Target Feeds Ltd, Whitchurch, UK) containing 150 g CP kg^{-1} and 11.5 MJ ME kg^{-1}. After switching, poor diet acceptance rapidly reduced growth rate and increased within-group bodyweight coefficient of variance (CV). The reason for this poor acceptance was unknown but likely to relate to an aspect of diet quality. Consequently, birds were switched back to the original diet on day 33 and fed this for the remainder of the experiment.

Feeding regime (day 1–41)

All birds were fed *ad libitum* during the first week and a restricted allowance during the second according to producer recommendations (Aviagen 2007). From 14 days, birds were fed according to their treatment protocol. *Ad libitum* birds were fed *ad libitum* for the study duration. Feed intake was measured once daily between 0800–0845h via a weigh-back technique to ascertain feed intake for the previous 24-h period. For all other treatment groups, birds were fed once daily at 0845–0915h until day 42. All birds were individually weighed daily at 0800–0900h (before being fed) until day 49 and twice weekly thereafter. The Control group were fed to maintain them on the recommended growth curve for Ross 308 broiler breeders reared to have 5% egg production at 25 weeks of age (Aviagen 2007), with quantities adjusted as necessary. This is the most common rearing strategy adopted worldwide by producers of Ross 308 parent stock. The average feed intake per bird per day was calculated daily for the *Ad libitum* and Control birds and used to calculate feed allowance for birds in the Forty% and Eighty% groups. Therefore, the Control group experienced the most severe level of feed restriction, The Eighty% group the least severe and the Forty% group were intermediate between these two groups.

Individual birds in the Forty% and Eighty% groups received an allowance according to the following formula:

Allowance = mean control intake + (P × [mean *ad libitum* intake – mean control intake])

Mean intake refers to intakes recorded on the previous day and the P-values were 0.4 and 0.8 for the Forty% and Eighty% treatments, respectively.

The formula was used instead of using the more simple approach of either calculating feed intake for the different feed-restricted treatment groups as a proportion of *ad libitum* intake or as a multiple of the commercial quantity of feed restriction. The rationale for adopting this approach was to ensure that the relative degree of feed restriction was constant between groups at all times.

Feeding regime (day 42–72)

Between days 42 and 48, the Control, Forty% and Eighty% birds were fed 1/5 of the Control birds' daily ration five times per day at 75-min intervals in preparation for training and testing. The Forty% and Eighty% birds were fed the remainder of their feed allowance at the end of the day. Unconsumed feed was removed between 2000 and 2200h and added to the same bird's end-of-day ration the following day. This was only necessary occasionally for some Eighty% birds and was never needed for the Forty% birds. This feed removal protocol was maintained until the end of the study.

Experimental apparatus

Both rooms housed an identical experimental set up. The experimental apparatus comprised a plywood Y-Maze (see Figure 1 for dimensions) and 12 wooden goal boxes (pens containing a food bowl) with manually operated trapdoors. The food bowls were circular (diameter: 18 cm, height: 6 cm, volume: 0.5 L) allowing immediate visual assessment of the quantity of feed contained by the relative amount of the base of the bowl that was covered by feed. The Y-Maze was mounted on castors to make it easy to move, allowing rapid sequential testing of several birds. The arms lined up with the goal-box openings. Each bird had access to the same two goal boxes during each free-choice trial. The start pen had an opaque roof and a clear Perspex trapdoor. Removable painted wooden inserts fitted the insides of both arms, which allowed either arm to be coloured black or white. A camera was attached by a rod to the back of the start box and angled to allow all activity that occurred in the Y-maze (excluding the start box) to be observed. The camera was connected by cable to a DVR system (Xvision, Croydon, Surrey, UK) that was remotely located in a separate room.

Testing procedure

General procedure

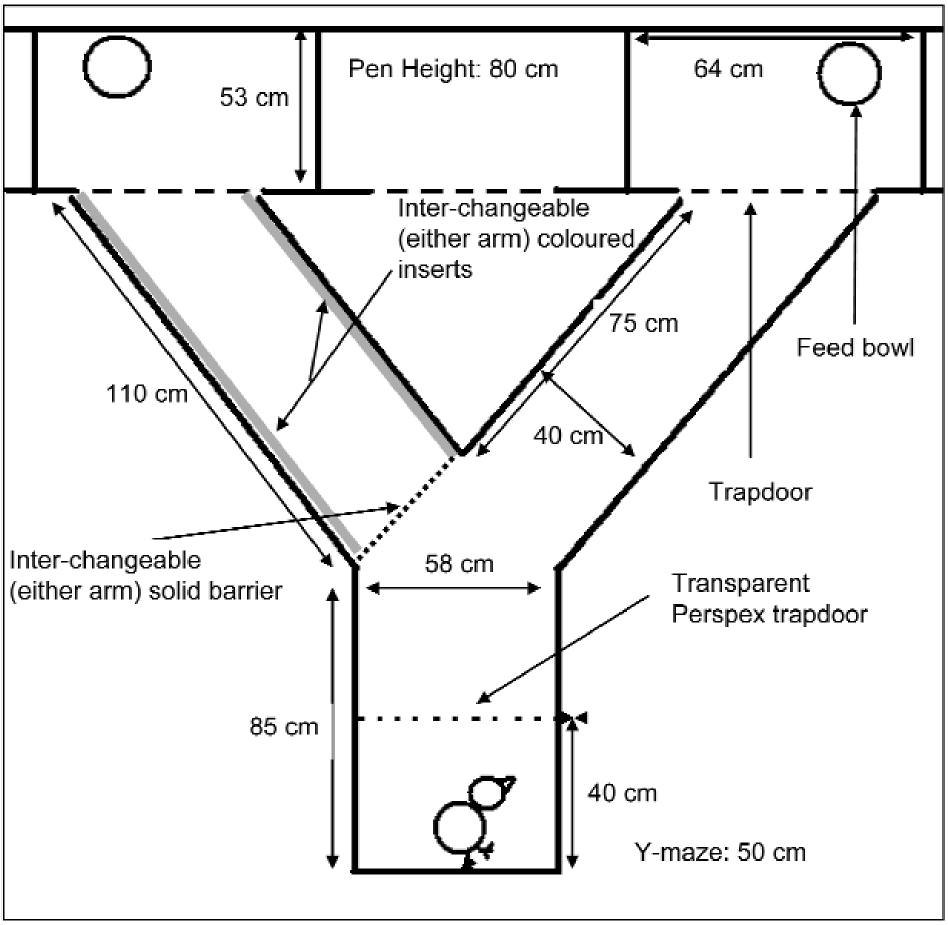
The task was to associate the black and white arms of the Y-maze with large and small food rewards (or *vice versa*). The black arm was associated with the larger reward for half of the birds (selected at random within treatment) and with the smaller reward for the remainder. The feed rewards were supplied within the goal boxes (one reward per goal box, with the feed supplied in identical bowls).

