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TEMPORAL PATTERNING OF ORAL STEREOTYPIES IN RESTRICTED-FED FOWLS: 2. INFLUENCE OF MEAL FREQUENCY AND MEAL SIZE

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ABSTRACT: Expression of oral stereotypies directed at the drinker (drinking) and empty feeder (pecking), by young, caged, restricted-fed broiler breeder fowls, was investigated in three experiments in which either the frequency of feeding or meal size was varied. Behaviour was measured from regular 15-min videorecordings. In Experiment 1, birds were provided with either one (1A), two (1B) or four (1C) hourly meals of 5 g in the morning, and a single balance meal in the afternoon. Treatment 1C caused increases in drinking and pecking, compared with 1A and 1B, but effects of meal number and the total weight of food eaten during testing were indistinguishable. In Experiment 2, birds were provided with four meals of equal size in the morning, at either 1.5, 1 or 0.5 hr intervals, with a balance meal in the afternoon in the first week only. There was no difference among these treatments in drinking or pecking at any time, and neither stereotypy responded to variation in inter-feeding interval length in the ways predicted by two alternative theoretical models, constructed for adjunctive behaviours. Additional information from Experiment 1, and a comparison between Experiments 1 and 2, indicated that both stereotypies were correlated positively with meal size and/or the total amount eaten during testing. In Experiment 3, birds were provided with two meals (only) of unequal size at 09.00 and 12.00 h, and were conditioned to receiving either the large meal (32 g) first, the small meal (8 g) first, or large and small meals in random order. The main finding was that pecking declined from the first to the third hour after the small meal only when the small meal came first, and did not do so after the large meal. This suggests that the rate at which stereotyped pecking declines after eating may depend on the amount that is eaten.

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INTRODUCTION

Growing parent stock (breeders) of meat-type chickens (broilers) are routinely fed on restricted rations in order to limit body weight at sexual maturity, and thereby improve health and fertility (Hocking et al., 1989). Typically, they eat only a third as much as they would with free access to food, and are highly motivated to feed at all times (Savory et al., 1993). They are more active than ad libitum-fed control birds, and show increased pacing before a single daily meal and increased drinking and pecking at non-food objects afterwards. Their expression of these activities is often stereotyped in form (i.e. invariable, repetitive, no apparent function; Odberg, 1978) and is correlated positively with the level of restriction imposed. The oral stereotypies have been interpreted in terms of frustration of feeding motivation (Kostal et al., 1992; Savory & Maros, 1993), and persistence of unfulfilled foraging behaviour (Lawrence & Terlouw, 1993; Savory & Kostal, submitted).

Abnormal stereotypic behaviours are also shown by hungry animals exposed to more frequent intermittent feeding. Such "schedule-induced" activities can be categorised according to their temporal location in inter-feeding intervals. Thus, interim, or adjunctive, activities occur at the beginning of each interval, and (anticipatory) terminal activities near the end (Anderson & Shettleworth, 1977; Staddon & Simmelhag, 1971; Staddon, 1977). Adjunctive activities are subject to greater individual variation (Staddon & Simmelhag, 1971), and can be explained neither in terms of physiological deficit, nor as a "superstitious" result of their adventitious pairing with food delivery (Falk, 1961, 1966, 1971). A bitonic (inverted U) relationship between their rate of occurrence and inter-feeding interval length was first reported for schedule-induced polydipsia in rats (Falk, 1966), and is considered to be a common property of these activities (Bond, 1973; Allen & Kenshalo, 1976; Jozsvai & Keehn, 1990; Robinson et al., 1990).

Killeen et al. (1978) argued that expression of adjunctive behaviours is raised to supernormal levels by "excessive" arousal (as defined by Delius, 1970) generated by periodic delivery of food or other incentives. Each incentive activates a small amount of arousal which decays exponentially over time. If the interval separating successive incentives is short enough, the arousal accumulates, building to an asymptotic level which depends on the size of the arousal increments, their rate of decay, and the interval between them.

According to this ("Killeen") model, the asymptotic level of arousal (and rate of occurrence of adjunctive behaviours) increases as the inter-feeding interval decreases. Hence, the relationship between the level of adjunctive behaviour and inter-feeding interval according to the Killeen model is fundamentally different to the bitonic function referred to above (Tuyttens, 1994).

The purpose of the present study was to investigate effects of different feeding schedules on drinker and feeder directed oral stereotypies in caged restricted-fed broiler breeders (Kostal & Savory, 1994; Savory & Kostal submitted), and to see whether expression of these activities varies in the ways predicted by the Killeen model or the bitonic function for adjunctive behaviours. One experiment examined the effect of different numbers of food deliveries, with a constant inter-feeding interval, and another investigated the effect of different intervals between a fixed number of meals. Comparison between these trials indicated a specific effect of the quantity of food eaten during testing. Influence of meal size on the stereotypies was therefore examined in a third experiment, in which possible effects of anticipation of, and change from, expected meal size were also considered. Crespi (1942) reported so-called "elation" and "depression" effects on locomotor behaviour in rats given food "incentives" that were larger or smaller than expected.

EXPERIMENT 1: METHODS

Subjects and husbandry

Thirty six female broiler breeder chicks (Ross 1, Ross Breeders Ltd., UK) were kept in a multi-unit brooder until 25 days of age, with ad libitum supplies of water and a conventional "starter" mash diet (200 g/kg protein and 11.5 MJ/kg metabolisable energy).

At 25 days they were divided randomly into three groups of 12 (IA, IB, IC) and housed individually in identical batteries in three identical light-proof rooms. Each battery consisted of three tiers of 4 cages. Each cage measured 30 x 45 x 41 cm (w x d x h) and had solid sides, back and ceiling, and a front with vertical bars through which the bird could feed from a plastic container and drink (ad libitum) from a 1 litre plastic container situated adjacently outside the cage. Birds could see neighbours on the same tier when their heads were out of the front of the cage, but not birds on other tiers. In each room the lights were on

from 07.00 to 19.00 h, ambient temperature was maintained at 21°C, and white noise minimised any disturbance from extraneous sounds.

Procedure

After the move to cages, all birds were deprived of food for two days to increase their feeding motivation. Thereafter they were fed on weighed rations of the starter diet in pellet form (3 mm diameter), according to the restricted feeding programme in the Ross 1 Parent Stock Management Manual (authorized by UK Home Office Licence). Small meals (5 g per bird) were given one, two or four times per day to groups IA, IB and IC, respectively. In every case the first food delivery was at 09.00 h and the interval between successive deliveries was 1 hr. These deliveries formed only part of the daily ration, and the balance was given in a single meal at 15.00 h, so that in weeks 1, 2 and 3 of the experiment each bird's total ration was 38, 42 and 46 g/d, respectively. Water was available ad libitum, drinkers being filled daily at 09.00 h. All birds consumed the 5 g food deliveries in <10 min (Tuyttens, 1994), so subsequent pecking at the empty feeder could be considered as being non-functional.

Behaviour measurements began three days after the feeding schedules started, when birds were 31 days old. They were made on two consecutive days in each week for three weeks, by recording the behaviour of all 12 birds in each room on videotape for every alternate 15 min, commencing at 08.15 h and ending at 14.00 h. There was thus a 15 min interval in recording after every food delivery, when the 5 g meal was eaten. The recording was done remotely with equipment in a fourth room, and involved no disturbance to the birds.

From the videorecordings, measurements were made in each 15-min period by noting each bird's behaviour every minute from a single "on the dot" observation (Slater, 1978), according to one of seven mutually exclusive categories. These were: sitting (only); standing (only, with head inside the cage); head out (of the front of the cage while standing and often pushing against the bars); pacing; preening (nearly always while standing); drinking (interspersed with, and indistinguishable from, pecking at the water or drinker without drinking); pecking (at the empty feeder or parts of the cage). Although the last two activities were only truly stereotyped (according to the definition of Odberg, 1978) when they occurred at higher frequencies, they are considered in this paper as oral stereotypies. Computer software used for this analysis was written by L. Kostal in Turbo Pascal

(Borland International, USA).

Statistical analyses

Statistical analyses were carried out on mean proportions of time spent drinking and object pecking in each week, calculated for each bird from all 15-min observation periods in the two days recording. These values were $\log_e$-transformed to give approximately equal variances to all treatments, and compared by split-plot ANOVA, with birds as plots, to measure significance of effects of bird, treatment, age (week), and treatment by age interaction. Specific differences between treatments within weeks were identified from t-tests.

Mean proportions of time spent drinking and pecking were also calculated for every 15-min period separately, from the two days recording in the third week only. With each of these activities and each treatment, a Wilcoxon signed rank test was used to compare the average of the two values before 09.00 h (baseline) with every subsequent value, the value after the first food delivery with those after subsequent deliveries, and the first and last values within inter-feeding intervals. This allowed conclusions to be drawn about any change in the oral stereotypies with time of day, any progressive increase in the stereotypies after successive food deliveries (cf. the Killeen model), and any difference in the stereotypies between the beginning (interim activity) and end (terminal activity) of inter-feeding intervals. Other activities were not analysed statistically because this investigation was concerned specifically with the stereotypies.

EXPERIMENT 1: RESULTS

Overall mean proportions of time spent in different activities were 1.7% sitting, 48.7% standing, 11.4% head out, 9.6% pacing, 17.7% preening, 6.4% drinking, and 4.5% object pecking. From ANOVAs, there were significant ($p<0.001$) effects of bird with both oral stereotypies, and of treatment and age with drinking only.

Mean proportions of time spent drinking and pecking in each week are shown in Figure 1. From t-tests, time spent drinking was significantly greater ($p<0.05$ or $p<0.01$) with treatment IC (4 x 5 g meal) than with treatments IA (1 x 5 g) and IB (2 x 5 g) in all three weeks, and there was no such difference between IA and IB. With pecking, IC was greater ($p<0.05$) than IA in week 1, and greater

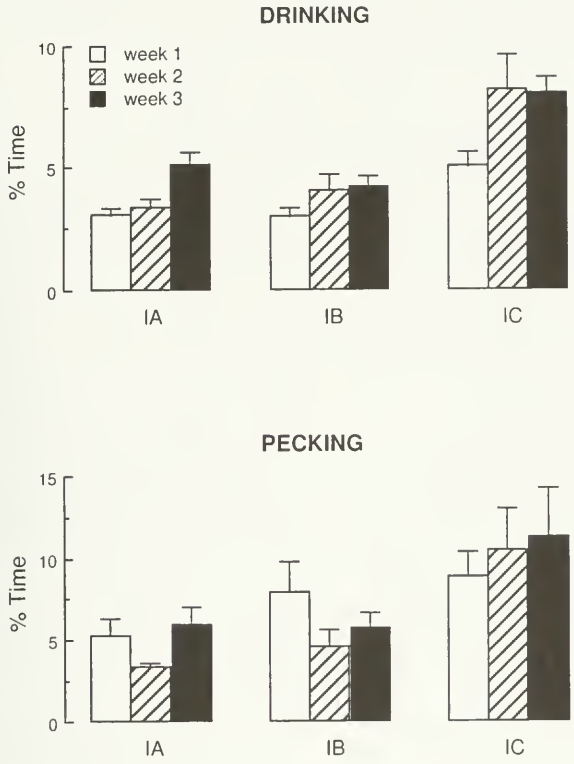

Figure 1. Mean (n=12) proportions of time spent drinking and pecking in each week of Experiment 1, by birds given either one (IA), two (IB) or four (IC) hourly meals of 5 g during testing. Vertical bars indicate standard errors.