The two dietary rewards were 1/5 of the Control bird's daily ration + or –25% (12 versus 7.2 g, average pay-off if no preference was shown: 9.6 g per trial). These quantities were modified after the 20 forced trials (4 days) and 60 free-choice trials (12 days) had been completed to 1/5 of the Control bird's ration at 67 days + or –50% to increase the contrast between the two options and recruit additional 'successful' birds (15 vs 5 g, average pay-off if no preference was shown: 10 g per trial). Learning the colour-portion quantity association enabled birds to supplement their diets by an additional maximum of 12.5 g per day (trials 1–60) and 25 g per day (trials 61–100).

Each bird was given five trials per day (75 min apart). Birds were held in the start box for 30 s prior to release. Each trial ended with entry into one of the goal boxes which was then closed and the bird given approximately 20 min to consume the ration. The end-of-day ration was unaffected by individual performance during trials.

Any of the feed in the goal box that was chosen by the bird but not consumed during each trial, irrespective of whether the larger or smaller option was selected, was added to the end-of-day ration of that individual bird. The feed associated with the option not chosen by the bird was discarded.

Figure 1



Experimental set-up showing Y-Maze and test pen (goal box) dimensions (not to scale).

Although this was not recorded systematically, it was noted that Control birds never left feed obtained on the daily trials, while birds in the Forty% group occasionally left a 'fine covering' and the Eighty% group frequently left substantially more (even when the portion of feed obtained was the smaller of the two possible options).

Test apparatus habituation

Days 42–48: Each bird was given five 20-min exploratory sessions (once daily for five days) within the Y-Maze to habituate them to the apparatus. Part of the birds' daily feed allowance was sprinkled throughout the maze to encourage exploration.

Forced-choice trials

Days 49–52: Birds in the treatment groups Control, Forty% and Eighty% were each given 10 white runway forced trials and 10 black runway forced trials over the four days. These were balanced to ensure that the birds experienced the black arm and the white arm on the right side of the maze five times and *vice versa*. The feed quantities associated with the black and white arms and the feeding protocol are outlined in the general procedure section above.

Free-choice trials

Days 53–72: Birds experienced 100 free trials in which the bird could choose which Y-maze arm to enter. All other conditions (including feed quality and availability) remained the same. Feed quantity and contrast was increased after 60 free trials.

Measurement of latency to enter a goal box

All trials (forced and free) were video-recorded for later analysis of latency to make a choice. Latency to make a choice was measured from the time point at which the Perspex barrier was lifted until the time point the bird's head reached the feed bowl located in the one of the two goal boxes (measured in s).

Six days of free-choice footage were selected for analysis. These were days 53 and 54, days 61 and 62 and days 69 and 70, representing the start, middle and end of the test period. Latencies were recorded for all trials that occurred on these days. All latency measurements were carried out twice by the same person. Where a difference between recorded latency occurred (< 10% of clips watched), the clip was viewed a third time and the mean of the two closest measurements recorded. Where a difference was observed this was never more than 1 s.

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Statistical analysis and blocking

Blocking

Treatments were balanced across the two rooms. Within room, birds (n = 18) were blocked into three groups (n = 6) (balanced for treatment/colour-diet quantity combination) and testing order initially randomised within block (this order was maintained for the study duration).

During free trials, within-bird trials were grouped into blocks of 20 consecutive trials. Within blocks, trials were balanced for colour/side presentation with order of presentation randomised within and between birds.

Success criterion

Individual birds were defined as having learnt the task if they choose the larger feed reward ≥ 15 out of 20 times per trial block ($P \leq 0.042$, individual binomial probability). In the analysis of the effect of colour combination on task success, only data recorded in blocks during which birds had learnt the task were included.

Statistical analysis

Individual bird performance was analysed using Probability Distribution Calculations for Binomial data. The Generalised Linear Mixed Models (GLMM) statistical test (logit-transformed binomial distribution, Schall method) was used to analyse dietary treatment level performance and to generate logit-transformed predicted means (group means per phase and overall performance). The variable of interest was 'food option chosen' and the fixed effects investigated included treatment, phase (1–2), trial block (1–5), room, and colour associated with the larger food option. Bird was used as the random effect (with trial nested within bird). Phase one represented the first 60 free-choice trials (trial blocks 1–3), phase two the last 40 trials (trial blocks 4–5) and overall performance all 100 free-choice trials (trial blocks 1–5). The statistical package used was Genstat version 11.1 (VSN International Ltd, Hemel Hempstead, UK).

Using the logit-transformed predicted means, *post hoc* group analyses of differences from 0.5 were calculated using χ^2 to compare for differences from 0 at 1 degree of freedom using a Chi-squared (χ^2) distribution table (Petrie & Watson 1999). Due to the unplanned removal of one Eighty% bird after 60 trials, 'success' data was transformed from number of birds to proportion of birds that met the individual success criterion/treatment group before graphical representation.