($p<0.01$) than IA and IB in week 2, but there was no significant difference in week 3. The reason why there was no overall treatment effect with pecking (by ANOVA) was because individual variation in pecking was high. In week 3, for example, coefficients of variation (standard deviation divided by the mean) in birds' mean values were 0.57, 0.52 and 0.92 for pecking, and 0.35, 0.43 and 0.31 for drinking, with IA, IB and IC respectively.

Mean proportions of time spent drinking and pecking in each 15-min observation period in week 3 are shown in Figure 2. With treatment IA, the 09.00 h meal was followed by a significant increase in pecking (at the empty feeder) in the first 15 min, compared with the mean (baseline) value before 09.00 h. None of the subsequent pecking values differed from the baseline, and there were no such differences

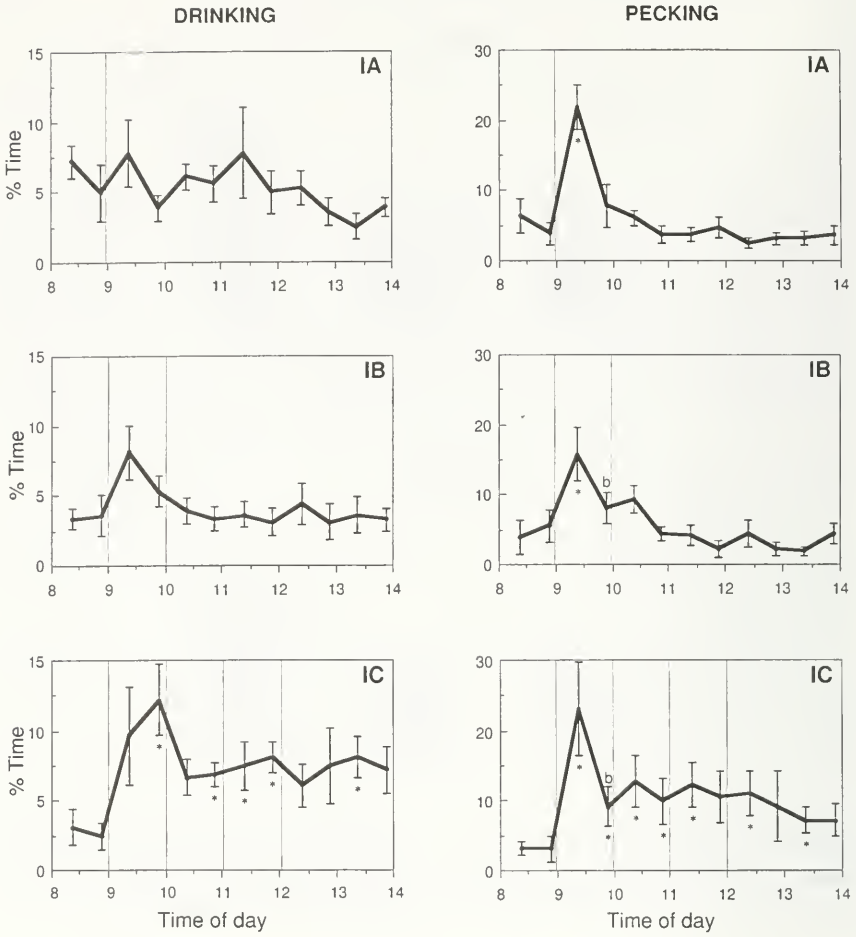

Figure 2. Mean (n=12) proportions of time spent drinking and pecking in alternate 15 min periods in the third (final) week of Experiment 1, by birds given either one (IA), two (IB) or four (IC) hourly meals of 5 g during testing. Vertical bars indicate standard errors, vertical lines from top to bottom indicate feeding times, * indicates where values differ significantly ($p<0.05$, by Wilcoxon test) from the corresponding baseline (average of the two values before 09.00 h), b indicates where values in the latter part of an inter-feeding interval differ significantly ($p<0.05$, by Wilcoxon test) from the first value in the same interval.

with drinking. With IB, pecking increased after the first (09.00 h) meal, then declined in the next 15 min, and did not increase after the second meal or subsequently. Drinking also increased after the first meal, but

not significantly so. With IC, pecking again increased after the first meal and declined in the next 15 min, and although it did not rise after the three subsequent meals, it remained higher than the baseline level. Drinking increased after the first meal, significantly so in the second 15 min, then fell after the second meal to a level that also remained higher than baseline.

For week 3 only, measurements were made of times spent drinking and pecking 45-60 min after the larger balance meal (range 18-41 g) at 15.00 h, which all birds ate in <10 min (Tuyttens, 1994). Mean proportions in the afternoon (9, 15, 11 for drinking, 31, 31, 18 for pecking, with IA, IB, IC, respectively) were nearly all greater than corresponding values 45-60 min after the first 5 g meal at 09.00 h (4, 6, 12 for drinking, 8, 8, 9 for pecking). This suggestion that larger meals may generate higher levels of the oral stereotypies was tested in Experiment 3, and was the reason for the change to no balance meal in Experiment 2. It is also possible that at least some observed effects of treatment in Experiment 1 could be associated with the total weight of food consumed between 08.15 and 14.00 h (5, 10, 20 g with IA, IB, IC), rather than with the number of food deliveries per se. This possibility was reinforced by a subsequent comparison between Experiments 1 and 2.