A Linear Mixed Model was used to investigate effects of treatment on latencies and comparisons between latencies at the start, middle and end. Within group tests to compare changes between latency at the beginning and end of the study were performed using the matched-pairs Student's *t*-test. Two birds in the Eighty% group were excluded from the latency analysis due to either incompleteness of data (one bird) or aberrant behaviour (latency increased during the experiment, probably due to leg problems).

Ethical considerations

This study was carried out under the Animals (Scientific Procedures) Act 1986 and approved by the Scottish Agricultural College's and Roslin Institute's ethics committees. The Home Office Code of Recommendations for the housing of poultry was met or exceeded at all times. Birds were euthanised by an approved Schedule One method (barbiturate anaesthetic overdose). The relevant predetermined humane end-points used in this study were as follows: (i) birds weighing less than 90% of the target commercial weight at any stage were to be fed supplementary feed and any that failed to gain sufficient weight by supplementary feeding were to be euthanised (no birds were euthanised on this basis); (ii) although this study was designed to finish before birds would reach high bodyweights and associated problems, such as lameness and respiratory problems, and birds showing signs of such problems were to be removed from the study and euthanised: one bird (Eighty% group) was removed due to lameness, two birds (*Ad libitum* group) due to lameness and the study was terminated 4 days early (day 72) because of thermal discomfort related to high room temperatures.

Results

Treatment growth curve and feed intake

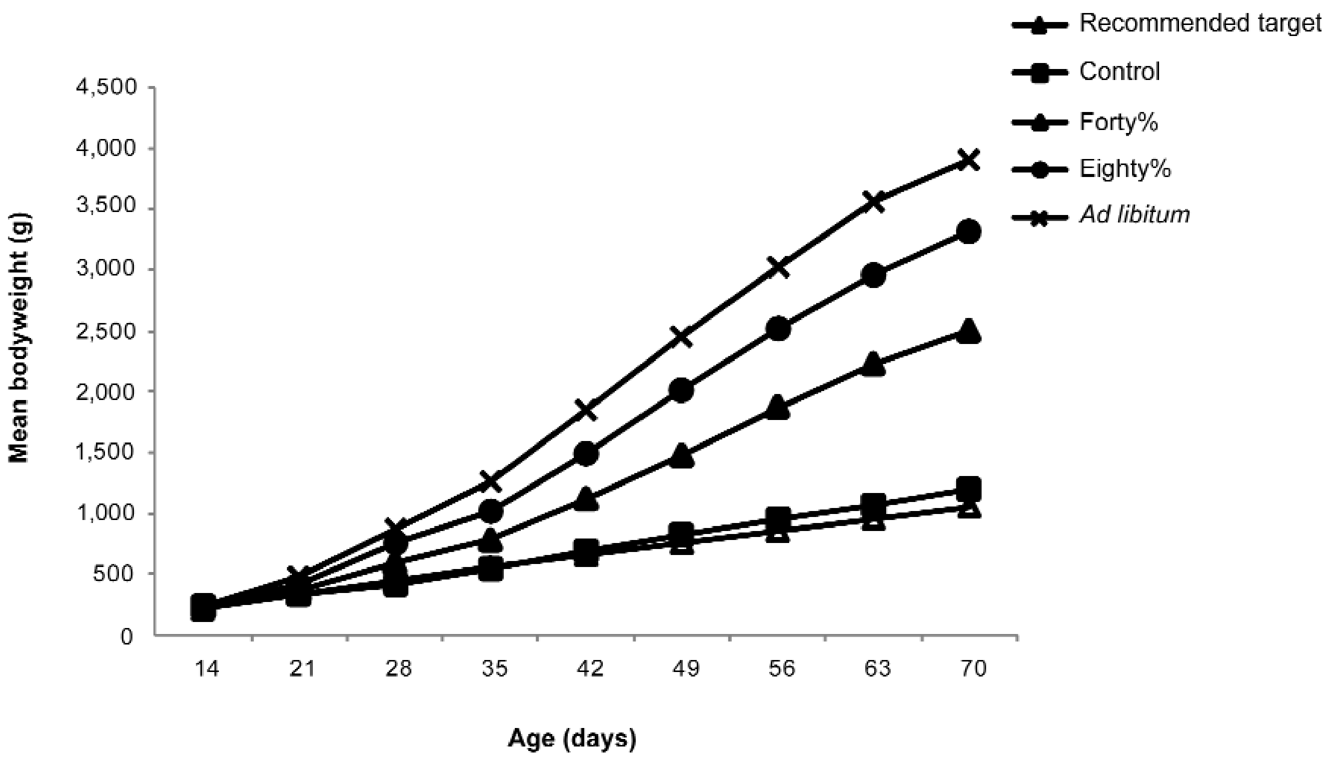
The growth curve of the control birds was similar to that of the producer's recommended target growth rate up to the start of the trial at 49 days of age (Figure 2). Birds on all treatments were successfully reared to their target growth curves, with only a small amount of variation. The mean (± SEM) coefficient of variation (CV) across time points and standard deviation associated with each treatment group was: *Ad libitum* group: 5.2 (± 0.9)%; Control group: 4.7 (± 1.5)%; Forty% group: 3.8 (± 1.3)%; Eighty% group: 5.0 (± 1.7)%. No overlap in bodyweights between groups was observed between days 21–70. This CV was small and well within producer recommended standards (Aim: < 12%; Aviagen 2006).

The average daily intake of the *Ad libitum* birds increased from an average of 46.3 g on day 14 to 235.1 g on day 70. During this same period, the average daily feed allocation to the Control birds increased from 29 to 50g.

Effect of treatment and stage of testing on latency to enter a goal box

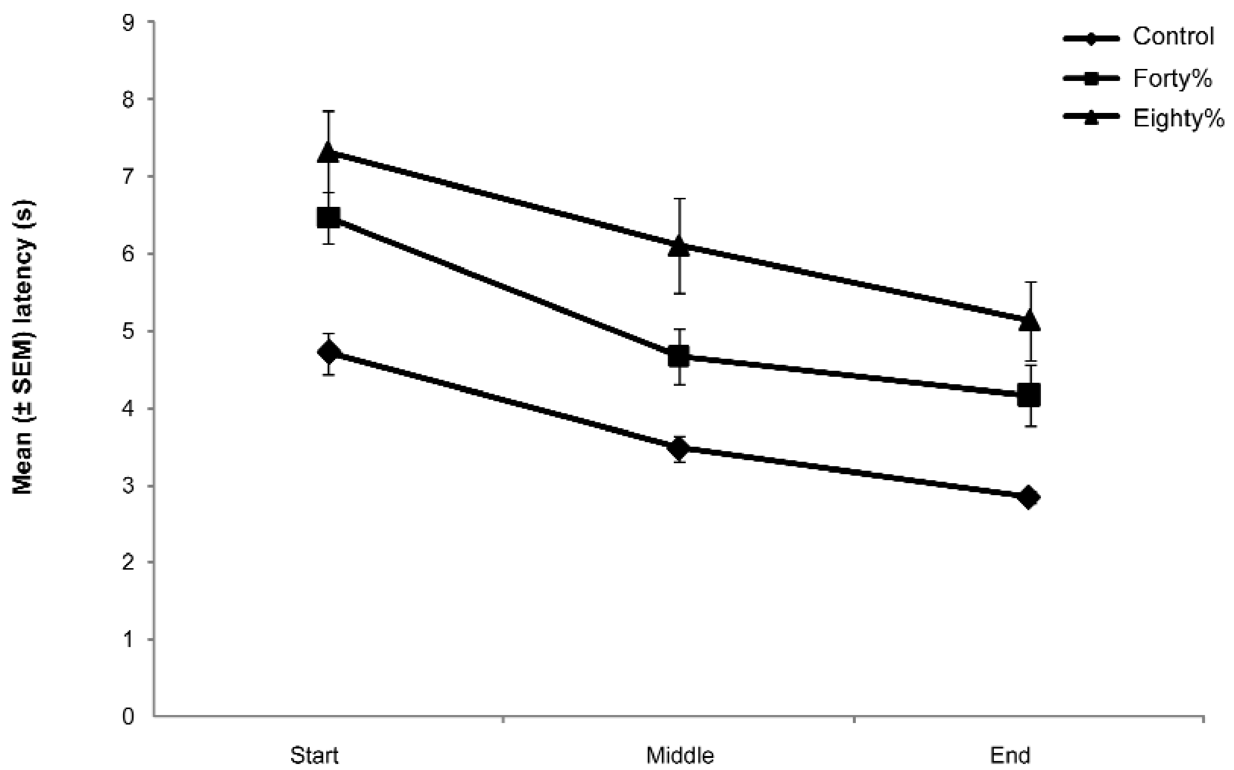
Treatment ($F_{2,31}$ = 12.84, $P < 0.001$) and stage of testing (start/middle/end) ($F_{2,62}$ = 103.8, $P < 0.001$) affected latency to enter a goal box but there was no interaction between treatment and stage of testing ($F_{4,62}$ = 1.13, $P = 0.352$). *Post hoc* testing using a series of paired Student's *t*-tests indicated that birds from all treatment groups ran faster as they learnt to associate the ends of the Y-maze with food (Eighty% group, $t = 6.48$, df = 9, $P < 0.001$; Forty% group, $t = 8.51$, df = 11, $P < 0.001$; Control group, $t = 7.11$, df = 11, $P < 0.001$). However, as can be seen from Figure 3, the more severe the feed restriction the faster the birds ran at all stages of testing.

Figure 2



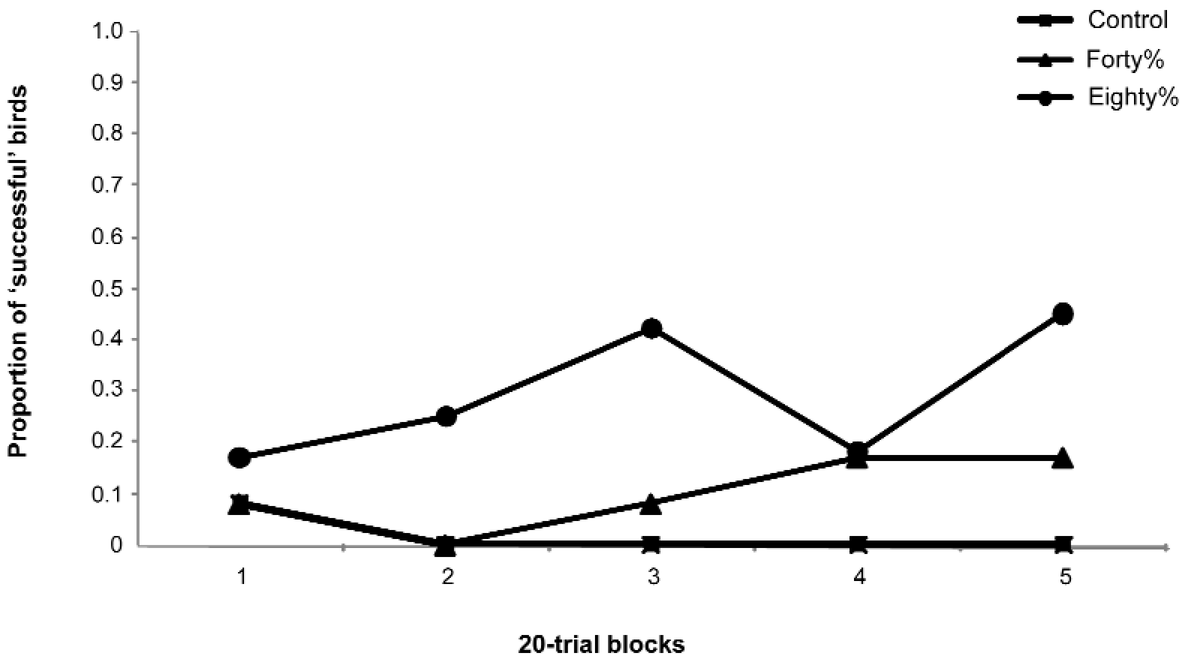
Bodyweight (g) by broiler breeder age and treatment group. Recommended target represents the producer's recommended target growth rate for feed-restricted broiler breeders grown to have 5% production at 25 weeks of age (shown for comparison). No error bars are shown as the SEM was so small as to be graphically indiscernible. The average SEM for each treatment was as follows: *Ad libitum* group = 23 g; Control = 25.5 g; Eighty% group = 25.6 g; Forty% group = 25.5 g.