EXPERIMENT 2: METHODS

Subjects and husbandry

Another 36 female broiler breeder chicks were treated in exactly the same way as described for Experiment 1 until the start of Experiment 2 feeding schedules at 28 days of age.

Procedure

Experiment 2 lasted four weeks. In week 1, all three treatment groups received four 5 g meals of the pelleted food plus a single 18 g (balance) meal at 16.00 h. Groups IIA, IIB and IIC received the four 5 g meals at 1.5, 1 and 0.5 hr intervals, respectively, with the first food delivery at 09.00 h in every case. In weeks 2, 3 and 4, the complete daily ration was divided equally between these four food deliveries, with fixed meal sizes of 10.5, 11.5 and 12.5 g in the respective weeks, and there was no balance meal. The smaller (5 g) meals in week 1 were

because birds could not consume larger meals in <15 min then; and the minimum inter-meal interval was 0.5 hr to allow 15 min videorecording after all food was eaten.

Behaviour measurements began five days after the start of the feeding schedules, and they and the statistical analyses were the same as described for Experiment 1. Week 1 results were not included in the split-plot ANOVAs in order to avoid confounding any treatment by age interactions with the large change in meal size between weeks 1 and 2. The small changes in meal size between weeks 2, 3 and 4 were assumed to be insignificant for the growing birds.

EXPERIMENT 2: RESULTS

Overall mean proportions of time spent in different activities were 4.0% sitting, 35.6% standing, 15.2% head out, 8.0% pacing, 13.1% preening, 9.5% drinking, and 14.6% pecking. From ANOVAs, there were significant ($p<0.001$) effects of bird with both stereotypies, and of age with drinking only, but no effect of treatment.

Mean proportions of time spent drinking and pecking in each week are shown in Figure 3. Varying the inter-meal interval between four meals, from 1.5 (IIA) to 1 (IIB) and 0.5 hr (IIC), had no significant effect on drinking or pecking in any week. Times spent drinking and pecking were always lower in week 1, when meal size was smaller, than in the other weeks ($p<0.01$, by t-test). With all groups, drinking increased progressively (week 4>week 2, $p<0.01$), but pecking remained the same in weeks 2, 3 and 4.

Mean proportions of time spent drinking and pecking in each 15-min observation period in week 4 are shown in Figure 4. With all treatments, levels of drinking and pecking in the periods from 09.00 to 14.00 h were nearly all significantly higher than respective mean (baseline) values before 09.00 h. With treatments IIA and IIB, pecking was always higher in the first 15 min than in the subsequent 15 min period(s) within inter-feeding intervals. This was not the case with drinking, which remained consistently high in most periods after 09.00 h. Levels of drinking and pecking immediately after the first meal were not exceeded significantly after subsequent meals.

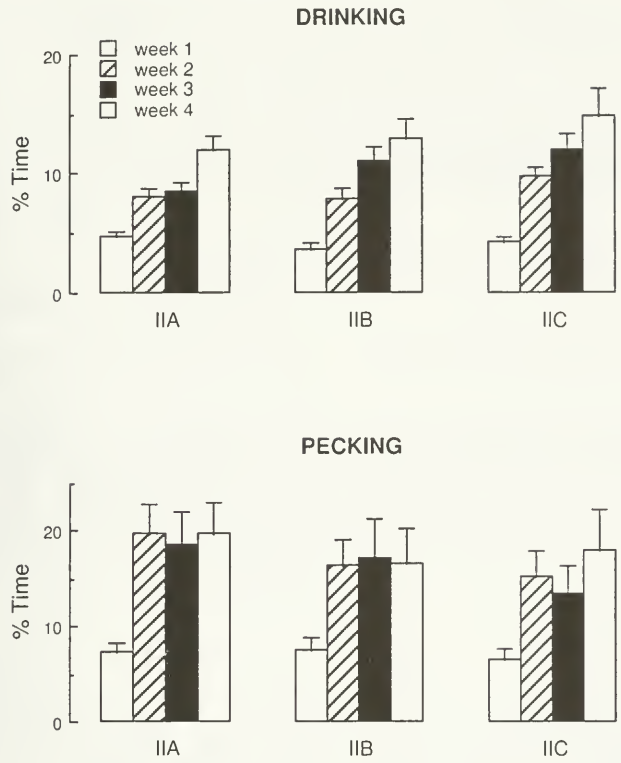

Figure 3. Mean (n=12) proportions of time spent drinking and pecking in each week of Experiment 2, by birds given four meals of equal size (5, 10.5, 11.5, 12.5 g in weeks 1, 2, 3, 4, respectively) during testing, at either 1.5 (IIA), 1 (IIB) or 0.5 hr (IIC) intervals. Vertical bars indicate standard errors.