Figure 3



Latency to enter goal box by treatment and stage of testing. Two Eighty% birds were omitted from the analysis (see text).

Figure 4



The proportion of birds by treatment and block achieving ≥ 15/20 choices for the larger food option (ie 'successful' birds). A score of 15/20 was associated with $P = 0.042$ (binomial probability). n = 36; n = 12 per treatment (for Eighty% n = 11 for blocks 4–5 as one bird was euthanised).

Effect of treatment on ability to learn task

Overall, six Eighty% birds, three Forty% birds and one bird in the Control group were considered to have learnt the task. One Forty% bird and one Control bird achieved this criterion on the first or first and second free-choice testing blocks but subsequently performed no better than chance for the remainder of the blocks.

A significant preference for the smaller reward option was never observed in any of the 180 individual blocks (36 birds × 5 blocks). Furthermore, only one Control bird was successful, in trial block one only, but two Forty% and five Eighty% birds (not including one successful Eighty% bird that was euthanised earlier in the study) were successful at the same time.

Analysis of group performance indicated that treatment affected the ability of the birds to learn the task ($F_{2, 30.8} = 4.88$, $P = 0.014$). *Post hoc* analysis revealed that, at the group level, only birds in the Eighty% group showed a preference for the larger feed option over the first sixty trials (Phase one)($\chi^2 = 8.16$, $P < 0.01$), the last forty trials (Phase two) ($\chi^2 = 6.76$, $P < 0.01$) and across all trials ($\chi^2 = 8.60$, $P < 0.01$). The other treatment groups showed no preference. There were no significant effects of room ($F_{1, 29.2} = 0.12$, $P = 0.729$) or colour associated with the larger food reward on the performance of successful birds ($F_{1, 6.7} = 2.4$, $P = 0.167$).

Effect of level of feeding motivation on maintenance of response once learnt

Using all bird data, there was no effect of number of free-choice trials (analysed in blocks of twenty consecutive trials) on performance ($F_{4, 279.2} = 0.43$, $P = 0.788$) and no interaction between treatment and block number ($F_{8, 348.6} = 0.60$, $P = 0.775$) with the average treatment performance remaining similar across all blocks of twenty trials. The numbers of 'successful' birds were too low to repeat the analysis using only these birds. Figure 4 shows the proportion of birds in each treatment group that were successful over each of the five consecutive blocks.

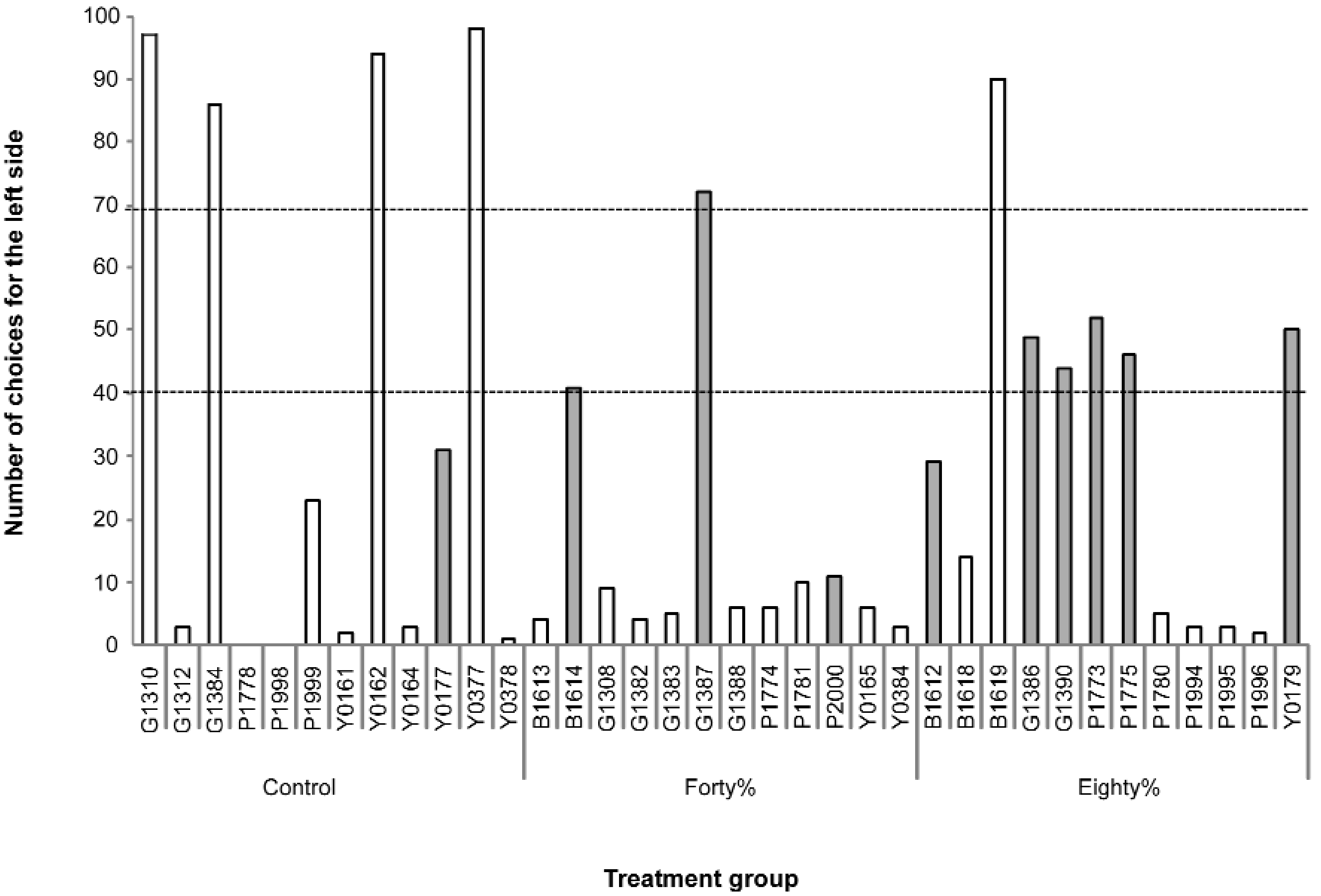
Due to a lack of sufficient individuals within each treatment group meeting the task criterion for success, it was not possible to investigate the effect of feeding motivation on maintenance of the learnt response.