DISCUSSION: EXPERIMENTS 1 AND 2

In Experiments 1 and 2, the feeding schedules (and ages) of treatment groups IC and IIB were the same in week 1, when both received four meals of 5 g at 1 hr intervals in the morning, and a larger (balance) meal in the afternoon. In week 2, group IC's schedule remained unchanged, but group IIB received four meals of 10.5 g at 1 hr intervals in the morning, and no meal in the afternoon. The effect of meal size and/or total quantity eaten during the test period (08.15 to 14.00 h), on drinking and pecking, can therefore be assessed from treatment by age interactions in split-plot ANOVAs, with birds as plots, IC and IIB as treatments, and weeks 1 and 2 as ages. Such treatment by age interactions were significant with both drinking ($p<0.05$) and

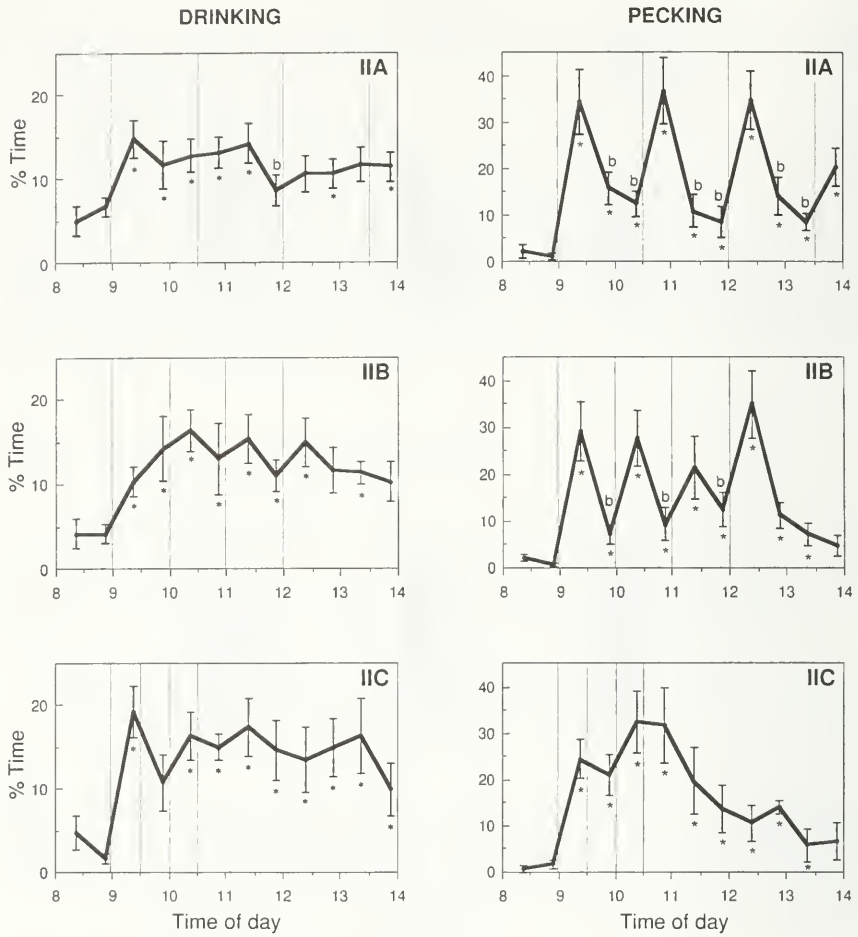

Figure 4. Mean (n=12) proportions of time spent drinking and pecking in alternate 15 min periods in the fourth (final) week of Experiment 2, by birds given four meals of 12.5 g during testing, at either 1.5 (IIA), 1 (IIB) or 0.5 hr (IIC) intervals. Vertical bars indicate standard errors, vertical lines from top to bottom indicate feeding times, * indicates where values differ significantly ($p<0.05$, by Wilcoxon test) from the corresponding baseline (average of the two values before 09.00 h), b indicates where values in the latter part of an inter-feeding interval differ significantly ($p<0.05$, by Wilcoxon test) from the first value in the same interval.

pecking ($p<0.001$), indicating that the increases in these activities from weeks 1 to 2 with treatment IIB (Figure 3) could have been associated specifically with the concomitant increase in the amount of food delivered.

This conclusion must necessarily be qualified, because groups IC and IIB were from different hatches and were not exposed to identical conditions before testing. Nevertheless, it concurs with the finding (see above) that times spent drinking and pecking in week 3 of Experiment 1 were greater after the large afternoon meal than after the first 5 g meal in the morning.

EXPERIMENT 3: METHODS

Subjects and husbandry

Twenty four female broiler breeder chicks were treated in the same way as in Experiments 1 and 2 until the start of Experiment 3 feeding schedules at 30 days of age, except that they were moved at 28 days to two 12-cage batteries (same as before) situated adjacently in the same room.

Procedure

During Experiment 3, which lasted 14 days, all birds were provided daily with 40 g of the pelleted food in two meals of unequal size (large meal 32 g, small meal 8 g) at 09.00 and 12.00 h. For the first 13 days, 8 birds (IIIA) always received the large meal first, 8 birds (IIIB) always received the small meal first, and 8 birds (IIIC) received large and small meals in different random sequences. On the final day the order of meal size in IIIA and IIIB was reversed, and IIIC remained random. Systematic distribution of treatments among cages and tiers was based on Latin squares, such that no two adjacent birds had the same treatment. The treatments were designed to separate any effects of anticipation of either a large or small meal from direct effects of meal size, and the reversed order on the final day with IIIA and IIIB was intended to test the "Crespi (1942) effect" (see Introduction) .

Behaviour measurements were made as in Experiments 1 and 2 from videorecordings of all birds in every alternate 15 min from 08.45 until 15.00 h, on each of the last four days in Experiment 3. There were thus three days (Days 1-3) when birds on treatments IIIA and IIIB were recorded on the order of meal size to which they were conditioned, and one day (Day 4) when that order was reversed. With IIIC, numbers of birds receiving large and small meals first were equal on all recording days. All birds finished their meals in <15 min, so videorecordings that

began at 09.15 and 12.15 h did so after eating had ceased.

Statistical analyses

From the 15-min observations were calculated proportions of time spent drinking and object pecking by every bird in each hour between 09.00 and 15.00 h on each day. These values were used to calculate mean proportions in the three hours after each meal (i.e. 09.15 to 12.00 h and 12.15 to 15.00 h), and changes in the proportions between the first and third hours after each meal. The mean proportions from three-hour periods were transformed by angular (arcsine root) transformation (Bartlett, 1947) before analysis, to give approximately equal variances, but this was not necessary with the changes between first and third hours. Because the experimental design was unbalanced (conditions were the same on all four days with IIIC but not with IIIA and IIIB), data were examined by "residual maximum likelihood" analysis (Patterson & Thompson, 1971), allowing for fixed effects (day(s), treatment, meal size) and random effects (bird, cage position). Specific questions concerned with meal size (see Results) were addressed by making appropriate comparisons among means, and dividing the resulting differences by their standard errors to obtain z values which were compared with the normal distribution (Wald tests).

EXPERIMENT 3: RESULTS

Overall mean proportions of time spent in different activities were 2.8% sitting, 45.7% standing, 15.5% head out, 4.1% pacing, 7.0% preening, 6.5% drinking, and 18.5% pecking. In the 15 min before the first meal at 09.00 h, mean proportions of time spent drinking and pecking were 1.3% and 4.2%, respectively.

Drinking and pecking responses in the three hours after large and small meals, with treatments IIIA, IIIB and IIIC, are shown in Figure 5. The following five questions were addressed.

1. Is any effect of meal size independent of anticipation of meal size? Considering data from IIIC only (no anticipation of meal size), the only significant effect of meal size was with the change in time spent drinking between first and third hours, which was greater after the large meal ($z = 3.12$, $p<0.01$).

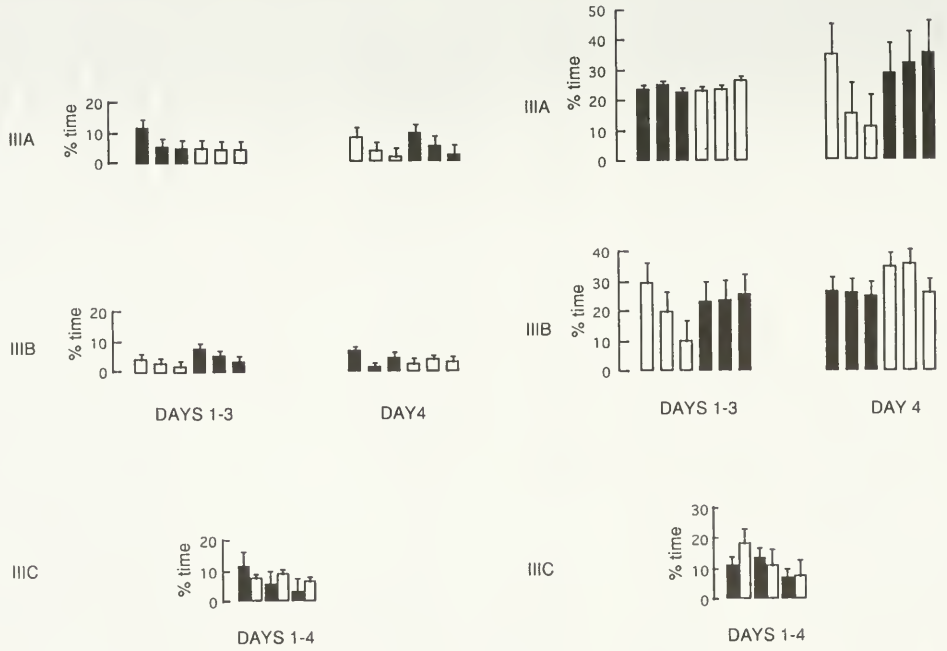

Figure 5. Mean (n=8) proportions of time spent drinking and pecking in the three hours after large (32 g, black columns) and small (8 g, white columns) meals at 09.00 and 12.00 h. On Days 1-3, (conditioned) birds received either the large meal first (IIIA), the small meal first (IIIB), or large and small meals in random sequences (IIIC). On Day 4, the order of meal size in IIIA and IIIB was reversed, and IIIC remained random. Vertical bars indicate standard errors.

2. Is any effect of meal size influenced by anticipation of meal size?
There were no significant differences between effects of meal size with IIIC and average effects of meal size with IIIA and IIIB.

3. Is there any effect of anticipation of meal size per se?
There were no significant differences between overall effects (regardless of meal size) of IIIC and average overall effects of IIIA and IIIB.

4. Is any effect of meal size influenced by order of presentation?
Comparing IIIA and IIIB, there was a significant effect of order on the difference between large and small meals in the change in time spent pecking between first and third hours (Days 1-3, $z = 2.75$, $p<0.01$; Day 4, $z = 1.81$, $p = 0.07$). Thus, with both IIIB and IIIA, there was a marked decline in pecking after the small meal only when the small meal came first (Figure 5). On Day 4, there was also a significant effect of order on the mean proportions of time spent pecking in three-hour periods ($z = 2.47$, $p<0.02$). Thus, (on Day 4 only), mean time spent pecking was greater after the second meal than after the first meal, regardless of meal size. There were no other effects of order.