Effects of Phase one and Phase two on performance

A comparison between group (ie analysed at the treatment group level) bird performance in Phase one and Phase two demonstrated that there was no significant increase in performance across these two phases ($F_{1, 91.7} = 0.11$, $P = 0.737$) and no interaction between phase and treatment group ($F_{2, 92.2} = 0.09$, $P = 0.910$).

One additional Forty% bird achieved the inclusion criteria during Phase two in which there was a greater contrast between the feed rewards. Three of the six 'successful'

Figure 5



Prevalence of side biases over the 100 trials, as indicated by the number of choices for the left side of the Y-maze, according to each individual bird in each treatment group. The grey bars indicate the birds that met the criterion for success (picking the larger option ≥ 15/20 times in a single block) and the white bars indicate that they did not meet this criterion. The study was balanced such that the larger diet option could be found at the end of the left and the right arm of Y-maze an equal number of times. The dashed lines indicate the highly significant (*P* < 0.001) threshold (< 34/100 choices for the left side or > 66/100 choices for the left side). NB Bird P1773 (Eighty% group) was euthanised after 60 trials. Her number of choices have been adjusted (original: 31/60) and all results are therefore expressed as a proportion.

Eighty% birds showed a temporary decline in performance during the first 20-trial block in Phase two but all three birds showed a significant preference (≥ 15/20 choices for the larger feed reward) by the second 20-trial block in Phase two.

Side biases

Side biases were prevalent with most birds (n = 30) demonstrating a highly significant side preference (ie they selected their preferred side more than 66 times out of 100 trials, $P < 0.001$). Figure 5 illustrates the severity of the side biases where present with most birds picking their preferred side on more than 90% of all trials.

All of the birds that did not meet the criterion for success (n = 26) demonstrated a highly significant side bias ($P < 0.001$). Of the birds that did meet the 'success criteria', four also showed a highly significant side preference ($P < 0.001$).

An analysis of the two birds that met the inclusion criterion initially but then lost this preference indicated that the birds deviated from their chosen side preferentially to select the colour associated with the larger feed reward. The Forty% bird deviated from her preferred side (right side) nine times in 100 trials, in all cases when the larger feed reward was on the left side (9/9 deviations occurred when the larger food reward was associated with the left side; $P = 0.02$).

The Control bird that initially met the inclusion criteria significantly preferred the right side overall (69 choices for the right side; $P < 0.001$). Over the first five days of the free-choice tests (she met the success criterion in block one, days 1–4) she deviated from the right side only when the left side was associated with the larger feed reward (8/8 deviations; $P = 0.008$).

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Discussion

The data indicated clearly that chronic feed restriction negatively affected the birds' ability to learn a complex feed quantity discrimination task. However, feed restriction did not totally prevent the birds from learning anything. Rather, it influenced what was learnt. The birds entered a goal box faster (irrespective of treatment) with time indicating that the all birds learnt to associate the end of the Y-maze with a positive outcome (food) and that there was an increase in associative strength with the number of trials. Increased speed seems unlikely to be due to larger birds being able to run faster (since the size of the birds increased over the experiment; see Figure 2). In support of this, it was noted that the weight of the Controls at the end was similar to the Forty% birds at the start of the trial but the latency was shorter in the Controls at the end compared to the Forty% birds at the start. Thus, in the absence of learning the association, the default strategy of 'unsuccessful' birds appeared to be to access feed as quickly as possible.

These findings are interesting when placed in the context of other research that has investigated the effect of feed restriction on cognitive processes (eg Nicol & Pope 1993; Diano *et al* 2006; Ferreira *et al* 2006; Deng *et al* 2009). Broadly speaking, the effects of feed restriction can be divided into two areas: firstly, those caused by nutritional stress (specific nutritional deficits having effects on the animals physiological status) and, secondly, those caused by psychological stress (the experience of hunger). The broiler breeders in our study were experiencing different degrees of feed restriction from two weeks of age. In a review of the cognitive effects of early malnutrition, Strupp and Levitsky (1995) report that early nutritional stress is associated with increased emotional reactivity, cognitive inflexibility, and attentional changes with a more narrow focus of attention that endures post malnutrition. These suggest that malnutrition is associated with changes in neuronal development, so this is a plausible explanation for our findings. However, it is important to note that commercial broiler breeders are feed restricted to levels equivalent to our controls to optimise physical health and no other physical signs of mal- or under-nutrition have been identified. Although it remains possible that there are negative effects of feed restriction on broiler-breeder cognition, despite the birds being in good health, it seems more likely that treatment differences in this study resulted from hunger stress rather than direct nutritional effects on brain development.