5. Is any effect of meal size influenced by unexpected change in order of presentation? ("Crespi effect")
There was no significant effect of the change in order of presentation (on Day 4) on mean proportions of time spent drinking and pecking in either the first hour or all three hours after the first meal, with either the large meal (IIIA on Days 1-3 vs IIIB on Day 4) or the small one (IIIB on Days 1-3 vs IIIA on Day 4).

GENERAL DISCUSSION

The aim of Experiments 1 and 2 was to see whether the oral stereotypies of caged restricted-fed broiler breeders (drinking and object pecking) respond to variation in feeding frequency in the ways predicted by the Killeen model (Killeen et al., 1978) for adjunctive behaviours.

The results of Experiment 2, in which four meals of the same size were provided at either 0.5, 1 or 1.5 hr intervals, did not concur with these predictions. There was no difference between treatments in overall levels of either drinking or pecking during testing, and no evidence within treatments of accumulation in either stereotypy between successive food deliveries. Similarly, there was no evidence of such

accumulation in Experiment 1, when either two (IB) or four (IC) meals of the same size were provided at 1 hr intervals. There was also no evidence in Experiment 2 of the bitonic relationship between behavioural expression and inter-feeding interval length, reported by others to be characteristic of adjunctive behaviours (see Introduction).

The question arises, therefore, whether drinking and pecking stereotypies of broiler breeders, with low frequencies of feeding, are truly analogous to the adjunctive behaviours of animals with higher frequencies of feeding. Both types of behaviour do have features in common. Their level of expression is correlated positively with the degree of food restriction (Falk, 1971; Savory & Maros, 1993); they are persistent, excessive and stereotyped in some individuals; and they are rarely seen before the first food delivery (Figures 2 and 4; Kostal et al., 1992; Savory & Kostal, submitted). Drinking, however, cannot be regarded as an interim adjunctive activity here because it was not focussed immediately after feeding (Figures 2 and 4), unlike schedule-induced polydipsia (Staddon, 1977). Pecking did appear to be focussed after feeding, but only with the larger meals in Experiment 2 (Figure 4). Also, there was consistently greater individual variation in pecking than in drinking in these experiments, and this is typical of adjunctive behaviours (Staddon & Simmelhag, 1971). It is quite possible that, with more (small) meals and shorter intervals than those tested here, the oral stereotypies of broiler breeders would respond in ways predicted by the Killeen model or the bitonic function.

In Experiment 1, regular provision of four small meals in the morning (IC), together with a single balance meal in the afternoon, was associated with greater and more prolonged increases in drinking and pecking during testing (08.15 to 14.00 h) than were either of the other two treatments with fewer meals (Figure 2). One possible explanation for this is that neural elements controlling these activities become sensitised through repeated stimulation, leading to exaggeration and stereotyping of the activities (Dantzer, 1986), and this happens sooner with more meals per day. This process depends on the arousal generated by intermittent delivery of insufficient food (Cabib, 1993), and on associated increases in feeding motivation and general activity (Baumeister et al., 1964; Savory et al., 1996). The sorts of activity it affects reflect the extent to which behavioural expression is constrained or "channeled" by the environment (Lawrence & Terlouw, 1993).

However, as well as the above effect of meal number, there may have been an additional effect due to more food being eaten during testing with treatment IC (20 g) than with IA (5 g) and IB (10 g). It is

impossible here to separate effects of meal number and the amount eaten, but there is other evidence from Experiments 1 and 2 indicating that meal size and/or total amount eaten may be important (assuming a fixed level of food restriction). First, the increases in drinking and pecking from weeks 1 to 2 with treatment IIB (Figure 3) could have been caused by the concomitant increase in the amount of food delivered (inter-experimental comparison). Second, in week 3 of Experiment 1, times spent drinking and pecking after the large afternoon meal were nearly all higher than corresponding levels after the first 5 g meal in the morning (Experiment 1 Results). Third, levels of drinking and pecking were consistently high after each of four hourly meals of 12.5 g in Experiment 2 (IIB, Figure 4), but dropped after the first of four hourly meals of 5 g in Experiment 1 (IC, Figure 2).

In Experiment 3, there was no apparent effect of meal size on mean times spent drinking and pecking in three-hour periods after two meals of unequal size (large - 32 g, small - 8 g) provided at 09.00 and 12.00 h. With treatment IIIC (random order, no anticipation of meal size), the change in time spent drinking between first and third hours was greater after the large meal than after the small one (Figure 5). This may be because food-related thirst was presumably greatest in the first hour after the large meal. Another effect was with time spent pecking, which declined from the first to the third hour after the small meal only when the small meal came first (i.e. IIIB on Days 1-3 and IIIA on Day 4), and did not do so after the large meal. The results suggest that the increase in stereotyped pecking after the first meal may be relatively independent of meal size, but the rate at which pecking declines afterwards may be greater with small meals than large ones. If this effect also applies to differences in total food eaten during testing, as in Experiment 1, then it might have contributed to the more prolonged increases in drinking and pecking observed with IC (Figure 2). There also appeared to be no effects on oral stereotypies in Experiment 3 that could be attributed specifically to either anticipation of meal size or unexpected change in (anticipated) meal size (cf. Crespi, 1942).

In conclusion, the oral stereotypies of restricted-fed broiler breeders did not respond here, to variation in inter-feeding interval length, in the ways predicted by either the Killeen model or the bitonic function for adjunctive behaviours. This might have been because the minimum interval tested in Experiment 2 (0.5 hr) was too long for these predictions to be realised. Drinking and pecking levels in Experiment 1 were higher with four hourly food deliveries per day than with either two or one, but effects of meal number and the total weight eaten during

testing were indistinguishable. Results of Experiment 3 indicate that the rate at which stereotyped pecking declines after eating may depend on the amount that is eaten.

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REFERENCES

Allen, D.A. & Kenshalo, D.R. Jr. (1976). Schedule-induced drinking as a function of inter-reinforcement interval in the rhesus monkey. *Journal of the Experimental Analysis of Behavior, 26,* 257-267.

Anderson, M.C. & Shettleworth, S.J. (1977). Behavioural adaptation to fixed-interval and fixed-time food delivery in golden hamsters. *Journal of the Experimental Analysis of Behavior, 25,* 33-49.

Bartlett, M.S. (1947). The use of transformations. *Biometrics, 3,* 39-52.

Baumeister, A., Hawkins, W.F. & Cromwell, R.L. (1964). Need states and activity level. *Psychological Bulletin, 61,* 438-453.

Bond, N. (1973). Schedule-induced polydipsia as a function of the consummatory rate. *Psychological Record, 23,* 377-382.

Cabib, S. (1993). Neurobiological basis of stereotypies. In A.B. Lawrence & J. Rushen (Eds.), *Stereotypic animal behaviour: fundamentals and applications to welfare* (pp. 119-145). Oxon: CAB International.

Crespi, L.P. (1942). Quantitative variation of incentive and performance in the white rat. *American Journal of Psychology, 55,* 467-517.

Dantzer, R. (1986). Behavioral, physiological and functional aspects of stereotyped behaviour: a review and re- interpretation. *Journal of Animal Science, 62,* 1776-1786.

Delius, J.D. (1970). Irrelevant behaviour, information processing and arousal homeostasis. *Psychologische Forschung, 33,* 165-188.

Falk, J.L. (1961). Production of polydipsia in normal rats by an intermittent food schedule. *Science, 133,* 195-196.

Falk, J.L. (1966). Schedule-induced polydipsia as a function of fixed interval length. *Journal of the Experimental Analysis of Behavior, 9,* 37-39.

Falk, J.L. (1971). The nature and determinants of adjunctive behavior. *Physiology and Behavior, 6,* 577-593.

Hocking, P.M., Waddington, D., Walker, M.A. & Gilbert, A.B. (1989). Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by food

restriction during rearing. *British Poultry Science, 30,* 161-174.

Jozsvai, E. & Keehn, J.D. (1990). Effects of inter-reinforcement interval on dimensions of schedule-induced polydipsia: group and individual differences. *Psychological Record, 40,* 139-151.

Killeen, P.R., Hanson, S.J. & Osborne, S.R. (1978). Arousal: its genesis and manifestation as response rate. *Psychological Review, 85,* 571-581.

Kostal, L., Savory, C.J. & Hughes, B.O. (1992). Diurnal and individual variation in behaviour of restricted-fed broiler breeders. *Applied Animal Behaviour Science, 32,* 361-374.

Kostal, L. & Savory, C.J. (1994). Influence of pharmacological manipulation of dopamine and opioid receptor subtypes on stereotyped behaviour of restricted-fed fowls. *Pharmacology Biochemistry and Behavior, 48,* 241-252.

Lawrence, A.B. & Terlouw, E.M.C. (1993). A review of behavioral factors involved in the development and continued performance of stereotypic behaviors in pigs. *Journal of Animal Science, 71,* 2815-2825.

Odberg, F.O. (1978). Abnormal behaviours: (stereotypies). In: (Editorial Garsi), *Proceedings of the 1st world congress on ethology applied to zootechnics* (pp. 475-480). Madrid: Industrias Graficas Espana.

Patterson, H.D. & Thompson, R. (1971). Recovery of inter-block information when block sizes are unequal. *Biometrica, 58,* 545-554.

Robinson, J.K., Flory, R.K. & Dunahoo, C.L. (1990). The effects on schedule-induced attack of covarying meal size and spacing. *Physiology and Behavior, 47,* 259-263.

Savory, C.J. & Maros, K. (1993). Influence of degree of food restriction, age and time of day on behaviour of broiler breeder chickens. *Behavioural Processes, 29,* 179-190.

Savory, C.J., Maros, K. & Rutter, S.M. (1993). Assessment of hunger in growing broiler breeders in relation to a commercial restricted feeding programme. *Animal Welfare, 2,* 131-152.

Savory, C.J., Hocking, P.M., Mann, J.S. & Maxwell, M.H. (1996). Is broiler breeder welfare improved by using qualitative rather than quantitative food restriction to limit growth rate? *Animal Welfare, 5,* 105-127.

Savory, C.J. & Kostal, L. (1997). Temporal patterning of oral stereotypies in restricted-fed fowls: 1. Investigations with a single daily meal. *International Journal of Comparative Psychology, 9,* 117-139.

Slater, P.J.B. (1974). Data collection. In P.W. Colgan (Ed.), *Quantitative ethology* (pp. 7-24). New York: Wiley.

Staddon, J.E.R. & Simmelhag, V.L. (1971). The "superstition" experiment: a re-examination of its implications for the principles of adaptive behavior. *Psychological Review,* 78, 3-43.

Staddon, J.E.R. (1977). Schedule-induced behavior. In W.K. Honig & J.E.R. Staddon (Eds.), *Handbook of operant behavior* (pp. 125-152). New York: Prentice-Hall.

Tuyttens, F.A.M. (1994). *The influence of the feeding schedule on the level and development of oral stereotypies in young, restricted-fed, broiler breeder females (Gallus gallus domesticus L.).* Unpublished Honours thesis, University of Edinburgh.