Most studies using feed restriction as the psychological stressor or motivator do not use food-rewarded tasks when examining the effects of feed restriction on learning and memory. This is presumably because as feed restriction increases the motivation to obtain food (Conrad 2010), the hunger-stress and motivation effects on performance would be confounded. Where food has been used as a reward, the task has been a simpler food/no food reward paradigm. In such cases, a positive association was found between the degree of feed restriction and task acquisition, because of the effect of restriction on motivation (Eisman *et al* 1956: deprived of food for 4 h, 22 h and 45.5 h before training; Richman *et al* 1970: adult rats feed restricted to maintain 75, 85 and 95% of *ad libitum* feed bodyweight). To the authors' knowledge, there is no published research looking at the effect of feed restriction on ability to learn a feed-restriction-relevant complex discrimination task in which both options are food rewarded. This may be due, in part, to the confounding variable of learning ability and motivation in this type of task. However, there are relatively few studies that ask an animal to learn a discrimination task in which both options are rewarded. However, there are occasions in which this approach may be appropriate and determining the preferences of feed-restricted broiler breeders for qualitative or quantitative dietary restriction is one of these. The effects of feed restriction on broiler-breeder learning ability could have been quantified in a non-food-rewarded paradigm. However, the results of this approach may not have translated into learning ability when faced with a task that is likely to be highly arousing to severely feed-restricted birds.

The Yerkes-Dodson Law predicts that the optimal arousal level for learning difficult tasks will be lower than for simple tasks (Yerkes & Dodson 1908). Whilst this study was not an explicit test of the Yerkes-Dodson Law, the results partially support this interpretation: a lower level of arousal (ie a lower level of chronic feed restriction) was necessary for successful learning of this complex task. By comparison, in a previous study (Buckley *et al* 2010), more severely restricted birds (equivalent to the Controls in this study), were able to learn a simpler food/no food task.

In some studies, using non-food rewarded tasks in rats, different levels of chronic feed restriction resulted in an inverted U-shape relationship with learning or memory or both (Ferreira *et al* 2006; Deng *et al* 2009). Ferreira *et al* (2006) compared memory and learning in rats chronically feed restricted to 70 and 40% of *ad libitum* intake with rats fed *ad libitum* throughout the study. They found that feed restriction improved learning but that the less severely feed-restricted rats showed evidence of more rapid avoidance learning and showed improved memory of this learning than either the *ad libitum* or 40% feed-restricted rats. Deng *et al* (2009) found that mild feed restriction (80% of *ad libitum* intake) resulted in improved long-term memory, whereas it was unchanged from *ad libitum* performance in rats feed restricted to 40 and 20% of *ad libitum* intake. Different levels of injected *ghrelin* (an appetite-stimulating hormone) produced similar effects when mice (*Mus musculus*) were tested on T-maze tasks (Diano *et al* 2006). This indicates that cognitive processes are sensitive to the degree of feed restriction. Further, synapsin-deficient animals (synapsin proteins are associated with learning and memory) have been shown to be memory-impaired (see, for example, Michels *et al* 2005; Porton *et al* 2010). Deng *et al* (2009) found that synapsin production was up-regulated with relatively mild feed restriction (80% of *ad libitum* intake), similar to *ad libitum* levels at 60% restriction but down-regulated with increasingly severe feed restriction

(40 and 20% of *ad libitum* intake). However, in the present study, there was no evidence of an inverted U-shaped pattern to task-learning ease. Instead, the relationship was linear: the less hungry the bird, the greater the likelihood that it would learn the task. This was interesting because although the 80% group were the least 'hunger-stressed' they would also have been the group least motivated by a food reward. It is possible that this inverted U-shaped curve could have been observed if *ad libitum*-fed birds had been used in the choice test but this seems unlikely. The 'successful' birds in the 80% treatment group frequently did not eat the entire portion of feed they had access to which suggests that, although motivated to access food rewards, these birds were not as hungry as the other treatments. Low levels of arousal may partially explain why half of the 80% group failed to learn the task. However, overall, the least hungry birds found the task easiest to learn.

In our study, we believe that the birds on different treatments differentially experienced hunger-stress. Although we did not formally measure either physiological or behavioural indicators of stress, there is sufficient scientific evidence to support this interpretation (eg Hocking *et al* 1993, 1996; de Jong *et al* 2002, 2003). In agreement with these reports, we observed spot-pecking, stereotypic behaviour (pacing) and excessive drinker manipulation in our control birds indicating that the birds were frustrated by being feed restricted. It is considered that, in addition to the chronic stress of feed restriction, the birds also experienced acute arousal during training/testing (due to the association between the apparatus and food). Acute stress or arousal may enhance learning where there is convergence in time between the stressor and the learning task and where learning the task removes the stressor (Joels *et al* 2006, but see Schwabe & Wolf 2010). However, chronic stress is a potent negative barrier to effective learning and memory (Joels *et al* 2006; Conrad 2010). Severe levels of chronic feed restriction (50% of *ad libitum* intake) are associated with poor cognition in juvenile rats (Young & Kirkland 2007). This level of feed restriction roughly approximates to our 40% group during training/testing. The Control group were considerably more feed restricted (circa 25–33% of the intake of *ad libitum*-fed birds of the same age).

In our study, the task was food rewarded and therefore relevant to reducing the stress of feed restriction. This aspect should have increased the likelihood of the birds learning the task. The potential relative gains (proportional extra daily feed allowance) were higher for the Control group. Therefore, these birds had a much greater incentive to learn. However, this was not realised in terms of performance in the Y-maze.

Schwabe *et al* (2010) point out that stress affects both the quantity and quality of the learning experience. Stress affects the quantity of information processed in various ways that lead to both increased and reduced performance in cognitive tests dependent upon what is measured (Mendl 1999). The quantity of information processed by the birds may have been negatively affected by chronic feed restriction in several ways.

Firstly, the birds may have experienced attentional narrowing. Attentional narrowing can be defined as focusing of attention on the central features of a task or event whilst ignoring more peripheral or less salient features of the same task or event (see Mendl 1999). Severe chronic feed restriction in growing rats leads to a failure of the rats to attend to environmental stimuli (reduction in perceptual learning) that were apparently unconnected to immediate biological needs (Rogers *et al* 1986). Stress also decreases attendance to 'redundant' cues (cues that are introduced to a training situation which provide no additional information regarding the correct response; Levitsky [1979], reported by Rogers *et al* [1986]). These studies indicate that 'attentional narrowing' can occur under conditions of stress. Easterbrook (1959) highlights that when peripheral cues are important for task performance, ignoring these cues leads to performance error. However, it is also possible that, in our study, the birds that failed the task did so because they attended to too many cues and, therefore, failed to sufficiently attend to the cues that were relevant to learning the task.

Secondly, Mendl (1999) suggests that stress/arousal may increase errors by speeding up decision-making such that the animal does not attend to all the relevant information before making a decision. Although birds were given an enforced period of observation before making a decision (30 s in the start box) the birds may have attended more to the Perspex barrier between them and food and only attended to runway stimuli once released. In our study, the hungriest birds ran faster, probably reflecting their greater motivation. Therefore, these would have had less time to assimilate the colour information.

Finally, holding birds in the start box for 30 s prior to release may have further increased arousal resulting in a concurrent reduction in learning. Van Rooijen and Metz (1987) found that feed-restricted pigs (*Sus scrofa*) working for food in a food/no food T-maze task failed the task when held in the start box for 5 min. Reducing the time to 30 s significantly improved performance (although this was confounded with the additional number of trials). Thus, holding the birds for less time might have improved performance. However, we consider this unlikely as the birds (especially controls) were highly aroused generally and focused on trying to escape both the home pens (prior to testing) and the start box. Therefore, we think it is more likely that they simply did not process the relevant information prior to release from the start box.

It is likely that the poor performance also reflected changes to the quality of learning. The default strategy of all birds that failed to learn the task was to show a positional bias irrespective of treatment. Chickens have been demonstrated to show low levels of spontaneous alternation (Hughes 1989; Haskell *et al* 1998). Increased perseverance in this study was reinforced by the provision of a food reward. With hindsight, this was a study weakness that could be addressed in any future work utilising a Y-maze, through the use of forced trials and occasional 'probe' choices in which the animal could choose which arm to enter. Nonetheless, positional biases were more common among the hungrier treatments.

The stress of feed restriction may have reinforced the tendency to persevere as a function of habit. Hunger stress has been associated with positional biases in both pigs (Van Rooijen & Metz 1987) and starlings (*Sturnus vulgaris*) (Talling *et al* 2002). Shocking mice upon entry to one of the goal boxes in a T-maze reduced stimulus-response learning (avoidance of shocks) and increased habitual responding that resulted in increased exposure to electric shocks (Mitchell *et al* 1985). In food devaluation studies, stressed humans show a habitual, rather than a goal-directed, strategy (Schwabe & Wolf 2009). In our study, one Control bird and one Forty% bird initially showed a significant preference for the larger reward in the first trial block after the forced trials but then developed strong side biases. The pattern of deviations from the preferred side suggests this initial preference was genuine and not due to chance. As the trials progressed, it is expected that the level of feed restriction became increasingly severe. Stress-induced habitual learning may have resulted in the much poorer performance in subsequent trial blocks, including reluctance to change behaviour even when quantity contrast was increased.

Despite the fact that feed restriction did affect the birds' ability to learn the task in this experiment, it is also clear that it was difficult to learn even for birds in the least feed-restricted group. It is not clear why. However, several factors may have affected this: the tendency of chickens to show low spontaneous alternation (Hughes 1989; Haskell *et al* 1998), combined with the free-choice methodology in which side biases were reinforced by food rewards may have stimulated the likelihood of side biases. Alternatively, insufficient trials, inter-trial length (but see Sarason *et al* 1956; D'Amato 1960) or absolute or relative food quantities (the smaller the contrast the more difficult discrimination will be and the longer the task takes to learn: see Hill & Spear 1963; Clayton 1964) may have affected performance. However, it is worth noting that most of the 'successful' birds had learnt the task within 60 free-choice trials. Alternatively, a species-specific difficulty associating relatively distal colour cues with food quantities rather than food location *per se* could have affected task performance. However, Phillips and Strogan (2007) found layer hens could associate feed qualities with colours with far fewer trials, suggesting that the task was potentially learnable. Combined with our previous work (Buckley *et al* 2010), this study suggested that the free-choice Y-maze method used here would not be particularly useful in evaluating broiler breeder preferences for qualitative or quantitative dietary restriction.

Animal welfare implications and conclusion

Chronic feed restriction is a potent stressor that negatively affected broiler breeder performance in this complex task, even though the task was relevant to removal of the stressor, a factor known to improve task success. Therefore, most of the birds did not express a preference for a larger food reward in this choice test. This study further demonstrates the negative effects that commercial feed restriction has on broiler breeders, in this case by reducing the broiler breeders' performance in a food-quantity discrimination task. Although the mechanism leading to reduced performance is unclear, in the wider context, this may provide additional support for the concerns (Mendl 1999) that, firstly, stressors may render choice tests for identifying 'wants' problematic and, secondly, stressors may negatively affect an animal's ability to function in its environment by reducing its ability to assimilate information favourable to its welfare.

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